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Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient

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Abstract Dead wood biomass can be a substantial fraction of stored carbon in forest ecosystems, and coarse woody debris (CWD) decay rates may be sensitive to climate warming. We used an elevation gradient in Colorado Rocky Mountain subalpine forest to examine climate and species effects on dead wood biomass, and on CWD decay rate. Using a new radiocarbon approach, we determined that the turnover time of lodgepole pine CWD (340 ± 130 years) was roughly half as long in a site with $2.5\text{--}3^\circ\text{C}$ warmer air temperature, as that of pine (630 ± 400 years) or Engelmann spruce CWD (800 ± 960 and 650 ± 410 years) in cooler sites. Across all sites and both species, CWD age ranged from 2 to 600 years, and turnover time was 580 ± 180 years. Total standing and fallen dead wood biomass ranged from 4.7 ± 0.2 to 54 ± 1 Mg ha⁻¹, and from 2.8 to 60% of aboveground live tree biomass. Dead wood biomass increased 75 kg ha⁻¹ per meter gain in elevation and decreased 13 Mg ha⁻¹ for

every degree C increase in mean air temperature. Differences in biomass and decay rates along the elevation gradient suggest that climate warming will lead to a loss of dead wood carbon from subalpine forest.

Keywords Coarse woody debris · Decomposition · Ecosystem carbon balance · Subalpine forest · Climate

Introduction

Standing and fallen dead trees are ecologically significant components of forest ecosystems, contributing fuel to forest fires (Tinker and Knight 2000), sources of nutrient availability (Hart 1999), and habitat for a wide range of plant and animal species (Harmon et al. 1986). Dead wood can also account for a substantial fraction of forest biomass and stored carbon (c). Temperate forests contain highly variable amounts of standing (snags) and fallen dead trees, or coarse woody debris (CWD), depending on management history, species composition, and environmental conditions (Harmon et al. 1986). Forests with the highest CWD biomass are typically old-growth Douglas fir forests of the Pacific Northwest, while forests in the montane western USA are at the low end of the range for temperate forests (Fahey 1983; Harmon et al. 1986). However, where dead wood biomass is relatively low in absolute terms, it can account for a large fraction of ecosystem biomass (Arthur and Fahey 1990).

Measurement of dead wood biomass is complicated by spatial variation and lack of suitable allometric equations relating snag volume or mass to girth and height, and estimates of dead wood turnover time are extremely difficult to obtain with high confidence. In addition, few studies have performed complete inventories of C stored in all living and dead biomass, and provided an estimate of the fraction of C stored in dead wood and its turnover time relative to other ecosystem C pools. As a result, this heterogeneous C pool is not well represented in ecosystem models, though it is a significant component of the forest C cycle.

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Tree mortality and CWD decay rate determine the mass of dead wood stored in forests. Reported decomposition rates for snags and CWD are highly variable, but are often quite slow due to the low nutrient content of woody tissue, low surface to volume ratio of large logs, unfavorable climatic conditions, low oxygen in saturated logs, or in some cases, high concentrations of anti-microbial compounds (Harmon et al. 1986). Using decomposition rate constants from sites that vary in temperature due to differences in latitude and elevation, researchers have found that a 10°C increase results in a 240–250% increase in the decomposition rate ($Q_{10}=2.4\text{--}2.5$) (Chambers et al. 2000; Mackensen et al. 2003), though within a narrower temperature range the pattern is less consistent (Harmon et al. 2000). This suggests that with anticipated climate warming, the turnover time of this important pool of ecosystem C will decrease, contributing a positive feedback to atmospheric warming, if CWD production remains the same. These Q_{10} calculations are a first approximation of the sensitivity of CWD decay rates to temperature, and do not remove the often interactive effects of tree species or site water balance. They highlight a need for more comparative measurements of CWD decomposition and its climate sensitivity within ecosystems vulnerable to climate change.

Measuring the decay rate of dead wood is difficult due to its long turnover time relative to the time frame of an individual research project (or career). As a result, various imperfect approaches have been developed. Directly measuring mass loss from individual pieces of newly fallen wood typically requires decades, and can introduce artifacts if the surface-to-volume ratio is larger than for full logs (Laiho and Prescott 1999; Stone et al. 1998). More often, researchers use indirect approaches to measure CWD decomposition. The chronosequence approach is most common, whereby historic windfall, fire, wave regeneration, or harvest events can be used to determine the amount of time logs have been undergoing decay. Relating the density or mass (after correcting for changes in log volume) of logs to the time they have been undergoing decay yields a decay rate (e.g., Busse 1994; Fahey 1983; Lambert et al. 1980). This approach is often applied after catastrophic disturbances, such as harvest or fire, that can significantly alter environmental conditions (e.g., increasing penetration of sunlight and heat to the ground surface). In addition, it requires a series of study sites affected by the same kind of disturbance event and knowledge of the exact timing and extent of the events, making it difficult to employ in new or remote research areas. Finally, the chronosequence approach tends to favor more recent events where there is higher confidence in records, and therefore may exclude older, highly decayed logs.

To obtain dates of tree death in sites with little recorded disturbance history, some researchers have turned to dendrochronology, matching the tree-ring patterns of live trees with those of fallen trees to determine how long ago a tree died (e.g., Brown et al. 1998; Daniels et al. 1997). This approach integrates a greater diversity of log ages

within a single site and can be used in remote forests that do not have carefully documented disturbance histories. However, it is impossible to obtain tree-ring records from logs in advanced stages of decay, again biasing studies towards the early stages of decay.

Finally, researchers have measured rates of C mineralization in decaying logs directly by measuring microbial respiration rates in the field and lab. These measurements can be difficult to relate to longer term measures of decay due to variation in wood temperature, moisture, density and decay states, but can improve our mechanistic understanding of the decay process (Chambers et al. 2001; Mackensen and Bauhus 2003; Wang et al. 2002).

In this study, we used radiocarbon to determine the age of 42 fallen logs, and then used the exponential relationship between log tissue density and time since tree death to estimate CWD decomposition rates. Natural abundance radiocarbon dating is increasingly used to estimate time constants for ecological processes including soil C turnover (Gaudinski et al. 2000; Torn et al. 1997; Trumbore 1993; Trumbore et al. 1996), fine root turnover (Gaudinski et al. 2001), and tree growth rates in forests without strong seasonal signals (Chambers et al. 1998). Radiocarbon has also been used to estimate the age of highly decomposed logs, but the resulting information has not been used to help estimate decay rates (Daniels et al. 1997; Harvey et al. 1981). Radiocarbon dating can be used on logs of any age (though with highly variable time resolution), and in any site not directly influenced by fossil fuel-derived C emissions (i.e., sources of ^{14}C -free CO_2). By measuring CWD and snag biomass at 11 sites and decomposition rates at three sites along an elevational climate gradient spanning two forest types, we examined how climate and tree species affect dead wood biomass and decomposition.

Materials and methods

Study sites

We measured CWD biomass and turnover along an elevation gradient centered at 38°43'27.21"N latitude and 106°39'3.92"W longitude, in the Fossil Ridge Wilderness, Gunnison Co., Colo., USA (Fig. 1). The Fossil Ridge Wilderness is a 12,840-ha roadless area on the western slope of the Rocky Mountains, designated as federally protected Wilderness in 1993. A fence currently prevents cattle from entering the research watershed, though grazing was permitted historically. The fire regime in Rocky Mountain subalpine forests has been minimally impacted by twentieth century fire suppression efforts, due to the difficulty of accessing higher elevations and to 100+ year fire return intervals (Sherriff et al. 2001; Turner et al. 2003). The last fire in the Fossil Ridge Wilderness was in 1980, burning about 80 ha of lodgepole and bristlecone pine (G. Chonka, US Forest Service, personal communication), though there was no evidence of this fire near any of our study plots. There is no recorded history or direct evidence (e.g., stumps) of logging in or near our

research sites. The largest current direct human impact in this forest is private and commercially guided hunting, which results in local wood gathering for campfires. Overall, this area has been minimally impacted by historic and current human activities, allowing us to assume that most differences along the gradient are due to environmental and ecological factors.

Vegetation along the gradient is largely determined by elevation and associated differences in climate (Peet 2000). The forest is dominated by lodgepole pine (*Pinus contorta*) at lower elevations and Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) at upper elevations, with all three tree species co-occurring in an ecotone between 3,300 and 3,400 m. The sparse understory is composed of common juniper (*Juniperus communis*), *Vaccinium myrtillus*, and other low shrubs, tree seedlings, graminoids and flowering plants. We selected 11–30×30 m research plots ranging in elevation from 3,040 to 3,550 m, establishing three plots in the pine forest, three in the spruce-fir forest, and five in the ecotone (Fig. 1). The highest elevation plot was approximately 50 m below treeline. We quantified tree species composition and aboveground biomass (AGB) of each plot from surveys of all trees ≥ 1.4 m tall in 1999, using species-specific allometric equations to estimate AGB (Kueppers 2003). AGB was 100% lodgepole pine in the pine forest, >75% Engelmann spruce in the spruce-fir forest, and 20–87% lodgepole pine in the ecotone (Table 1), with total AGB ranging from 90 to 233 Mg ha⁻¹ (Table 3). All plots had northwest aspects with slope angles <30°, similar

stand densities, and were in forest patches at least 130 years old. The plots were on the Schofield–Peeler gravelly to very stony sandy loam soil series, classified as a *Typic cryoboralf* derived from Pre-Cambrian granite (Fox 1977). The soils are very rocky with strong horizonation, having thicker organic horizons at higher elevations.

Climate

Mean annual air temperature and mean total annual precipitation at the nearby National Weather Service Taylor Park weather station (2,800 m) are 0.2°C and 425 mm respectively. Monthly mean temperature peaks in July at 13.3°C. Peak total monthly precipitation occurs in August with monsoon rain, although precipitation is spread fairly evenly throughout the year. We measured microclimate variables directly in every plot, using dataloggers linked to one air and five soil temperature sensors per plot to measure annual temperatures, and using five samples of gravimetric soil moisture per plot taken three times during the growing season to quantify relative differences in soil moisture (Kueppers 2003). Mean annual air and soil temperature varied among the plots by 2.92 and 2.45°C, respectively (Table 1). Growing season soil moisture, date of snowmelt and other climate indices also varied among the plots, with all variables well correlated to each other. Colder, wetter plots with longer winters occurred at higher elevations, and warmer, drier plots with

Fig. 1 Location of study plots along an elevation gradient in the Fossil Ridge Wilderness, Gunnison Co., Colo., USA

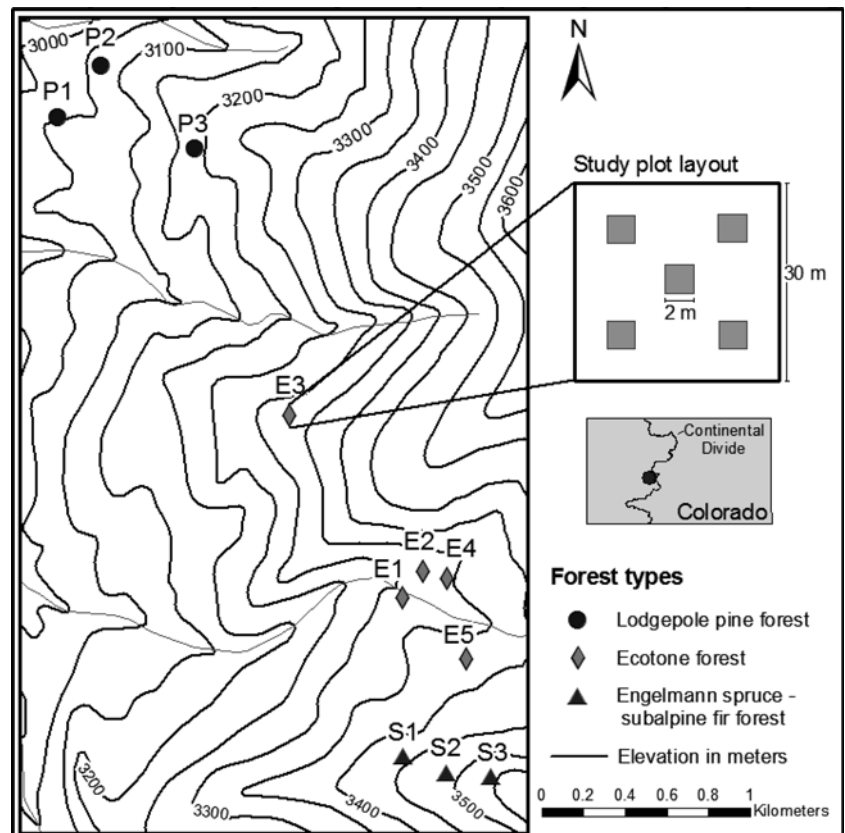


Table 1 Microclimate and tree species composition for plots along an elevation gradient, Fossil Ridge Wilderness, Colorado. Engelmann spruce trees account for the balance of AGB, although S1 has

23%, S2 has 8%, and the Ecotone plots have ~1% subalpine fir. In all other plots trembling aspen and fir biomass account for <1% of tree biomass

Plot	Forest type	Elevation (m)	Mean temperature		Growing degree days (°C)	Soil moisture ^a (%)	Date of snowmelt (Julian day)	Winter length (days)	Lodgepole pine AGB (%)
			Air (°C)	Soil (°C)					
P1	Pine	3,040	1.88	2.81	920	28.4	129	195	100
P2	Pine	3,072	2.20	3.93	1,001	15.9	125	176	100
P3	Pine	3,200	1.86	3.60	923	18.5	125	176	100
E1	Ecotone	3,308	-0.72	2.08	529	24.2	146	223	71
E2	Ecotone	3,323	0.02	2.54	630	21.4	144	211	81
E3	Ecotone	3,328	0.82	2.93	761	20.2	140	205	87
E4	Ecotone	3,334	-0.38	2.74	562	40.2	142	209	52
E5	Ecotone	3,392	-0.46	2.31	566	58.8	147	213	20
S1	Spruce-fir	3,456	-0.13	1.59	644	60.2	156	234	0
S2	Spruce-fir	3,520	-0.58	1.48	560	79.2	152	223	0
S3	Spruce-fir	3,552	-0.37	2.23	605	52.9	150	226	0

^aMedian growing season gravimetric soil moisture

early snowmelt occurred at lower elevations (Table 2). The plot with the coldest air temperature (E1) occurred in the mid-elevation ecotone forest, probably as a result of local cold air drainage. The two wettest plots (S1 and S2) also had the latest snowmelt dates, which may have allowed the plots to remain moist through most of the growing season.

Coarse woody debris and snag biomass

We included all pieces of fallen dead wood with diameters ≥ 10 cm at the widest point in our 2001 survey of CWD biomass. We first assigned each log in a study plot to a qualitative decay class (0–V, where 0 is least and V is most decomposed) based on amount of bark, bole shape, condition of branches, accumulation of litter and herbaceous growth, and wood fragmentation after schemes by Arthur and Fahey (1990) and Busse (1994). We then calculated the log's volume using the equation for a cylinder, based on the log's average diameter (from three equally spaced measurements), and length. For irregularly shaped pieces we used measurements and equations for the most relevant geometry. We only included the fraction of CWD laying inside plot boundaries in our measurements.

To more accurately convert CWD volume measurements to mass we calculated decay-class and species-specific log tissue densities from a subset of 42 logs in or near three plots, later using these same logs for radiocarbon analyses. We measured tissue density from two lodgepole pine and two Engelmann spruce logs in each decay class, I–V, in the forest types where each species occurred (i.e., pine in pine and ecotone forest, and spruce in spruce-fir and ecotone forest). For decay class 0, one pine log was measured from the pine forest, and one spruce log was measured from the spruce-fir forest. We measured the tissue density of three evenly spaced cross-sections from each log by calculating cross-section volume geometrically in the field, drying the cross-sections at 65°C, weighing them, and averaging the densities of the samples. For recently fallen logs from which it was impossible to obtain large cross-sections with a handsaw, we took at least one cross-section and multiple quantitative core samples using a tree-coring tool. CWD tissue density corresponded well to qualitative decay class assignments (Fig. 2).

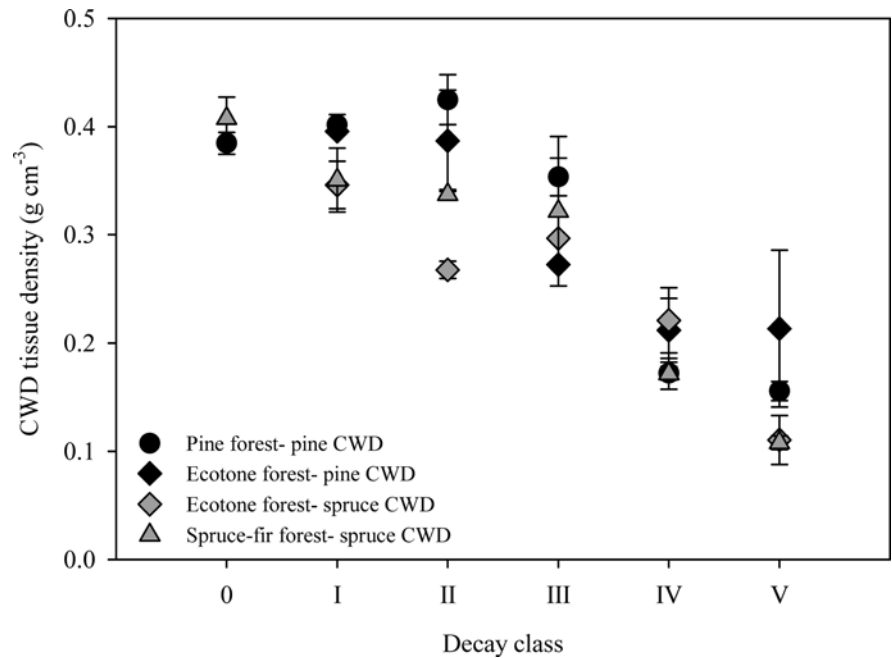
Total CWD biomass for each plot was calculated as,

$$\text{CWD Biomass} = \sum_{i,j} \sum_{k=1}^n V_{k,i,j} \times \rho_{i,j}, \quad (1)$$

Table 2 Pearson correlation, (*r*), matrix of climate and species composition characteristics for the plots. Data for correlations are given in Table 1. All correlations are significantly different from zero with $P < 0.05$ ($n=11$). Correlations significant after a Bonferroni correction for multiple comparisons are in italics

	Elevation	Air temperature	Soil temperature	Growing degree days	Soil moisture	Snowmelt date	Winter length
Elevation	<i>1.00</i>						
Air temperature	<i>-0.84</i>	<i>1.00</i>					
Soil temperature	<i>-0.78</i>	<i>0.83</i>	<i>1.00</i>				
Growing degree days	<i>-0.81</i>	<i>1.00</i>	<i>0.81</i>	<i>1.00</i>			
Soil moisture	<i>0.76</i>	<i>-0.64</i>	<i>-0.79</i>	<i>-0.60</i>	<i>1.00</i>		
Snowmelt date	<i>0.90</i>	<i>-0.91</i>	<i>-0.93</i>	<i>-0.88</i>	<i>0.75</i>	<i>1.00</i>	
Winter length	<i>0.83</i>	<i>-0.89</i>	<i>-0.94</i>	<i>-0.87</i>	<i>0.68</i>	<i>0.97</i>	<i>1.00</i>
Fraction pine	<i>-0.89</i>	<i>0.75</i>	<i>0.81</i>	<i>0.71</i>	<i>-0.93</i>	<i>-0.87</i>	<i>-0.81</i>

Fig. 2 Coarse woody debris (CWD) tissue density for various decay classes. Error bars are one standard error of the mean log tissue density ($n=2$ logs) for classes I through V, and one standard error of the mean tissue density of single logs for decay class 0



where V is the volume of any piece (k), i and j label decay class and forest type, ρ is the appropriate CWD tissue density, and the sum is across all pieces and decay classes within each plot.

We also measured the biomass of standing dead trees, or snags, in 2001. We measured the diameter at breast height (dbh) and full height of all snags using a steel tape and clinometer. We estimated individual snag volume using species-specific allometric equations for aspen (a very minor component of snag biomass), lodgepole pine, and Engelmann spruce developed in similar forests in Colorado and Wyoming (Edminster et al. 1982; Myers 1964; Myers and Edminster 1972). We used a generic equation for subalpine fir and snags that we could not identify to species, 32 of 191 snags across all plots (Newbould 1967). All equations estimated the volume of the stem (including the stump and top) but not branches, so the resulting volumes were underestimates. These pine, spruce and fir trees typically have a single central bole with radiating branches that fall off as the snag ages. We estimate that total snag volumes are 5–20% greater than those calculated. We assumed that snag tissue density was similar to that of CWD in early stages of decay, and estimated snag biomass by multiplying each snag's volume by the average tissue density of decay classes 0, I, and II CWD. We used forest type-specific averages (0.41, 0.35, and 0.36 g cm⁻³ for pine, ecotone and spruce-fir forest respectively).

Radiocarbon (¹⁴C) sampling and analysis

We used radiocarbon dating to determine the probable years of tree death for the same 42 logs described above for measurements of CWD tissue density. These logs were

stratified by decay class and therefore captured CWD in all stages of decay. We sampled the outermost growth rings from intact sections of CWD, typically with at least a shred of bark still remaining, using a hole saw to remove two 5 cm diameter, 1 cm thick disks of wood from each log. We shaved any bark from the outer face of the disk and then removed 20–60 mg of thin shavings using a scalpel. For second, older ring samples, we used the scalpel to smooth a part of the back of the disk and again removed thin shavings. In some cases, growth rings were extremely thin such that one to three rings were sampled to get enough tissue for analysis. In all cases, we counted the number of rings between the outer and inner samples, recording uncertainty in the time gap between the sampled rings for later input into the tree-ring dating program.

We treated the wood shavings using an acid/alkali/acid (AAA) procedure followed by bleach prior to radiocarbon analysis to remove resins, sugars, and some lignin that may have formed more recently than the tree ring cellulose. The AAA method or acid plus bleach has been used to construct most of the radiocarbon calibration curve from tree ring samples (Stuiver et al. 1998b), and when compared to alpha cellulose methods AAA has yielded very minor differences (Stuiver and Quay 1981; Tans et al. 1978). We treated the shavings with 1 N HCl, 1 N NaOH, and then 1 N HCl heated to 95°C on a block for 25 min, repeating each treatment until the solution remained clear. We then treated the shavings with 1 N NaOH and commercial bleach in a sonicator until they were pale yellow to pure white, rinsed them three times with deionized water and dried them overnight at 65°C. We oxidized the C in the shavings in sealed quartz tubes, and then reduced it to graphite on a vacuum line. We analyzed the graphite targets for their ¹⁴C/¹²C ratio on the accelerator mass spectrometer at Lawrence Livermore National Laboratory. We also analyzed ¹⁴C-free coal

samples treated as above to detect contamination during laboratory processing.

We express the radiocarbon data as $\Delta^{14}\text{C}$ (per mil or ‰), the difference between the $^{14}\text{C}/^{12}\text{C}$ ratio in the sample and that of a universal oxalic acid standard decay corrected to 1950, and as conventional ^{14}C ages (years B.P.) (Stuiver and Polach 1977). So that we could accurately adjust the radiocarbon ratios for biological fractionation of C isotopes during photosynthesis (Peterson and Fry 1987), we analyzed the treated shavings from each outermost ring for their $^{13}\text{C}/^{12}\text{C}$ ratio on a gas phase isotope ratio mass spectrometer at UC Berkeley, and calculated $\delta^{13}\text{C}$ values relative to the PDB standard (Dawson et al. 2002). We corrected outer ring ^{14}C values using sample-specific $\delta^{13}\text{C}$, and inner ring values using a mean $\delta^{13}\text{C}$ of -22.7‰ . After chemical pretreatment and correction for photosynthetic fractionation and radioactive decay, the ^{14}C signature of the samples should reflect that of the atmosphere at the time the growth ring was formed (Grootes et al. 1989; Hua et al. 1999). All outer ring ^{13}C and ^{14}C values are given in electronic supplementary Appendix S1.

Estimating calendar year of tree death

To estimate the year of tree death, we matched our sample radiocarbon values against a time series of atmospheric radiocarbon. Atmospheric radiocarbon ratios are defined by two eras. In the historic era, variation in ^{14}C was due to solar activity, atmospheric circulation, and since the nineteenth century, dilution due to emission of ^{14}C -free, fossil fuel-derived CO_2 (Stuiver and Braziunas 1998; Stuiver and Quay 1981). The “bomb” or “post-bomb” era is defined by a spike in atmospheric radiocarbon due to aboveground nuclear weapons testing in the late 1950s and early 1960s (Cain and Suess 1976; Grootes et al. 1989). The temporal and spatial pattern of this atmospheric pulse of radiocarbon has been affected by oceanic and ecosystem uptake and release of C, as well as atmospheric mixing (Randerson et al. 2002). Samples of organic matter that are thousands of years old can usually be dated to within a few decades (Stuiver et al. 1998a) because the rate of production was relatively constant over most of this period and radioactive decay since then has been significant. Organic matter that was created in the last 50 years can be dated to within 1–2 years because the spike and subsequent radioactive decay of ^{14}C resulted in large year-to-year changes in atmospheric radiocarbon ratios that are well documented. Over the ~450 years prior to 1950, there was considerable variation in cosmogenic production of ^{14}C , such that for any measured radiocarbon ratio in a sample that is ~50–500 years old, there are several possible date ranges from which it could have originated.

An approach called “wiggles matching” has been used to match series of tree ring radiocarbon ratios to the temporal variations, or “wiggles”, in the atmospheric radiocarbon record (Bronk Ramsey et al. 2001; Cain and Suess 1976). This technique can be used during any time period when the temporal resolution of the record and sample are

compatible, and is particularly useful in periods when atmospheric radiocarbon production has varied widely. To wiggle match all of our sample pairs and obtain estimates for the years the trees were last alive, we created a single, continuous, annually-resolved reference curve of northern hemisphere atmospheric radiocarbon ratios from 1510 to 2001, bridging the historic and bomb eras. We merged primary records that have been published elsewhere and are widely used (Levin and Kromer 1997; Levin et al. 1985; Stuiver et al. 1998b), interpolated or extrapolated missing years, and added a small amount of new data. We list both $\Delta^{14}\text{C}$ and ^{14}C age for each calendar year in the record, but used only ^{14}C ages for wiggle matching because that is the unit used by the tree-ring dating program.

While ^{14}C age approximates the number of years before ‘present’ (1950) that a sample in the more distant past was taking up atmospheric radiocarbon, for the past ~500 years and since 1950 this approximation is not valid. For all of the samples and reference curve data reported here, ^{14}C age can not be assumed to equal a number of calendar years before the present day or a 1950 reference date, but instead should be considered a standardized unit of measurement. For example, the ^{14}C ages of samples reflecting the post-1950 atmosphere are negative. Our reference curve and more detailed methods for its development are given in electronic supplementary Appendix S2.

We used our annually resolved, growing-season average, atmospheric radiocarbon record as the reference curve in the tree-ring dating program OxCal v. 3.8 2002 (Bronk Ramsey 1995, 2001; Bronk Ramsey et al. 2001) to wiggle match the CWD radiocarbon ratios. OxCal used the (positive or negative) ^{14}C ages from both the inner and outer growth rings, the estimated number of years between them, errors in all input values, and the reference curve itself to find all possible points of intersection between the measurements and reference curve. The program then calculated the relative probabilities for each match. We saved these probability distributions, summing separately to 68.2% of all probable dates (1- σ errors; $P=0.32$) or to 95.4% of all probable dates (2- σ errors; $P<0.05$) for each sample. For one sample (S2 IV Spruce) we used a different, decadal reference curve, INTCAL98 (Stuiver et al. 1998a), to generate date ranges and probabilities because the sample was older than the oldest date in our annually resolved curve.

Coarse woody debris decay constants and turnover times

Because many of the sample pairs yielded several probable ranges of years within which the outer tree ring could have formed, we could not simply calculate a single CWD decay curve. Instead, we wrote a Monte Carlo routine using Matlab v. 6.5.0 (MathWorks 1984–2002, routine script available upon request) to repeatedly draw combinations of year of tree death from the OxCal probability

distributions and CWD tissue density for each sample. The routine selected a range of years according to the OxCal relative probabilities and then a single year assuming a normal distribution centered in the chosen range. Time since death was calculated by subtracting the selected year from 2001, the year we measured CWD tissue density. The routine then selected a CWD tissue density from a normal distribution centered over the mean density for that sample, with one standard deviation equal to the standard error of the measurement mean. We then fit an exponential decay curve from the first set of dates and densities (across samples) using linear regression analysis with log-transformed CWD tissue density values,

$$\text{Ln}(\text{Tissue density}) = a - k \times t, \quad (2)$$

where t is time since tree death. Regression statistics and parameters (a , k) were saved, and the cycle was iterated to obtain families of curves. We calculated mean parameter values from families of 500 curves based on all samples ($n=42$), or based on samples grouped by site and species ($n=10-11$). Results generated from date ranges taken from 1- σ and 2- σ probability distributions are reported separately, although they do not differ greatly. We calculated turnover times as $1/k$ for each group of samples.

By using tissue density as our index of mass loss during decomposition, we did not correct for any concomitant change in log volume. We also did not control for initial log density. The mean diameter of the CWD samples was 15.6 ± 0.88 cm across all samples, ranging from 8.6 to 30.0 cm. All samples were ≥ 10 cm diameter at their widest point.

Statistical analysis

For CWD and snag biomass, we report standard errors calculated either from measurement error or as the standard error of the mean when plots were combined. We used Gaussian error propagation to estimate error. For CWD decomposition parameters, we report the standard

error of the parameters using first order, second moment error propagation, which combines uncertainty in the dates of tree death, in CWD tissue density, and in the spread of points used in each curve fit.

Because four of the ecotone plots were located near a semi-permanent hunting camp (E1, E2, E4, E5), and were probably affected by wood collection for campfires, we excluded these plots from analyses of CWD (but not snag) biomass. We used linear regression analysis to relate CWD and snag biomass to climate variables along the gradient, using Systat v. 8.0 (SPSS 1998) to compute regression statistics. We used a t -test to make pair-wise comparisons of CWD turnover times between sites and species. We report statistical significance when $P < 0.05$, unless noted.

Results

Coarse woody debris and snag biomass

Where not affected by wood gathering, CWD biomass ranged from 2.57 ± 0.09 to 34.3 ± 0.6 Mg ha⁻¹ (Table 3). CWD biomass was highest in the spruce-fir forest, both in absolute amount (23 ± 6 Mg ha⁻¹) and as a fraction of live AGB ($20 \pm 10\%$). The amount of CWD biomass tended to increase with elevation, though the effects were not statistically significant. Snag biomass ranged from 0.20 ± 0.01 Mg ha⁻¹ in one of the pine forest plots to 25.0 ± 0.9 Mg ha⁻¹ in one of the spruce-fir forest plots (Table 3), and generally increased with elevation ($R^2=0.59$, $P=0.006$) and soil moisture ($R^2=0.42$, $P=0.03$). Snag biomass also decreased with increasing soil temperature ($R^2=0.57$, $P=0.007$, $n=11$ in all cases).

Together, CWD and snag biomass totaled from 4.7 ± 0.2 to 54 ± 1 Mg ha⁻¹ across all plots, with the greatest biomass in the spruce-fir forest. CWD and snags contained $2.8 \pm 0.1-60 \pm 1\%$ as much biomass as live tree AGB (Table 3), with the highest ratio of dead:live in the spruce-fir forest. Total CWD and snag biomass increased strongly with elevation ($R^2=0.90$, $P=0.001$; Fig. 3), soil moisture ($R^2=0.67$, $P=0.02$), date of snowmelt ($R^2=0.77$, $P=0.01$), and winter length ($R^2=0.72$, $P=0.02$); and decreased with

Table 3 Coarse woody debris and snag volume and biomass for plots along an elevation gradient, Fossil Ridge Wilderness, Colorado. Standard errors (SE) were calculated from measurement error. Total AGB is given for reference

Plot	Forest type	AGB (Mg ha ⁻¹)	CWD		Snags	
			Volume (m ³ ha ⁻¹)	Biomass (Mg ha ⁻¹)	Volume (m ³ ha ⁻¹)	Biomass (Mg ha ⁻¹)
P1	Pine	206	36.99 (0.18)	6.99 (0.14)	9.86 (0.32)	4.02 (0.14)
P2	Pine	110	73.15 (0.28)	12.25 (0.23)	0.49 (0.01)	0.20 (0.01)
P3	Pine	117	98.82 (0.94)	16.04 (0.34)	4.05 (0.26)	1.65 (0.11)
E1	Ecotone	173	19.11 (0.10)	3.84 (0.13)	35.36 (1.21)	12.34 (0.53)
E2	Ecotone	168	10.80 (0.13)	2.96 (0.11)	4.99 (0.34)	1.74 (0.15)
E3	Ecotone	212	10.14 (0.11)	2.57 (0.09)	51.21 (1.60)	17.87 (0.69)
E4	Ecotone	233	6.18 (0.08)	1.61 (0.05)	22.79 (1.04)	7.95 (0.45)
E5	Ecotone	208	5.51 (0.05)	1.31 (0.04)	17.40 (0.89)	6.07 (0.38)
S1	Spruce-fir	151	65.13 (0.26)	13.64 (0.34)	70.20 (2.46)	25.04 (0.94)
S2	Spruce-fir	210	96.30 (0.28)	21.27 (0.41)	57.88 (1.71)	20.65 (0.66)
S3	Spruce-fir	90	137.59 (0.41)	34.30 (0.60)	55.14 (2.78)	19.67 (1.09)

increasing air ($R^2=0.87$, $P=0.002$) and soil temperature ($R^2=0.60$, $P=0.04$; $n=7$ in all cases). Dead wood biomass increased 75 kg ha^{-1} per meter gain in elevation and decreased 13 Mg ha^{-1} for every degree C increase in mean air temperature.

Coarse woody debris decomposition

According to radiocarbon dating, the logs we sampled had been dead between 2 and ~ 580 years. The tree determined to have died after the 1998 growing season was observed to have blown down alive in early spring 2001. Its last growth ring should have reflected the ^{14}C signature of the 2000 growing season atmosphere. This ~ 2 year discrepancy could be due to imprecise wood sampling, differences between actual atmospheric concentrations and the extrapolation used for this time period, differences between Colorado and northern Europe in atmospheric radiocarbon concentrations (Kromer et al. 2001), a different growing season than we assumed, and/or the tree using C assimilated in 1998 to form the 2000 ring or not producing new wood after 1998. However, a difference of ~ 2 years is well within the error associated with much of the historic radiocarbon curve, and should not have had a significant effect on our estimates of decomposition rates using these dates.

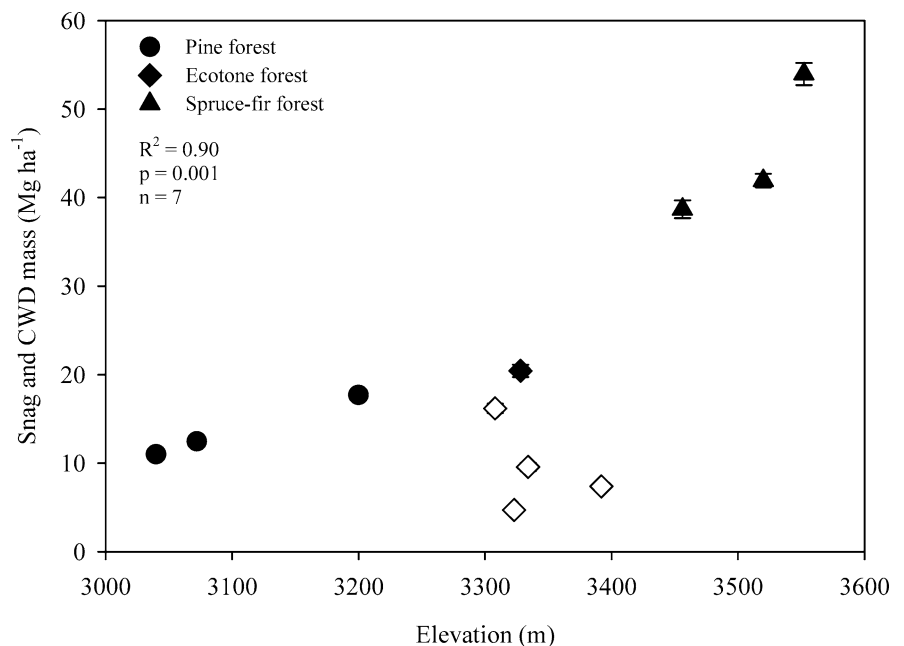
Of the 42 logs we sampled, 17 died in the 45 years since atmospheric nuclear weapons testing occurred (Appendix S1). These logs were all in the early stages of decomposition. More highly decomposed logs died in the preceding 550 years. Across all three elevations and both species, we estimated CWD turnover time to be 580 ± 180 years (Table 4). Overall, there were no statistically significant differences between turnover times at the different elevations or between species at the same elevation ($t < 1$

in all cases for $df=18$ or 19), due to high standard errors of the estimates. However, we found that our estimate of the turnover time for lodgepole pine logs in the mid-elevation ecotone forest (630 ± 400 years) was 1.9 times longer than that for pine logs in the low elevation pine forest (340 ± 130 years), suggesting that conditions for pine wood decay are better at lower elevations (Table 4). Within the ecotone forest, where both pine and spruce trees co-occur, the high uncertainty for the spruce logs gives low confidence in the comparison between species.

Table 4 Coarse woody debris decay rate and turnover time by species and plot. Mean parameters a and k are from 500 iterations of Eq. 2 in the text for each plot \times species combination. τ is the turnover time, calculated as $1/k$. 2- σ values consider date ranges for each sample for which associated probabilities summed to 95.4%, while 1- σ values consider date ranges for which probabilities summed to 68.2%

Plot	Species	n	a (g cm^{-3})		k (year^{-1})		τ (years)	
			Mean	SE	Mean	SE	Mean	SE
2- σ values								
All	Both	42	0.33	0.10	0.0017	0.0005	580	180
P2	Pine	11	0.42	0.15	0.0029	0.0011	340	130
E2	Pine	10	0.34	0.23	0.0016	0.0010	630	400
E2	Spruce	10	0.27	7.13	0.0013	0.0015	800	960
S2	Spruce	11	0.33	0.20	0.0015	0.0010	650	410
1- σ values								
All	Both	42	0.33	0.10	0.0017	0.0005	590	190
P2	Pine	11	0.41	0.15	0.0028	0.0011	350	130
E2	Pine	10	0.34	0.22	0.0016	0.0010	620	400
E2	Spruce	10	0.27	2.19	0.0011	0.0015	920	1200
S2	Spruce	11	0.33	0.21	0.0015	0.0010	660	430

Fig. 3 Snag and CWD biomass along the elevation gradient. Plots near a hunting camp (shown with hollow symbols) were excluded from the given analysis. Error bars represent measurement error



Discussion

Coarse woody debris and snags are important but variable components of the C cycle in temperate forests. Together they contained up to 60% as much biomass as live aboveground trees in our highest elevation sites. Engelmann spruce-subalpine fir forest dead wood averaged $35 \pm 12\%$ as much biomass as AGB, slightly less than the 52% measured by Arthur and Fahey (1990) for the same forest type in a slightly wetter location. Lodgepole pine forest dead wood biomass in our sites averaged just 14 Mg ha^{-1} , which is considerably less than the 39 Mg ha^{-1} (just CWD) reported by Busse (1994), or the $43\text{--}128 \text{ Mg ha}^{-1}$ reported by Fahey (1983) for the same forest type. Differences in stand age may partly explain the discrepancy. Of the three Fahey sites, the one with the least snag and CWD biomass had the oldest stand age (240 years, French Creek), while the one with the most biomass was surveyed 70 years after a stand replacing fire (Rock Creek). This could be because the fire itself kills but does not consume many trees, which then fall and undergo decay as the stand re-grows (Tinker and Knight 2000). In our lodgepole pine forest plots, the oldest trees were at least 130 years old (rings counted at breast height). Alternatively, CWD production may be lower or decay may be faster in Fossil Ridge pine forest, relative to the others mentioned.

Snag biomass was a substantial fraction of dead wood biomass in most of our plots, in some cases surpassing the amount of fallen wood. Snag biomass as a fraction of total dead wood was generally greater in the high elevation spruce-fir forest than in the low elevation pine forest, indicating that the causes of mortality at higher elevations may differ from those at lower elevations (e.g., more wind-throw at low elevations vs. more lightning strikes at high elevations), or that tree and/or stand architecture change with species composition and elevation (e.g., deeper roots or denser stands keep dead trees standing longer at high elevations).

The greater biomass of both snags and CWD at higher elevations where temperature tends to be cooler could be due either to greater rates of mortality or to lower decomposition rates. Mortality is difficult to measure over just a few years, but tree biomass increment surveys suggest that mortality did not vary with elevation, averaging 1.8 trees per plot, or 20 trees per hectare, between 1999 and 2002 (Kueppers 2003). This corresponded to an input of about 1.65 Mg ha^{-1} to the snag and CWD biomass pools over 3 years. However, because mortality is likely to be episodic and spatially heterogeneous, this rate of CWD and snag production probably does not represent an average input rate.

Decomposition of CWD is extremely slow in these subalpine forests. In the ecotone forest, our decay rate constants may be underestimates if hunters preferentially removed higher density CWD in the early stages of decay from the sampling area. However, we included logs at all stages of decay for each species and forest type, and decay constants for the pine and spruce-fir forests would not

have been affected. Our estimate of the decay constant across all sites and both lodgepole pine and Engelmann spruce logs ($0.0017 \pm 0.0005 \text{ year}^{-1}$) is slower than that reported for 40+ cm Douglas fir logs in the Pacific Northwest, for other temperate forests (Harmon et al. 1986), and for the same species measured by most other researchers (Busse 1994; Fahey 1983; Laiho and Prescott 1999). Using a dendrochronological approach, Brown et al. (1998) reported lodgepole pine and Engelmann spruce decay rates in similar Colorado forest to be linear with time, decreasing by 0.0004 and $0.0015 \text{ g cm}^{-3} \text{ year}^{-1}$, respectively. At these rates, the time for CWD to reach 37% of its original density is ~ 570 years for pine, comparable to our estimated turnover time of 340–630 years, and 140 years for spruce, which is much less than the 650–800 years we estimated. They also found that lodgepole pine decomposed more slowly than Engelmann spruce, while our results were inconclusive regarding species differences.

The extremely slow CWD decomposition in Colorado subalpine forests is probably because the cold climate impedes decomposition. While the large uncertainty in our estimate of decay constants did not result in significant differences between sites, we did find qualitative differences. Decay was fastest at the lowest elevation site where the climate is warmer and drier, suggesting that future increases in mean annual temperature or in the length of the growing season could speed decay. Previously published work suggesting a global Q_{10} value for this process of 2.4–2.5 (Chambers et al. 2000; Mackensen et al. 2003) is qualitatively consistent with the increase in the decay constant we observed from the two cooler, wetter sites to the warmer, drier site. If CWD decay in subalpine forest is temperature limited it may be more sensitive to temperature increases in cooler than in warmer sites. Among sites with mean annual air temperature below 10°C , there seems to be high variability in decay rates due to differences in genus-specific rates of heart wood decay, local moisture status, and size as well as temperature (Harmon et al. 2000). Future studies should use a comparative approach to more carefully quantify the temperature sensitivity of wood decay in high elevation sites vulnerable to future climate change.

Because we did not sample trees that all fell at the same time, nor did we control initial wood density or the microsites for decomposition, our decay constant estimates incorporate real heterogeneity in CWD decomposition. The oldest log we sampled was last alive in the early 1400s, though it was not the most highly fragmented or least dense log we sampled. It is likely that this log remained upright in the dry mountain air long after death, and only began decaying when it fell and came in contact with the relatively moist ground. The large amount of snag biomass in our research plots indicates that such a time lag in the onset of decay may not be unusual in these forests. We observed several kinds of mortality over the course of our study; spring windstorms toppled shallow rooted but otherwise apparently healthy lodgepole pine trees, and lightning and beetle infestation killed Engelmann spruce

and subalpine fir. Few studies of CWD decay report standard errors for their decay parameters that incorporate all sources of variation (in CWD density or mass, CWD age, and in the curve fit), as we have reported here. Because decomposition is an inherently heterogeneous process, more highly constrained estimates of mean decay rates require extensive sampling in most environments, and variance in estimates should be reported.

The radiocarbon dating method we used allowed us to date logs to within 2 years for recently dead logs, while a large fraction of the older logs had probable ranges for date of death spanning decades. By using a Monte Carlo sampling routine, we were able to account for these broad ranges and estimate decay curves without making any assumptions about, or needing any knowledge of, site history. Our approach could be used in any other research site, but would be particularly successful in sites with faster turnover times because a larger fraction of the samples would have died since 1950. For sites with slow turnover times, measuring the ^{14}C content of more than two rings for each tree that died in the interval 1800–1950, and measuring a greater number of samples in any one site will improve confidence in estimates of the decay constant. Alternatively, combining our approach with a dendrochronological approach for trees that died 50–150 years ago may also yield a better-constrained estimate.

Dead wood is an important component of forest C cycling that should be more systematically quantified. In the Fossil Ridge sites, the dead wood pool accounted for 3–60% as much biomass as live trees, and 2–17% of total ecosystem C, including soil C (Kueppers 2003). By simply multiplying the observed decay constants by the pools of dead wood, we estimate a steady-state C flux ranging from 15 to 40 kg C ha⁻¹ year⁻¹ in sites not affected by wood gathering. To model potential changes in the rates of C cycling and C storage in forest ecosystems under a changing climate, we need better estimates of decay rates of CWD, uncertainties in these estimates, and knowledge of the sensitivity of this sometimes large pool of forest C to changes in climate. Less CWD and snag biomass in warmer plots along our subalpine forest climate gradient suggests that long-term aboveground C storage may be smaller under a warmer climate, and a greater rate of CWD decomposition in a warmer site relative to rates in cooler sites suggests that climate warming in subalpine forests could lead to a loss of stored C from this pool. Changes such as these would affect not only the local forest structure, but also calculations of any potential atmospheric C sink in western subalpine forests.

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