

Environmental drivers of deadwood dynamics in woodlands and forests

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Abstract. Deadwood dynamics play a key role in many forest ecosystems. Understanding the mechanisms involved in the accumulation and depletion of deadwood can enhance our understanding of fundamental processes such as carbon sequestration and disturbance regimes, allowing better predictions of future changes related to alternative management and climate scenarios. A conceptual framework for deadwood dynamics has been generally accepted but has not been broadly tested with empirical data. We used a large ($n = 6191$) data set containing measurements of live and standing dead trees, and downed woody material, representing numerous woodland and forest types from throughout the Interior Western USA, to assess relationships between environmental factors and basic elements of forest structure, with particular focus on the various components of deadwood (i.e., fine woody debris, litter, duff and large deadwood, both standing and downed). Environmental gradients emerged as the most influential factors determining structure and deadwood dynamics of these diverse vegetation types. We found that dead components are approximately proportional to the live component and that all of the various components of structure can be ordered as a function of climatic gradients representing temperature and moisture. The postulate that maximum accumulation of biomass is associated with intermediate values of temperature and moisture was only partially supported by our results, indicating that conceptualizations of deadwood dynamics must be considered in the context of the particular disturbance regimes (e.g., fire, insect outbreaks, wind) most commonly associated with particular woodland and forest types. These findings are relevant to a wide range of applications, from ecosystem modeling to development of resource management plans under alternative future climates.

Key words: climatic gradients; coarse woody debris; disturbance regimes; fine woody debris; Rocky Mountains; snags.

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INTRODUCTION

Deadwood in forests and woodlands has been linked to a broad range of ecosystem processes and functions. It has, for example, a central role in carbon and nutrient cycling within terrestrial

systems (e.g., Laiho and Prescott 1999). Standing and downed dead trees are key elements of forest and woodland structure (Marzano et al. 2013), which are important components of habitat for wildlife species including amphibians, birds and mammals (e.g., Bull et al. 1997,

Sturtevant et al. 1997, Bunnell et al. 2002, Bednarz et al. 2004). Similarly, deadwood in all its forms and sizes (leaves, twigs, logs) is a key input to aquatic systems (e.g., Bilby and Ward 1991, Richmond and Fausch 1995, Gurnell et al. 2002, Everest and Reeves 2007). Deadwood dynamics of woodlands and forests play key roles in carbon sequestration and disturbance regimes, and understanding these dynamics will be central to predictions of changes in such processes under alternative management and climate futures. A conceptual framework for deadwood dynamics (e.g., Harmon et al. 1986, Sturtevant et al. 1997, Woodall and Westfall 2009) has been generally accepted but has not been broadly tested with empirical data. We critically examine the conceptual framework and reconcile differences between conceptual models and field observations. Our results will be relevant to a wide range of applications, from ecosystem modeling to development of resource management plans.

In this study, we focused on deadwood dynamics of woodlands and forests of the Interior West of the United States. This region spreads across 18 degrees of both latitude and longitude and includes broad ranges of elevation, topographic position and soils. Considerable structural and species biodiversity is associated with the resulting environmental gradients. Within the region, vegetation ranges from types characteristic of warm desert to alpine. An important quality of the Interior West is the presence of both lower and upper treelines (Long 2003). Broadly, lower treeline is thought to be determined by limiting moisture and upper treeline by limiting temperatures (Daubenmire 1954). The nature of the dominant disturbance regimes varies considerably among woodland and forest types. For example, natural fire regimes can be characterized by very frequent (e.g., <5 years)/low severity to very infrequent (e.g., >300 years)/high severity fires (Arno 1980, Agee 1998, Schoennagel et al. 2004). Structures of the types range from open, savanna-like woodland to closed canopy forest. The nature of deadwood also varies considerably. For example, there can be more than 10-fold differences in the amount of coarse woody debris (CWD), depending on vegetation type, site-specific environmental conditions and disturbance history (Woodall

and Westfall 2009).

Using a large data set containing measurements of live and standing dead trees, and downed woody material, and representing numerous woodland and forest types from throughout the Interior West, we assess relationships between environmental factors and basic elements of forest structure. We particularly focus on the various components of forest deadwood (i.e., fine woody debris, litter, duff and large deadwood, both standing and downed). Our general conceptualization is that details of the deadwood complex are indirectly influenced by environmental factors, which more or less directly influence potential productivity, decomposition rates, and disturbance history. Deadwood accretion (e.g., tree death by disturbance or competition) and depletion (e.g., combustion, decomposition) result from the combined effects of all these factors and processes. We postulate that increasing moisture and decreasing temperature are associated with important elements of stand composition and structure (e.g., volume of living trees, canopy cover, and density) indicative of the transition from open woodlands to closed canopy forests (Fig. 1A). This broad postulate is influenced by the fact that the Interior West of the United States does not have sites where high temperatures and high precipitation co-occur. We also postulate that these environmental gradients strongly influence structure and deadwood dynamics of woodland and forest communities such that maximum accumulations of both living and dead woody structures are associated with intermediate levels of temperature and moisture (Fig. 1B). Actual accumulations of deadwood are, of course, influenced by disturbance and local site factors. A basic conceptualization (Fig. 1C) represents, for example, interactions between pre-disturbance legacies, deadwood creation and transitions between structural components over time. Details of these relationships are expected to vary with vegetation type and the nature of disturbance. For example, insect outbreaks, fire and wind can generate different deadwood patterns over time. A near zero starting point for the live curve and a variable amount of downed dead would be characteristic of a severe, stand-replacing fire. A bark beetle epidemic, however, would likely leave a small

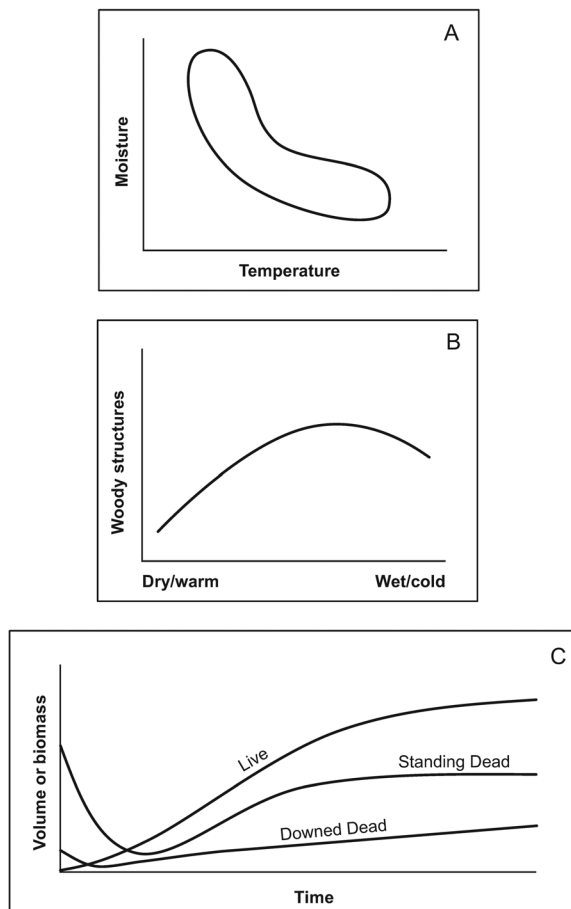


Fig. 1. Postulated relationships between environmental factors, disturbance and basic elements of forest structure: (A) distribution of woodland (occurring under dry/warm conditions) and forest (under increasingly wet/cold conditions) types with respect to precipitation and temperature gradients; (B) amounts of live and deadwood along a gradient of decreasing temperature and increasing moisture; (C) interactions between pre-disturbance legacies, deadwood creation and transitions between structural components over time.

live component and all of the legacy downed dead material. At the time of new stand establishment following a bark beetle outbreak, the standing dead component would be nearly equal to the combination of previously live and legacy standing dead components (in contrast to legacies of stand-replacing fire) and the downed dead component would likely increase quickly as the beetle-killed trees fall.

Specifically, for the important woodland and forest types in the Interior West, we examine how: (1) the various types are broadly arrayed with respect to temperature and moisture; (2) these environmental factors influence woody structure (i.e., the amount of living trees, standing dead trees, coarse and fine downed wood, litter and duff); and (3) the influence on woody structure of disturbance histories differs across environmental gradients and between vegetation types.

METHODS

Sampling design

The data used in this study were drawn from USDA Forest Service Forest Inventory and Analysis (FIA) annual surveys completed between 2006 and 2009 in the states of Arizona, Colorado, Idaho, Montana, Nevada, and Utah (Fig. 2). FIA annual surveys use a nationally standardized mapped plot design (Conkling and Byers 1993), meaning two or more conditions (e.g., stand types or ages, or forest and non-forest cover) can be present on the sample for a given site. For the purpose of this study, we eliminated multi-condition plots to ensure that the plot footprint sampled a relatively homogeneous condition; this reduced the number of conditions available for analysis from 8490 to 6253. As a result of this filtering, the terms plot, condition, and stand are effectively synonymous for our purposes. Hereafter we will use the term “stand” to refer to the sampled area at a given location. The sample was further reduced by eliminating non-stocked plots and minor forest types (e.g., Great Basin bristlecone pine, *Pinus longaeva*), leaving 6191 stands.

We consider the sample of 6191 stands included for analysis as primarily representing natural conditions and processes. Although most of the Interior West, like the rest of the U.S., has a modern history of human forest use, in most parts of the region there is currently little commercial forestry activity. FIA crews found evidence of treatment on just over 2% of conditions, with the year of treatment occurring up to 10 years prior to the plot visit. As a result, the per-annum rate of stand treatment is estimated to be minimal at this geographic scale. In cases where harvest evidence potentially oc-

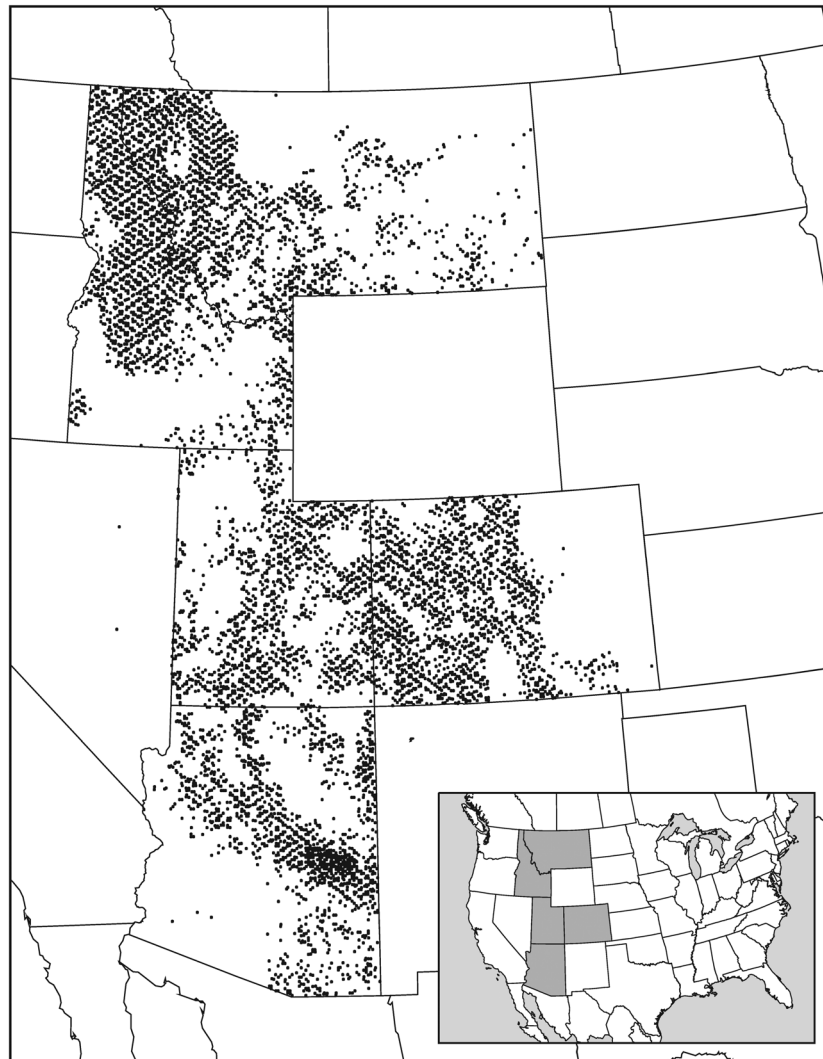


Fig. 2. Locations of USDA Forest Service Forest Inventory and Analysis stands used in this study, representing common woodland and forest types in the Interior Western USA.

curred long prior to plot measurement, we make the assumption that subsequent stand development or natural disturbances have largely overprinted the effects of harvest. Such is the case in northern Utah and southern Wyoming, for example, where forests that were heavily utilized during the era of Euro-American settlement are mature second growth, and in some cases have been subsequently affected by fire or bark beetle epidemics. Evidence of natural disturbances, such as fire, insects, disease, and windthrow was found on just over 17% of plots, across a similar time span. Approximately 20% of distur-

bance codes were recorded in young stands (<25 years), with another 30% of codes recorded in stands aged 75–125 years. The occurrence of disturbance was proportionately lower than average in maturing stands (25–75 years). We considered this distribution of disturbances by age class to be consistent with our definitions (e.g., that young stands are primarily the result of stand-replacing events) and our expectations of stand development over time (see Fig. 1C). Given that the exploration of woody material patterns over time and in response to disturbance was a primary goal of this study (with the other being

Table 1. List of variables adopted in this study. Variables are grouped by category (living trees, deadwood, and environmental descriptors). The data source is the FIA dataset, except for the climatic variables (†) that were computed from the PRISM dataset.

Variable	Units	Code
Living trees		
Basal area	m ² /ha	BA_Live
Trees density	trees/ha	TPA_Live
Stand Density Index		SDI_Live
Volume	m ³ /ha	VOLCF_Live
Stand age	years	STDAGE
Crown cover	%	CRCOV
Mean annual increment	m ² ·ha ⁻¹ ·yr ⁻¹	MAICF
Quadratic mean diameter	cm/yr	Dq
Regeneration density	seedlings/ha	SEEDS_Ac
Deadwood		
Snag basal area	m ² /ha	BA_Deal
Snag density	trees/ha	TPA_Deal
Snag Stand Density Index		SDI_Deal
Snag volume	m ³ /ha	VOLCF_Deal
Coarse woody debris volume	m ³ /ha	CWD_CF_AC
Fine woody debris volume	m ³ /ha	FWD_all_CF_AC
Duff depth	cm	DUFF_DEPTH
Litter depth	cm	LITTER_DEPTH
Total deadwood volume	m ³ /ha	DWM_VolCuffTotal
Environment		
Elevation	m a.s.l.	El
Slope	°	Sl
Aspect	°	As
Bare soil cover	%	Soil
Latitude	°	Lat
Longitude	°	Lon
Rain Factor†	...	RF
Aridity Index†	...	AI
Pluviothermic Ratio†	...	PR
Ombrothermic Index†	...	OI

the control of climatic factors on woody material abundance), we elected to do no further filtering of the data set. We considered that the very small number of treated stands would have little influence on the analysis, and that the distribution of disturbance codes was empirical evidence of the conceptually unbiased nature of the data set. As a result, all 6191 plots from the initial filtering were retained for analysis.

Data collection

Our dataset represents three main categories of variables: living trees, deadwood and environmental descriptors (Table 1). Live and standing dead trees are “core” components of the national FIA data set. Core field-collected variables for live and standing dead trees include, for example, diameter, height, decay class (in the case of standing dead), and species; these are used to compute variables such as volume and biomass. The Interior West FIA program also collects “core-optional” variables (such as mortality

year), which are collected at the discretion of each regional FIA program. In addition to core and core-optional variables is a third class of variables that is referred to as “regional add-ons”. These variables can include individual variables within a general area of the sampling scheme (e.g., plot, condition, or tree level), or can comprise an entire subsection of the general measurement protocol.

Our downed woody material (DWM) data come from a regional add-on DWM protocol that was piloted in 2004 and 2005, and implemented in 2006. Since the late 1990s, the national FIA program has collected DWM data on what was historically known as the Forest Health Monitoring plot system (Conkling and Byers 1993), more recently referred to as FIA Phase 3 (P3) plots. This plot system is a subset of the regular FIA production plots, which are commonly referred to as Phase 2 (P2) FIA plots. Due to user demand for more detailed information on DWM (e.g., ability for estimation at smaller scales), primarily

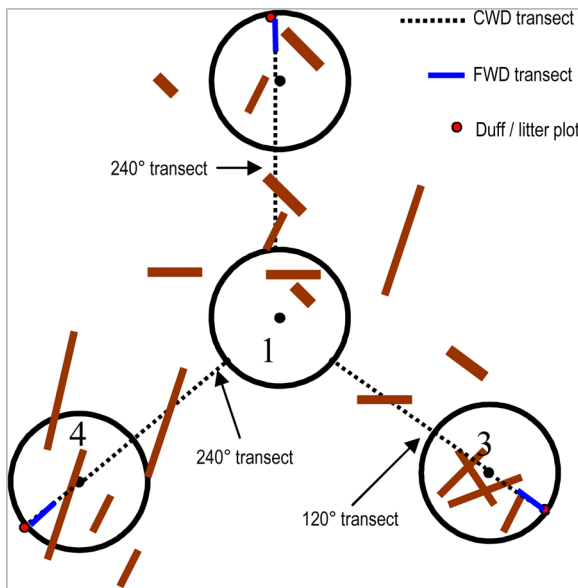


Fig. 3. Layout of the Interior West FIA P2 down woody material sampling transects showing a single-condition plot. Modified from Interior West FIA Field Manual version 3.0.

for fire and wildlife applications, the Interior West FIA program collects DWM data on all P2 plots as a regional add-on protocol. This provides approximately 16x the sampling intensity of the national FIA P3 DWM protocol (Woodall and Monleon 2008). Both the national FIA P3 methodology and the Interior West Regional P2 protocols are based on line-intercept sampling methods (Warren and Olsen 1964, Brown 1974). Woodall and Monleon (2008) discuss adoption of the line-intercept methodology by the national FIA program in detail. The Interior West P2 approach (Fig. 3) includes modifications to the P3 DWM protocol to provide for greater efficiency. Therefore, the compilation methods at the plot and population scale for P2 DWM measurements are the same as for P3 DWM (Woodall and Monleon 2008), but accounting for differences in transect layout (i.e. 12 7.3-m segments vs three 36.6-m segments). Manuals for Interior West FIA field procedures are available at: <http://www.fs.fed.us/rm/ogden/data-collection/field-manuals.shtml>. Raw and compiled data for the Interior West P2 DWM are currently archived within the regional FIA database, pending modification of the national FIA database to accept regional

variables.

For each stand, we summarized the basal area, stem volume, and density for living trees (>2.5 cm at 1.37 m stem height) on a per hectare basis. Other living tree variables at the stand-level were stand density index (Reineke 1933), crown cover, mean diameter, mean annual increment, stand age, and regeneration density. Quantity and characteristics of lying deadwood were described by: depth of litter and duff; volume of DWM segregated into fine woody debris (FWD) (>0.6 cm and <7.6 cm diameter, divided into small, medium, and large subfractions) and coarse woody debris (CWD) (≥ 7.6 cm diameter). The standing dead component (≥ 12.7 cm diameter) was characterized by volume, basal area, and stand density index.

We should note that there are conflicting uses of the term “coarse woody debris” in the literature. Harmon et al. (1986), for example, define coarse woody debris to include standing dead trees. For several reasons, we separate standing dead trees and downed dead material that is large enough to be classified as “coarse”. The FIA field manuals under which our data were collected define CWD as: “In this inventory, CWD includes downed, dead tree and shrub boles, large limbs, and other woody pieces that are severed from their original source of growth. CWD also includes dead timber and single stemmed woodland trees (either self-supported by roots, severed from roots, or uprooted) that are leaning >45 degrees from vertical.” (IW-FIA Field Manual Ver. 3.0, Sec. 11.0.3).

Formal definitions, for example, by the Society of American Foresters Dictionary of Forestry (<http://dictionaryofforestry.org/>) and the British Columbia Ministry of Forests, Lands, and Natural Resource Operations Biodiversity Guidebook (<http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/biodiv/biotoc.htm>), include only downed material in the definition of CWD. Use of the term “debris” to include standing dead trees is also something of a misnomer, because most definitions of debris describe material that is scattered, broken, or otherwise modified from its original form. Indeed, FIA sampling methodology recognizes the intact portion of a standing dead tree as a tree (broken or otherwise), and the fallen portion(s) as downed (coarse or fine) woody debris.

We used wood volume as the unit of measurement in our analysis. Volume is the most directly computed among the related variables (i.e., volume, biomass, carbon) that are maintained in the FIA database, because it is based on measured diameter and height. Volume equations are applied by species, ecoregion, and state, using the most appropriate equations at the regional scale. FIA estimates of tree and downed woody biomass, and secondarily carbon, are computed from volume using scalars (e.g., wood density), additional allometric models (e.g., biomass component ratios), and other adjustments (e.g., decay class). Examination of the CWD decay class showed that nearly 70% of tallied pieces were in classes 1 to 3 (i.e., most sound), with the remainder being in classes 4 and 5 (advanced decay). The advanced decay classes were well-distributed among forest types and stand age classes, indicating that any deductions would simply lower the overall magnitude of estimated volume, biomass, or carbon and not affect comparisons of relative abundance of any metric by forest type and stand age. While we acknowledge that incorporation of decay class would constitute a refinement to our estimates, we consider it more appropriate for investigations of within-class variation that are beyond the scope of this study.

Environmental descriptors included geographic (latitude and longitude), topographic (slope, aspect, elevation), site (bare soil) and climatic (Rain Factor, RF; Aridity Index, AR; Pluviothermic Ratio, PR; Ombrothermic Index, OI) variables. Geographic coordinates and topographic variables were measured or computed according to national FIA protocols (Interior West Forest Inventory and Analysis Field Procedures, Version 3.02; accessible at <http://www.fs.fed.us/rm/ogden/data-collection/field-manuals.shtml>). Precipitation and temperature data were obtained by intersecting the PRISM climate grid data (Daly et al. 1994) with our stand locations. Four climatic indices, both simple and compound, were computed to assess the influence of climatic gradients on the distribution of forest types and deadwood accumulation. Rain Factor (Lang et al. 1976) and Aridity Index (Martonne 1926) are based on mean annual precipitation and temperature values, while the Pluviothermic Ratio (Emberger 1942) involves averages of minimum

and maximum temperature. To take into account the role of the growing season we adopted the Ombrothermic Index (Rivas-Martínez 2004, Rivas-Martínez et al. 1999), which is calculated as a function of precipitation and temperature for days with temperatures above 0°C.

Forest types and groups

The FIA program recognizes a limited number of forest types, approximating those recognized by the Society of American Foresters (Eyre 1980). These types are classified by two methods: (1) by algorithm, using the tally trees measured on a condition (Arner et al. 2001), and (2) by field crew call. Each has advantages and limitations. For example recently-disturbed stands may not have sufficient numbers of trees to be classified by the algorithm and therefore be classified as “nonstocked”. Crew calls on such stands are necessarily subjective, but the more synoptic view of the crew, as compared to the plot footprint, will likely provide an accurate classification for stands that fail the forest type algorithm. The analysis dataset included 26 woodland and forest types representing vegetation types common enough to be represented in our data set by at least 15 stands (Tables 2 and 3). Stands in the dataset range from 31° 21'46" N to 48°59'43" N latitude, 102°10'4" W to 119°29'27" W longitude and 85–3593 m in elevation. The 26 types were assigned to one of four broad groups (Tables 2 and 3), the makeup of which followed, for the most part, characterizations by MacMahon (2000), Peet (2000), and West and Young (2000).

Woodland group.—The woodland group includes seven vegetation types that have been categorized in various ways by different authors. Most of the woodland group occupies sites just above what West and Young (2000) refer to as semi-desert scrub or shrub-steppe. They lump several of our types together as mountain mahogany-oak scrub. They also combine the various juniper and juniper-pine types in the broad category of pinyon-juniper (P-J) woodlands (i.e., various combinations of cembroid pines and *Juniperus* spp.). Collectively, the P-J woodlands occupy at least 17 million ha in the Interior West and within this huge range there is considerable variability in seasonality of precipitation. Nevertheless, the broad type is best characterized as

Table 2. Common and scientific names for the 26 vegetation types, by group, included in this study. The four letter codes are used in the presentation of results. Climatic data represent means for each type (ELEV = elevation; MAP = mean annual precipitation; MAT = mean annual temperature; OI = Ombrothermic Index).

Vegetation type	Type code	N	Mean ELEV (m)	MAP (mm)	MAT (°C)	Mean OI
Cascadian						
Grand fir (<i>Abies grandis</i>)	abgr	120	1273	1017	5.5	76.1
Mountain hemlock (<i>Tsuga mertensiana</i>)	tsme	22	1712	1394	4.8	93.9
Western hemlock (<i>Tsuga heterophylla</i>)	tshe	25	1110	1041	6.1	74.1
Western larch (<i>Larix occidentalis</i>)	laoc	68	1315	850	5.0	61.8
Western redcedar (<i>Thuja plicata</i>)	thpl	43	1055	1022	5.6	73.7
Montane						
Aspen (<i>Populus tremuloides</i>)	potr	243	2649	664	3.7	60.0
Blue spruce (<i>Picea pungens</i>)	pipu	15	2678	599	3.9	54.8
Douglas-fir (<i>Pseudotsuga menziesii</i>)	psme	1001	1825	741	4.6	60.2
Lodgepole pine (<i>Pinus contorta</i>)	pico	555	2209	829	3.0	71.8
Ponderosa pine (<i>Pinus ponderosa</i>)	pipo	594	1846	550	7.1	46.6
White fir (<i>Abies concolor</i>)	abco	47	2592	626	5.5	57.8
Subalpine						
Engelmann spruce (<i>Picea engelmannii</i>)	pien	123	2893	789	2.0	81.5
Engelmann spruce/subalpine fir (<i>Picea engelmannii</i> / <i>Abies lasiocarpa</i>)	esab	556	2475	1022	2.5	87.5
Subalpine fir (<i>Abies lasiocarpa</i>)	abla	191	2309	1080	2.9	84.0
Limber pine (<i>Pinus flexilis</i>)	pifl	34	2460	623	3.8	61.8
Whitebark pine (<i>Pinus albicaulis</i>)	pial	53	2670	908	1.7	90.6
Woodland						
Cercocarpus woodland (<i>Cercocarpus</i> spp.)	cerc	28	2293	528	5.7	43.6
Cottonwood (<i>Populus</i> spp.)	popu	14	1114	437	7.9	33.4
Deciduous oak woodland (<i>Quercus</i> spp.)	qude	242	2291	533	6.8	43.7
Evergreen oak woodland (<i>Quercus</i> spp.)	quev	115	1719	563	13.3	36.3
Intermountain maple woodland (<i>Acer</i> spp.)	acer	20	1917	660	6.7	48.3
Juniper woodland (<i>Juniperus</i> spp.)	juni	432	1700	360	10.7	25.4
Mesquite woodland (<i>Prosopis</i> spp.)	pros	87	1127	374	17.0	18.6
Pinyon/juniper woodland (<i>Pinus</i> spp./ <i>Juniperus</i> spp.)	piju	1441	1946	375	9.7	27.9
Rocky mountain juniper (<i>Juniperus scopulorum</i>)	jusc	80	1599	430	6.8	37.2
Western juniper (<i>Juniperus occidentalis</i>)	juoc	23	1736	442	6.5	30.8
Grand total		6172	2006	640	6.5	52.1

occurring on semiarid sites (West and Young 2000). Within our study area, mesquite woodlands are for the most part associated with ‘warm deserts’ (MacMahon 2000) and sites occupied by this type are the warmest and among the driest of our vegetation types (Table 2). The cottonwood type is represented by several *Populus* species (principally, *P. fremontii* and *P. angustifolium*). The type has limited area but can have considerable importance especially in landscapes where it is the only forest.

Montane group.—This group includes 10 vegetation types. These, in various combinations are represented in several of Peet’s (2000) ‘major vegetation types’, e.g., ponderosa pine woodland, Douglas-fir forest, and montane seral forests (e.g., forests characterized by aspen and western larch).

Subalpine group.—This group consists of five vegetation types, including three that Peet (2000) collectively considers spruce-fir forest. Our forest

types differentiate stands which range from predominately Engelmann spruce, to predominately subalpine fir, and mixtures of the two species. Two additional forest types in the Subalpine Group are characterized by whitebark pine and limber pine. Peet (2000) characterizes a broad category of ‘subalpine white pine forests’ which includes the Interior West’s five-needle pines occurring at high elevations. Of these six pines, only whitebark and limber pine forests are common enough to be represented in our data set by at least 15 stands. Limber pine (and the similar southwestern white pine, *P. strobiformis*) have unusually large elevation ranges. We have included limber pine in the Subalpine Group, but could have assigned it to the Montane Group.

Cascadian group.—Peet (2000) refers to these types as ‘Cascadian forests’ because they are characterized by tree species that dominate extensive areas of the Cascade Mountains of British Columbia, Washington and Oregon. In

Table 3. Common and scientific names for the 26 vegetation types, by group, included in this study. The four letter codes are used in the presentation of results. Stand structure data represent volume means for each type.

Vegetation type	Type code	N	Mean live volume (m ³ /ha)	Mean DWM volume (m ³ /ha)	Mean snag volume (m ³ /ha)
Cascadian					
Grand fir (<i>Abies grandis</i>)	abgr	120	277.5	145.2	19.8
Mountain hemlock (<i>Tsuga mertensiana</i>)	tsme	22	224.2	88.6	18.0
Western hemlock (<i>Tsuga heterophylla</i>)	tshe	25	255.4	135.5	13.0
Western larch (<i>Larix occidentalis</i>)	laoc	68	169.6	124.2	23.5
Western redcedar (<i>Thuja plicata</i>)	thpl	43	407.0	178.4	26.2
Montane					
Aspen (<i>Populus tremuloides</i>)	potr	243	121.4	71.3	13.8
Blue spruce (<i>Picea pungens</i>)	pipu	15	152.6	91.0	10.1
Douglas-fir (<i>Pseudotsuga menziesii</i>)	psme	1001	132.1	61.3	12.6
Lodgepole pine (<i>Pinus contorta</i>)	pico	555	137.5	84.7	21.4
Ponderosa pine (<i>Pinus ponderosa</i>)	pipu	594	93.3	33.5	3.7
White fir (<i>Abies concolor</i>)	abco	47	143.9	91.0	13.7
Subalpine					
Engelmann spruce (<i>Picea engelmannii</i>)	pien	123	194.9	94.4	21.3
Engelmann spruce/subalpine fir (<i>Picea engelmannii</i> / <i>Abies lasiocarpa</i>)	esab	556	191.4	128.5	33.7
Subalpine fir (<i>Abies lasiocarpa</i>)	abla	191	113.7	110.5	31.8
Limber pine (<i>Pinus flexilis</i>)	pifl	34	61.9	50.5	11.0
Whitebark pine (<i>Pinus albicaulis</i>)	pial	53	101.8	65.9	33.3
Woodland					
Cercocarpus woodland (<i>Cercocarpus</i> spp.)	cerc	28	28.2	10.5	1.9
Cottonwood (<i>Populus</i> spp.)	popu	14	87.7	83.2	6.9
Deciduous oak woodland (<i>Quercus</i> spp.)	qude	242	15.6	14.4	3.6
Evergreen oak woodland (<i>Quercus</i> spp.)	quev	115	31.9	19.3	1.6
Intermountain maple woodland (<i>Acer</i> spp.)	acer	20	29.5	25.3	1.0
Juniper woodland (<i>Juniperus</i> spp.)	juni	432	24	5.3	1.0
Mesquite woodland (<i>Prosopis</i> spp.)	pros	87	6.9	2.3	0.1
Pinyon/juniper woodland (<i>Pinus</i> spp./ <i>Juniperus</i> spp.)	piju	1441	43.8	17.2	3.1
Rocky mountain juniper (<i>Juniperus scopulorum</i>)	jusc	80	28.6	14.3	1.5
Western juniper (<i>Juniperus occidentalis</i>)	juoc	23	19.6	16.3	1.1
Grand total		6172	100.9	54.4	11.7

our study area, they are restricted to northern Idaho and western Montana. Pacific weather systems crossing the Cascade Mountains are associated with high precipitation and moderate temperatures in comparison to other parts of the western Rocky Mountains. At relatively low elevations, this results in forests dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*) and grand fir (*Abies grandis*). Another Cascadian forest type is characterized by mountain hemlock (*Tsuga mertensiana*); at middle latitudes, this species is most typically associated with high elevations in the western Cascade Mountains.

Data analyses

We examined the relationships between the various living tree and deadwood components of the woodland and forest types and we also examined their relationship to underlying gradients in moisture and temperature, both directly and as expressed by synthetic climatic indices

(e.g., OI). For this part of the analysis, we calculated, for each of the 26 vegetation types, means of the various metrics to focus on between-type variability.

We used a chronosequence approach to approximate the relative abundance of live and dead woody components over the course of stand development. Investigations of standing and downed woody dynamics are commonly limited to chronosequence approaches, primarily due to the relatively slow rate of change over the forward course of stand development. There are limitations in the use of space-for-time substitution for some applications (e.g., Johnson and Miyanishi 2008), including representativeness of the locations used to characterize the various points in time. In a summary of chronosequence studies, Harmon (2009:179) listed 19 studies that sampled stand age ranges of up to 515 years. Only seven of these studies sampled over 30 stands, and in several cases fewer than 10 stands were used to characterize chronosequences of

100 to 200 years. In such cases, sample size could be problematic because of potentially low replication of the selected time points. Given the systematic sample inherent in the FIA plot system (i.e., stand conditions are generally sampled in proportion to their abundance on the landscape), our large sample size, and the fact that we intended to characterize relatively broad relationships, we feel that averaging woody components by forest type and stand age at time of measurement provide a reasonably robust approximation of typical stand development over time. At the same time we acknowledge that “average” conditions are actually found in a fraction of stands, and that each site has a unique history and the stand sampled on a given site represents a small part of that history. Although it is possible for us to characterize the range of variation at population scales, analysis at that level of detail is beyond the scope of the current study.

Within each forest type, stands were grouped by stand age class. Stand age was used to characterize living and dead volume over time. The stand age computed by the FIA program is straightforward for even-aged stands. In cases where stands have irregular structures, stand age reflects the dominant size class. In classically uneven-aged stands, stand age will tend to describe the oldest cohort(s) in the stand. In the case of a two-aged stand where the younger cohort is capturing most of the growing space, e.g., a sapling stand with a few relic trees from a prior stand, stand age will usually describe the sapling component. Earlier in development of the younger cohort (i.e., seedling stage), stand age will describe the relict component.

We did not attempt chronosequence analysis for all of the forest types present in our sample, primarily due to the relatively small number of observations available for some types. While the small sample sizes used in the aforementioned studies (Harmon 2009) may have been appropriate for their respective study goals, similar sample sizes would be inadequate to provide temporal resolution and broad range of inference that are goals of our analysis. Therefore, we opted for a conservative approach and chose to limit our chronosequence to the first 150 years of stand development in the six most common types: aspen ($n = 242$), Douglas-fir ($n = 891$),

lodgepole pine ($n = 513$), pinyon-juniper ($n = 792$), ponderosa pine ($n = 556$), and spruce-fir ($n = 651$). In the cases of pinyon-juniper and spruce-fir, we combined data from closely allied types for the purpose of the chronosequence analysis (juniper woodland, Rocky Mountain juniper, and pinyon-juniper woodland in a combined pinyon-juniper type; subalpine fir, Engelmann spruce, and Engelmann spruce-subalpine fir in the combined spruce-fir type). These six types represent most of the breadth of climate, elevation, and latitude that is found in the full list of types, and the number of observations in each of these six types was sufficient to allow classification of the stands into relatively narrow age classes. We used age class 0–5 years to represent conditions immediately following stand disturbance and re-establishment, and 10-year classes thereafter. As a result the average sample depth by stand age $\times$ forest type class was 38, although the actual number of observations in each class varied due to the variation in stand age classes that prevails across the Interior West. Although there was considerable variation in the number of observations across all classes, from $n = 1$ in 150-year-old aspen to $n = 108$ in 90-year-old Douglas-fir, there was no indication that the sample size biased the estimates of woody components in any way. For each age class, we calculated average fine and coarse downed woody material volume, standing dead volume, and live volume.

RESULTS

Forest and woodland types and climatic gradients

The location of each woodland and forest type in Fig. 4 corresponds to the overall means of precipitation and temperature for stands of that type (Table 2). Types within the woodland group are arrayed across a substantially greater range in mean temperature (ca. 6.5–17°C) than those of the other groups combined. In contrast, the range of mean precipitation values (ca. 375–560 mm yr⁻¹) associated with the woodland types is substantially narrower than for the other groups. The forest types of the subalpine group are arrayed across a wide range of precipitation and, compared to the other groups, a narrow range of mean annual temperature (ca. 1.5–2.5°C).

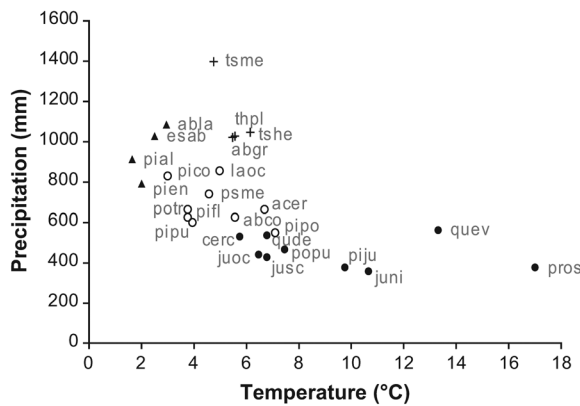


Fig. 4. Distribution of woodland and forest types with respect to type means for annual precipitation and month temperature. Type codes are defined in Table 2.

Consistent with our predictions, living and DWM volumes of the generally semiarid woodland types are substantially lower than for the forest types (Table 3). The cottonwood type is an exception to this generality. Within our study area, cottonwood occurs from warm desert to mid-elevations in mountain ranges and is typically restricted to riparian corridors (MacMahon 2000, Peet 2000, West and Young 2000). Type means of CWD are directly proportional to the volume of living trees (Fig. 5) and, across the various types, the ratio of CWD to living tree volume typically ranged from 1:3 to 1:2.

Important metrics of stand structure (e.g., volume, basal area, canopy cover, and mean annual increment of living trees) all have significant relationships ($P < 0.001$) with OI (Fig. 6). The relationships are positive and are best fitted using a power function, but in many cases the power function is only slightly more suitable than a linear fit. For the cooler, more mesic types the relationships appear to become asymptotic. Those types with mean OI less than 40 are exclusively semiarid woodland types (e.g., mesquite and the various pinyon and juniper types) (Table 2). Those types included in the subalpine and Cascadian groups all have mean OIs greater than 70. OIs between 40 and 70 include most of the montane group plus three of the higher elevation woodland types (i.e., *Cercocarpus*, Deciduous oak and Intermountain maple).

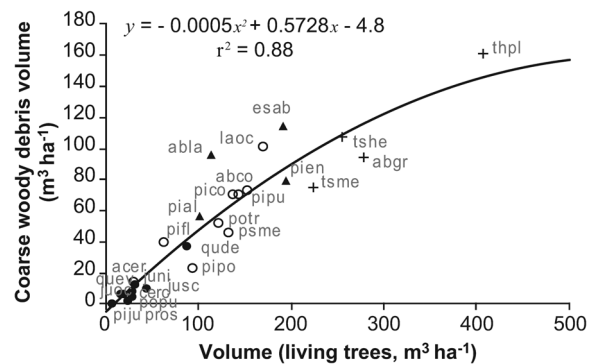


Fig. 5. Scatterplot of the 26 vegetation types ordinated by means of coarse woody debris and volume of living trees. The relationship is significant ($P < 0.001$) with an r^2 of 0.87. Type codes are defined in Table 2.

DWM, litter and duff were all related to OI (Fig. 7). Similar to the metrics of living stand structure (Fig. 6), the relationship between these features and OI (Fig. 7) was significant ($P < 0.001$) and generally positive; however, there appears to be a decline beyond an OI threshold of about 70. This pattern appeared somewhat more pronounced for the smaller detrital fractions (FWD, including sub fractions, duff and litter). Both the number and volume of snags were significantly ($P < 0.001$) and positively related to OI and there was no suggestion of a decline with higher OI (Fig. 7). The proportionality of various structural components is also related to OI. The ratio of standing deadwood to living volume is positively related to OI (Fig. 8A), whereas the ratio of fine woody debris to living volume is negatively related to OI (Fig. 8B).

Deadwood and time (stand age/disturbance history)

Regardless of stand age, volumes of fine and coarse woody debris of the six most common forest types tended to rank according to the temperature and moisture gradients. We illustrate the combination of stand age and climate in Figs. 9 and 10, which present the same data in two ways. In Fig. 9 all components are graphed separately, showing individual component trajectories over time. In Fig. 10, woody components are stacked to illustrate the relative contributions of each to total woody volume over time.

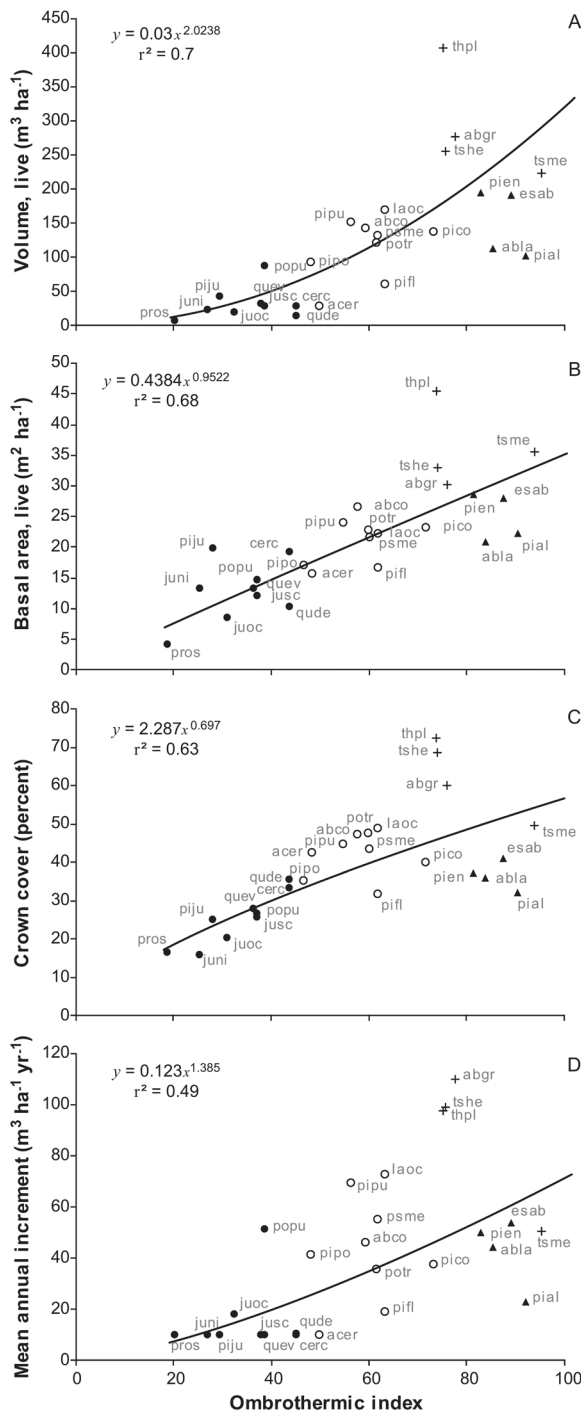


Fig. 6. Relationship of various metrics of living stand structure to OI: (A) stand volume; (B) basal area; (C) canopy cover; and (D) mean annual increment. All relationships are significant ($P < 0.001$). Type codes are defined in Table 2.

Spruce-fir stands tended to have seven to ten times the amount of downed woody material as pinyon-juniper stands (Fig. 9A, F). In all cases the amount of fine woody material appeared to be relatively constant from the time of stand establishment to age 150 years, although the absolute amount of fine material and the ratio of fine to coarse material both varied by type; coarse material accounts for the largest fraction and drives the temporal trend in downed material (Figs. 9 and 10). When fine and coarse material volumes are considered together, the temporal pattern appears to range from little discernible trend in the drier types to gradual accumulation in the wetter types (Fig. 10). The pattern of standing dead volume over time was more consistent among forest types (Figs. 9 and 10). All six types exhibited an early peak in standing dead volume, followed by a minimum that generally occurred between ages 30 and 60 years, and gradual accumulation thereafter. From the age at which the minimum occurred to age 150, the standing dead component at least doubled in most types, with the only exception being pinyon-juniper. In the case of pinyon-juniper, accumulation appeared to occur at a slow, constant rate and continues to accumulate to age 200 and beyond (not shown).

Snags and DWM existing prior to stand reestablishment (i.e., legacy material) strongly influence patterns of total woody biomass over time. When fine, coarse, standing dead, and live volumes are shown together, the conceptual pattern of legacy material, subsequent decrease in the legacy, and re-accumulation of total woody biomass emerges (Fig. 10). As expected, and consistent with FIA stand-age assignment, none of the stand types have a substantial live volume component at the beginning of the time series. Within a forest type, the magnitude and timing of the minimum total woody volume is primarily driven by the amount of legacy standing dead, its rate of decline, and, to a lesser extent, the dynamics of the coarse downed component. As the legacy components decline, live volume begins to increase and eventually becomes the majority of woody volume. The live component accounts for about half of the total volume by about age 60, approximately 20 years following the time when minimum total volume occurs. Then, combined dynamics of live and standing

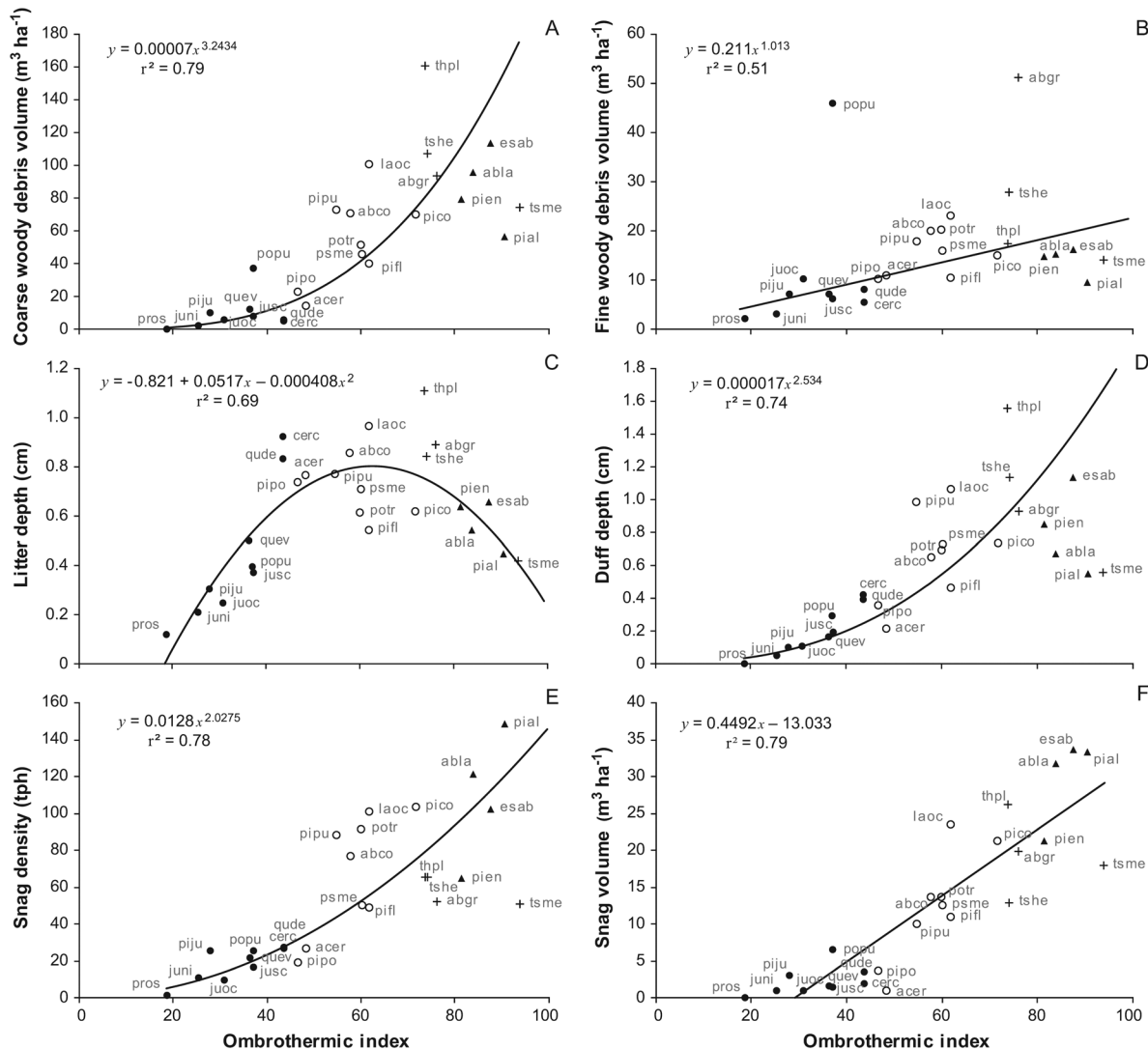


Fig. 7. Relationship of (A) coarse woody debris, (B) fine woody debris, (C) litter, (D) duff, (E) snag density, (F) snag volume to Ombrothermic Index. All relationships are significant ($P < 0.001$). Type codes are defined in Table 2. Outlying values for Cottonwood (popu) and grand fir (abgr) forest types in (C) are partially influenced by the effect of a few extreme values; in the case of Cottonwood, there is also an effect of higher production than expected from climatic factors, due to its unique status as a primarily riparian type in the Interior West (see text).

dead trees largely drive the transition of the aboveground woody component from a carbon source to a carbon sink, and live volume accumulation becomes the increasingly dominant component following this transition (Fig. 10).

DISCUSSION

Our results are consistent with the postulate (Fig. 1A) that broad gradients of temperature and

moisture influence the various compositional and structural elements, which differentiate closed canopy forests and open woodlands. In the Interior West, closed canopy forest types occur across a relatively narrow range of mean temperatures, but across much of the variation in mean annual precipitation found in the region (Fig. 4). In contrast, the woodland types occur across a comparatively wide range of mean annual temperatures, but as a group are associ-

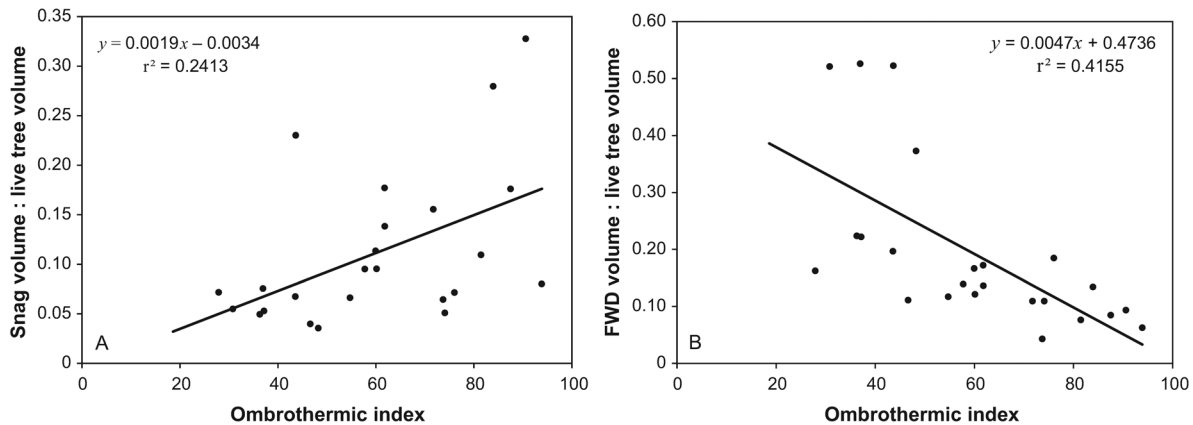


Fig. 8. Relationship of (A) the ratio of snag volume to live tree volume and (B) the ratio of fine woody debris (FWD) volume to live tree volume to Ombrothermic Index.

ated with a limited range of precipitation (Fig. 4). Several of our woodland types commonly occur at the ecotone between tree-dominated communities and shrub-steppe or grassland (West and Young 2000). The overall organization of our woodland and forest types is consistent with the premise that moisture limitations strongly influence lower treeline and that low temperatures are associated with upper treeline (Daubenmire 1954, Knight 1994, Driese et al. 1997).

Although the range of environmental conditions in which Interior West woodlands and forests occur is locally and regionally diverse—i.e., in some locations nearly the entire range of conditions can be found over a distance of tens of kilometers—it is a relatively narrow range in the global context. The scale of environmental gradients in the Interior West is intermediate to the broad range of temperature and moisture represented globally by major forest biomes (Fig. 11). Interior West woodlands and forests occupy sites of both decreased moisture and temperature relative to environmental conditions associated with maximum woody biomass, which occur near the centroid of the Temperate Moist Forest zone (Fig. 11).

Temporal patterns within forest types

Pinyon-juniper types accumulate live volume at very slow rates (Fig. 10A). Pinyon-juniper and juniper woodland stands are not the result of abundant regeneration following disturbance, after which the self-thinning process produces a

steady source of standing and downed deadwood. Instead, they are the result of gradual site re-occupancy following high severity disturbance. This is most commonly fire, but insects and drought can periodically result in high mortality (Shaw et al. 2005). Both stand structure and composition affect the proportions of downed woody components and changes over time. Because of small stature and multi-stemmed form, fine woody material constitutes a large proportion of live pinyon and juniper trees. This fine material is mostly consumed in the case of severe fire, but it also breaks down over a relatively short period of time in the case of insect attack or disease (Kearns et al. 2005). However, since it constitutes a large proportion of the material in live trees, pinyon-juniper is the only type in which the fine woody component is greater than or equal to the standing dead and coarse downed woody components.

Along the productivity gradient that covers our six major forest types, the ponderosa pine type is the next most productive after pinyon-juniper woodlands (Fig. 10B). However, at any point of development the average sum of live and dead components of the ponderosa pine type is 2–3 times greater than in pinyon-juniper woodlands and the difference tends to increase with stand age. As is the case with pinyon-juniper, the post-disturbance minimum volume is reached by 30–40 years, and the magnitude of change from immediately post-disturbance to the minimum is relatively small. During the past few

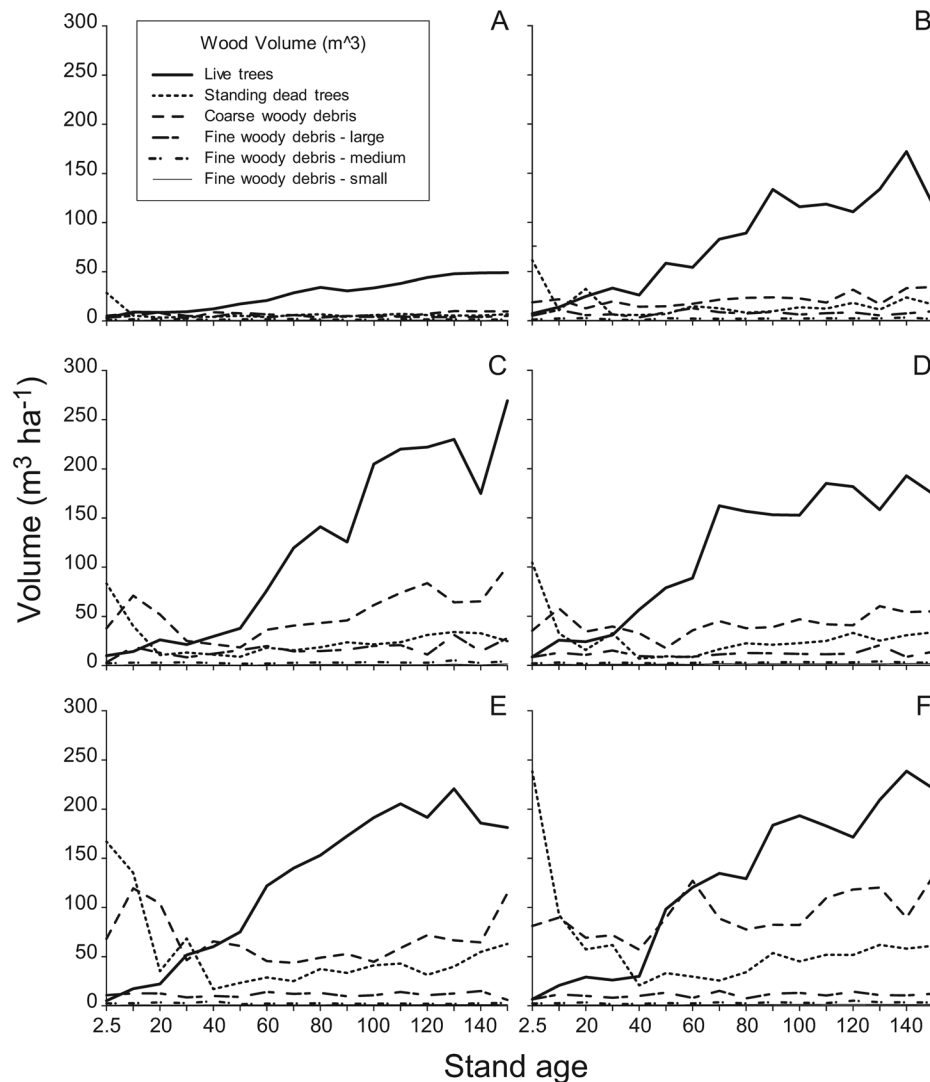


Fig. 9. Live tree and detrital component volumes with age for: (A) pinyon-juniper; (B) ponderosa pine; (C) Douglas-fir; (D) aspen; (E) lodgepole pine; (F) spruce-fir.

decades wildfires in the ponderosa pine type have tended to be severe (Agee and Skinner 2005), which is in contrast to the high-frequency, low-severity fire regime that is considered to be the norm for this type over the past several centuries (Swetnam and Baisan 1996). Passovoy and Fulé (2006) studied a chronosequence of 3–27 years in severely burned ponderosa pine in Arizona, and found that the CWD biomass was comparable between the 8- to 9-year and 27-year post fire periods. Few snags resulting from the fire remained by the 27th year. In our data and the chronosequences studied by Passovoy and

Fulé (2006) and Roccaforte et al. (2012), the transition from standing dead to downed dead appears to occur relatively quickly. In the stands studied by Savage and Mast (2005), ponderosa pine regeneration tended to be spread over a period of 15–35 years post-fire. Although the legacy of standing dead trees is relatively low on average, our data show that there are many stands in which relatively high volumes of standing deadwood occur during the period of stand reestablishment.

Except for situations where drought causes patchy mortality at the scale of clones or stands,

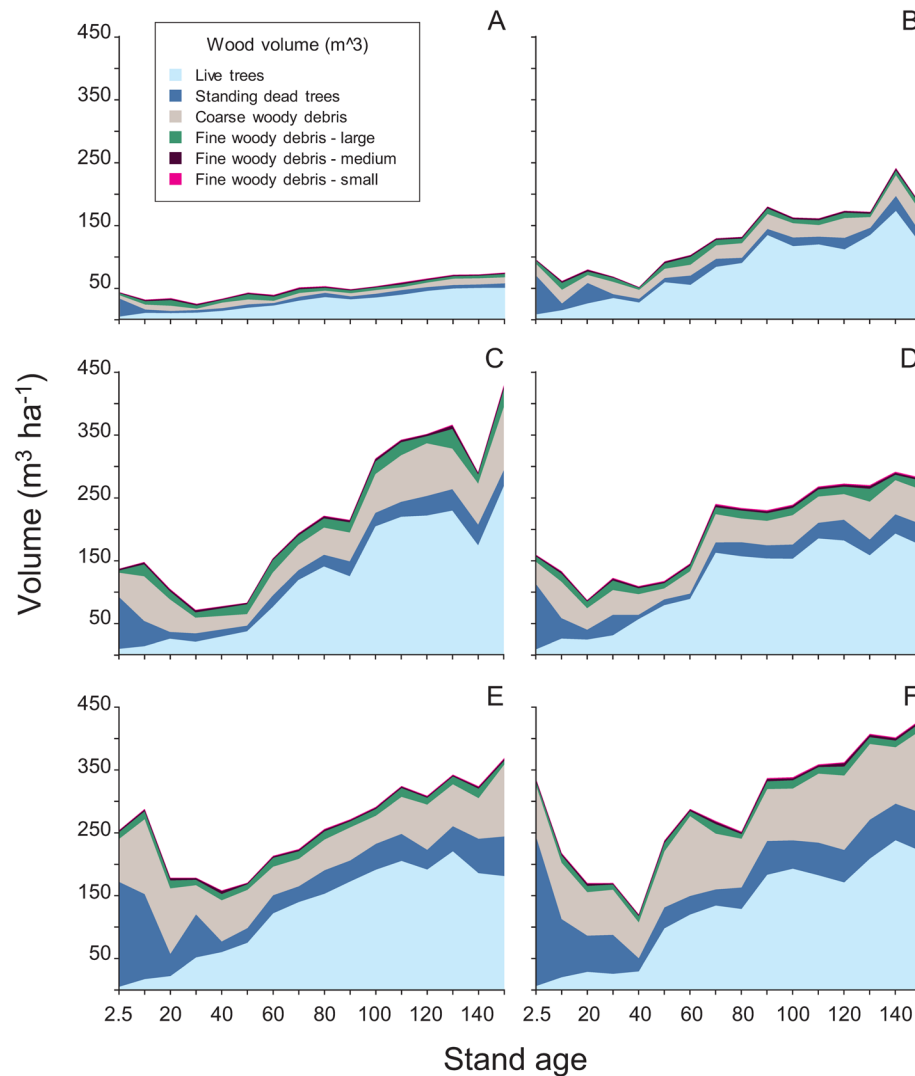


Fig. 10. Live tree and detrital component volumes with age displayed as stacked graphs for: (A) pinyon-juniper; (B) ponderosa pine; (C) Douglas-fir; (D) aspen; (E) lodgepole pine; (F) spruce-fir.

fire is the major stand-replacing agent in aspen. Compared to other types highlighted here, there are likely to be differences in longevity of standing and downed material due to differences in decomposition rates of aspen versus conifer associates. In a comparison of aspen stands in three age classes (23–26, 51–63, and 122–146), Lee et al. (1997) found that although the total volume of downed woody material did not differ significantly with age class, the distribution of volume among size classes (very fine, fine, medium, and coarse) did vary significantly. As would be expected, they found that the size

distribution of standing dead trees also varied, with the largest snags occurring in the oldest age class. Because of the wide potential differences in stand composition and structure prior to stand-replacing disturbance, aspen stands exhibit a wider range of variability in the standing dead component immediately following disturbance than is found in other forest types in the same age classes. In addition, it is possible that some of the stands classified as aspen at the time of measurement had been converted from other types by the disturbance. For example, in places where aspen is seral, associates such as Engelmann spruce and

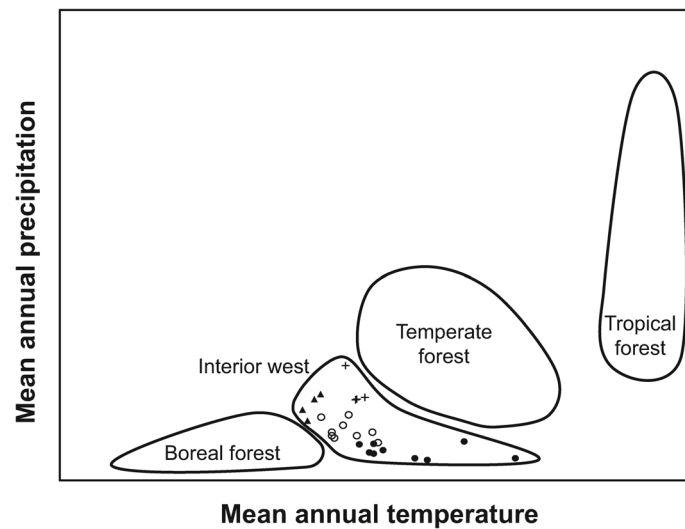


Fig. 11. Mean annual precipitation versus mean annual temperature and the generalized groupings of forest: boreal forest, temperate forest, and tropical forest after Keith et al. (2009), and the four type groups reported in this study for the US Interior West.

lodgepole pine are susceptible to attack by bark beetles. Post-disturbance forest type shifts are common after fire, because the root suckering ability of aspen can allow it to quickly assert dominance in severely burned stands where it was previously a minority component.

In contrast to aspen, the Douglas-fir chronosequence is less likely to involve transitions from a forest type to another one. Douglas-fir, while considered seral on many sites, is long-lived and not likely to yield dominance to other species over the length of our chronosequence. The propensity for Douglas-fir to self-replace in response to fire was observed by Pinchot (1899), who wrote that he “did not see a single young seedling of Douglas fir under the forest cover, nor a single opening made by fire which did not contain them”. In the Interior West, Douglas-fir does not generally experience high rates of mortality due to insects or disease, although in recent years (not reflected in our data) Forest Inventory and Analysis data appears to show a substantial increase in the area affected by the western spruce budworm (*Choristoneura occidentalis* Freeman). As with the previously discussed forest types, the minimum of total live and dead volume appears to occur by age 30–40, after which there appears to be a steadily increasing volume of the standing and downed coarse

woody components.

Lodgepole pine has the second-highest average amount of standing dead material present in regenerating stands (Fig. 10E). Lodgepole pine stands are known to experience partial replacement, but in many cases of fire and insect outbreak, mortality is nearly complete. We attribute the high mean volume found in regenerating stands primarily to the prevalence of insect-killed trees, in stands where most of the live and dead volume present in the preceding stand is preserved through the regeneration cycle. When comparing inventory data from 1997–2002 to 2002–2007, Thompson (2009) found that mortality rates had increased ten-fold in lodgepole pine stands in Colorado. Current Forest Inventory and Analysis data reflect similar increases in other Interior West states.

Spruce-fir types had the largest amount of legacy material in young stands (Fig. 10F). Because spruce-fir stands are, by definition, mixed and therefore not commonly subject to near-complete stand replacement by insects or disease, it is consistent that lodgepole pine still shows the greatest mean standing dead. Only fire is likely to convert all or most of a spruce-fir stand from live to dead, and in that process there is an inevitable loss of volume to consumption by fire and from standing to downed wood compo-

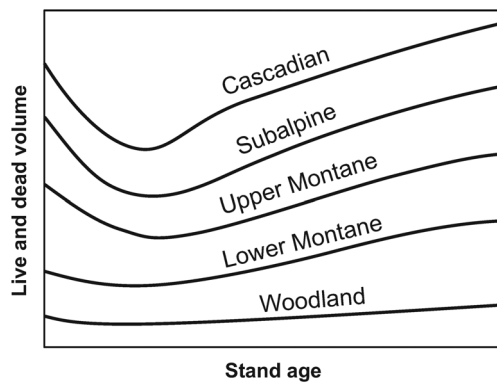


Fig. 12. Conceptual synthesis of woody volume with increasing Ombrothermic Index (as represented by generalized vegetation zones) and stand age. Curves in the figure are based on the temporal patterns found in woodland and forest types that are representative of the generalized vegetation zones, i.e., the stacked-component graphs shown in Fig. 10.

nents. This reinforces our interpretation that the combination of relatively pure stand conditions, potentially stand-replacing non-fire agent, and site conditions capable of moderately high live volume tends to produce the largest legacy volume of material following major disturbance.

Each forest type exhibits characteristic total woody volume, as dictated by the prevailing climatic conditions, and changes in woody volume over time, as affected by the nature and timing of disturbance in combination with stand growth. This suggests a model of woody volume change over time, while simultaneously considering the climatic gradient (Fig. 12). We note that although drought was not listed among the important sources of downed woody material by Harmon et al. (1986), recent mortality in the Interior West has shown it to be an important, if infrequently occurring agent. While drought is rarely considered the proximal agent of mortality, it can facilitate insect- and disease-related mortality (Shaw et al. 2005). In comparison to most other species, the junipers are essentially impervious to drought (Shaw 2006), so drought acts similarly to insects and disease in terms of its effect on deadwood components.

Influence of environmental factors

Among environmental variables, climatic variables emerged as being the most influential

factors affecting site productivity, described by stand density, volume, growth rate and canopy cover. Increasing moisture and decreasing temperature appear to drive not only species composition but also stand structure. That stand metrics such as absolute density, tree size, and stand age, are only weakly associated with environmental factors, we attribute to the confounding influence of disturbance history. A given stand volume or basal area might occur in a relatively young stand with many small stems per hectare or in a relative old stand with many fewer, but larger, stems. Disturbances affect stand age dynamics (e.g., Turner and Romme 1994); conversely, stand age and tree sizes can strongly influence disturbance occurrence (e.g., insect outbreaks and wildfire) and spread within a forest or a landscape (Taylor and Carroll 2004, Agee and Skinner 2005, Lyons-Tinsley and Peterson 2012).

The trends associated with increasing OI are indicative of the transition from open woodlands to closed canopy forests. The postulate that maximum accumulation of living biomass is associated with intermediate values of temperature and moisture (Fig. 1B) was only partially supported by our data (Fig. 6). The expected decline of living biomass associated with more mesic cooler sites was observed for some forest types, but overall above an OI value of about 60, living biomass was essentially asymptotic. An OI threshold between 40 and 50 separated the woodland and forest types. All of the woodland types fall below and all but three of the forest types are above the threshold. Exceptions to this generality, like the relative 'warm/dry' ponderosa pine type (mean OI = 46.6) are effectively transitional between the woodland and montane forest types. The whitebark pine type is an example of an apparent decline in productivity at higher values of OI, where the benefit of higher precipitation may be at least partially offset by temperature limitations. Whitebark pine has the lowest mean live volume among the subalpine and Cascadian types, and lower mean live volume than many of the montane types. Although whitebark pine is a slow-growing species that typically occurs in stands of short stature near treeline, the low mean live volume for the type is also likely reflective of recent range-wide elevated mortality due to insects and

disease (Logan and Powell 2001). This is consistent with our finding that whitebark pine ranks among the highest of all types in the total amount of standing dead.

The largest amounts of deadwood are found in moist and cool climates, where forest productivity and deadwood accumulation are high, but decomposition rates are reduced (Woodall and Liknes 2008). The greatest amounts of litter, duff and FWD were, as expected, associated with intermediate levels of OI (Fig. 7B, C, D). In contrast, the relationships between downed deadwood and snags (Fig. 7A, E, F) and OI are asymptotic. It is recognized that quantity and quality (e.g., piece size) of deadwood is directly affected by climate through its influence on decomposition rates (Zell et al. 2009). Moisture and temperature regimes of the substrate greatly influence decomposition rate (Dunn and Bailey 2012) with decomposition rates expected to increase with greater moisture availability and decrease at low temperatures (Harmon et al. 1986).

As previously mentioned, site productivity, and ultimately temperature and moisture, strongly influences the amount of litter, duff and the various sizes of downed wood. The positive association between site productivity and the total amount of deadwood has been found by others (Spetich and Guldin 1999, Siitonen et al. 2000, Castagneri et al. 2010). There is a particularly strong relationship between CWD and volume of living trees (Fig. 5). In contrast to downed woody material, snag recruitment is actually more directly linked with the disturbance history of the stands. Pulses of snags are produced by periodic severe disturbance events (Everett et al. 1999), while mortality due to competition or successional processes leads to more continuous and less abundant snag recruitment (e.g., Petritan et al. 2014). Snag pools are more ephemeral than CWD and are strongly influenced by short-term disturbance effects. Snag fall rate represents the main recruitment source to the downed deadwood population, and is the result of the complex interaction among several factors, related to snag size, species, stand history and disturbance regimes (Harmon et al. 1986, Garber et al. 2005, Angers et al. 2010). While individual snags can remain standing for centuries, on average snags

do not have great longevity (Morrison and Raphael 1993, Everett et al. 1999, Aakala et al. 2008).

As with the various components of living and dead structure, the proportionality among components also appears to be influenced by temperature and moisture gradients as reflected by OI. For the standing and downed woody components, this relationship is positive, i.e., these components make up a larger fraction of total woody volume with increasing OI (Fig. 8A). For FWD the relationship reverses, decreasing in proportion to the volume of live trees (Fig. 8B). The net effect is that the sum of coarse and fine woody components, when considered as a ratio of the live component, shows little or no trend with changing OI. Woodall and Liknes (2008) found fine woody debris carbon stocks to be less correlated with climatic variables than coarse woody debris carbon stocks. Considering the rapid decay and turnover of fine woody debris, several studies (e.g., Simmons et al. 1996, Malhi et al. 1999) argued that this component is relatively unaffected by changes in temperatures.

Stand and deadwood dynamics

Trends in accumulation of live and dead material are more nuanced than the postulated relationships (Fig. 1C). For example, differences among various vegetation types in potential productivity are predictably associated with differences in accumulation of woody volume at different stand ages. The different patterns are also associated with differences in disturbance regimes common in each type. Figs. 9 and 10 illustrate, for several important types, how the live, standing and downed dead components change with stand development. At some stages of stand development the downed dead components represent a relatively small fraction of total woody volume and therefore have a limited influence on total woody volume. It is changes in the standing dead component, coupled with the accumulation of live volume, which drive the temporal pattern of total woody volume most strongly.

Given that the accumulation of live volume of a forest type is dictated primarily by the prevailing climatic regime, and varies within the regime according to site quality, it remains that disturbance introduces much of the variability

ity in woody material components over time. Harmon et al. (1986) discussed the major sources of woody material inputs—wind, fire, insects, disease, and competition—and noted wide variation in rates of input. They provided several conceptual variations of the coarse woody component, based on the combination of legacy downed material, input from legacy standing trees killed by disturbance, and input from regrowth trees due to competition and other “background” mortality causes (Harmon et al. 1986). Harmon (2009) also examined the potential influence of delays in post-disturbance regeneration on the patterns of deadwood accumulation.

There are several note-worthy patterns of live tree and dead component volumes with age for the six forest types we examined with temporal detail. Early peaks in downed wood were evident for aspen, lodgepole pine, and Douglas-fir, but the patterns in pinyon-juniper, spruce-fir and ponderosa pine were much less obvious (Fig. 9). Second, at the end of our 150-year time series, downed woody material equaled or exceeded post-disturbance volume in five of the six types and the trough (bottom of the “U”) to peak volume difference was two times at most. For types where we had the data depth to examine time beyond 150 years (not shown), volume continues to rise beyond the early post-disturbance peak and suggests that the steady state is not achieved in the normal lifespans of these forest types.

Our interpretation is that the differences in these patterns have much to do with influence of disturbance regimes. While some types of disturbances are expected to preserve most or all legacy downed woody material, other disturbances will leave less. When averaged over an entire forest type, especially fire-dominated types as are common in the Interior West, the legacy volume can be lower than the amount present immediately prior to disturbance. We should also consider that the environmental conditions that the legacy downed wood is exposed to following disturbance will likely be much different than the environment of the preceding stand, so the amount of downed material might be subjected to different decomposition rates. Other factors likely to influence these patterns are differences in rates of input from the overstory. Our results

suggest that the transition of standing dead into the downed dead pool is relatively rapid, being nearly complete by age 40 or so on average. Only part of the decrease in the standing dead component is reflected in an increase in the downed woody component, possibly providing evidence that increased decomposition rates at least partly offset the potential “swamping” of the downed woody component by falling dead trees. Finally, the contribution of new growth (*de novo*, *sensu* Harmon 2009) to downed woody material is likely to be slow in developing. Fig. 10 shows that live volume at the time when the standing and downed dead components reach their minimum—i.e., age 30–40 years—is only about 20% of the volume achieved by age 150. Although the rate of input due to competition-related mortality in the developing stand will vary with site quality, in general, the rate is probably sufficiently low that decomposition is able to approximately keep pace. Our data show the most distinct minimum of woody material only when the live, standing dead, and downed woody components are considered together (Fig. 10).

This is likely why Woodall et al. (2013) failed to find a strong “U-shaped pattern” in the downed woody component over time. Such a pattern would not be strongly expressed in downed woody components because in young stands input is not immediate unless the dominant disturbance is wind (e.g., snag-fall would be more gradual following insect attack or fire), and in old stands the input due to competition-related mortality is gradual in the absence of major disturbance. Woodall et al. (2013) rightly expected that young stands with low relative density should potentially have relatively large amounts of downed material because a young stand is consistent with a “stand replacing” event. On highly productive sites, where high relative density and competition-related mortality produce relatively higher inputs of downed material, it is logical to conclude that the same factors that favor growth—moderate temperature and high moisture—also allow decomposition to keep pace with input. On low productivity sites, input from competition is slower, or in the case of pinyon-juniper woodlands, extremely low, so again it is likely that decomposition, though slow, is able to keep up

with input. This explains our finding of relatively stable to slightly increasing proportions, on average, of downed woody components over time, and the lack of a combination of old age and high proportions of downed dead material.

We must acknowledge that, given our approach based on the calculation of deadwood volume in plots without repeated measurements, we did not directly take into account decomposition rates, with possible consequences on temporal patterns. The decomposition of deadwood is considered a knowledge gap (Birdsey et al. 2006), whose importance is clearly linked with the possibility for instance to better predict ecosystems responses to global change derived from a more precise understanding of the variability of deadwood decomposition rates and associated C flux (Weedon et al. 2009). Few studies investigated the temporal dynamics of deadwood, particularly of downed woody debris, and fewer quantified mass loss through time (Russell et al. 2014). A recent investigation by Russell et al. (2014) provided estimates of down woody debris half-life, residence time and decay rate for 36 tree species of eastern US forests, coupling repeated measurements with models. This approach could provide new insights for the quantification of ecosystem functions related to deadwood dynamics. Several aspects associated with deadwood decomposition, and finally with carbon dynamics, need however to be further investigated, e.g., the process of heterotrophic respiration, whose neglecting could overestimate carbon flux, particularly in those forests where disturbances play a major role (Harmon et al. 2011).

CONCLUSIONS

Our analysis of standing and downed deadwood over a wide range of forest types, stand ages, and climatic conditions reveals two dominant patterns. First, averaged over all ages within forest types, the dead components are approximately proportional to the live component and both could be ordered as a function of climatic gradients. Second, there are common temporal patterns of live and deadwood, whose magnitude of change appears to be related to the disturbance and regeneration patterns of specific forest types. This results in changing proportions

of woody components over time.

Although we analyzed a regionally diverse range of forest types and climatic conditions, it is clear that these conditions occupy a fraction of the conditions that exist globally. For example, our low end of downed woody material accumulation is largely represented by low-productivity conditions, with limitations of either moisture or temperature. Our data and analysis do not encompass examples of low-volume downed woody material in high-productivity situations, as might be found in moist tropical settings. However, some of our conditions overlap with wide-ranging, analogous forest types elsewhere, such as in Eurasia (e.g., *Picea abies*, *Pinus sylvestris*, *Populus tremula*), so the validity of our generalizations should be testable. Given adequate data, temporal resolution such as shown in our analysis would be a valuable extension of our knowledge of maximum potential biomass (e.g., Keith et al. 2009), because, in the face of disturbance and fluctuating climatic conditions, the state of maximum saturation is a rare and temporary state.

Finally, we emphasize, as have others, that woody component dynamics across large landscapes are the result of interactions between disturbance regimes and productivity gradients. Although we did not focus on variability in this study, we note that both productivity and severity of disturbances within types are highly variable and overlapping among the forest types. Therefore, the potential effects of different disturbances are limited by, and operate within, the context of productivity and forest composition.

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