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Coarse woody debris in mature *Pinus ponderosa* stands in Colorado[1]

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ROBERTSON, PHILIP A. AND YVONNE HALL BOWSER. (Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901-6509). Coarse woody debris in mature *Pinus ponderosa* stands in Colorado. J. Torrey Bot. Soc. 126:255–267. 1999.—During summer of 1994, 328 0.1 ha circular plots were sampled to determine the volume of coarse woody debris (CWD) and standing dead density and basal area in 53 mature or older *Pinus ponderosa* stands in the Front Range and Southwestern mountains of Colorado. Standing dead volume was estimated using height derived from living trees in the plots. Generally, CWD amounts were lower in these forests than have been reported for *Pinus ponderosa* forests in Arizona and New Mexico and other forest types in North America. Mean volume for all plots was 15.9 m^3/ha ± 20.85 SD. Mass, estimated from published wood density values, was 3.4 Mg/ha ± 5.07. CWD in the Southwestern mountains of Colorado averaged about 7.5 m^3/ha > in the Front Range. Sixty-three percent of the CWD was in decay class 4 followed by class 5 with 16%. CWD showed considerable variation across stands and habitat types with generally higher amounts in more mesic conditions. No significant relationships existed between CWD and the various environmental factors measured. CWD volume and variability both increased with stand age. Standing dead density was highly variable with an mean density of 11.9 stems/ha. Most standing dead trees were small with a mean diameter of 34.6 cm and mean basal area of 1.25 m^2/ha. Eighty-eight percent of the class 1 CWD was standing dead, but class 1 comprised only 8% of the total CWD. High values of standing dead may be related to disturbance and stand age. In *Pinus ponderosa* stands, it appears CWD is affected by disturbance, such as fire, timber harvesting and insect infestation > by physical factors of the environment.

Key words: *Pinus ponderosa,* coarse woody debris, old-growth forests, standing dead, Colorado.

In the past 20 years, attention has been focused on the value and ecological characteristics of old-growth forests. In Colorado, *Pinus ponderosa* dominated sites have been of concern because these low-elevation forests have been severely affected by timber harvesting, recreation, development and fire suppression. Little is known about coarse woody debris (CWD) in these forests, particularly in mature or old-growth stands.

Coarse woody debris results from disturbance and from natural mortality as stands age. Coarse woody debris provides a view of stand history, and can affect future stand structure and function. CWD in forest stands is affected by, and will determine to some extent, future fire behavior and insect outbreaks (Spies et. al. 1988; Covington and Moore 1994a, 1994b; Fule 1996). A variety of invertebrates and vertebrates require or use CWD (Maser et al. 1979). Knowledge of coarse woody debris volume and mass along with the standing dead density can give managers information necessary to manage old-growth *Pinus ponderosa* stands for these attributes.

This report is part of a more comprehensive study to define the old-growth condition for *Pinus ponderosa* in Colorado. Coarse woody debris is not expected to have the same dynamics and structure as in other western coniferous forest types because of the high natural fire frequency and xeric conditions characteristic of this forest type. Confounding these characteristics of *Pinus ponderosa* forests in Colorado is the highly managed fire regime and human disturbance.

The objectives of this study were 1) to determine volume and estimate mass of CWD in mature or older *Pinus ponderosa* stands in the Front Range and Southwestern Mountains of Colorado, 2) to determine standing dead tree structural characteristics and 3) to determine relationships of CWD and standing dead to stand age, stand structure and habitat conditions.

Materials and Methods. FIELD METHODS. During the summer of 1994, 328 plots in 53

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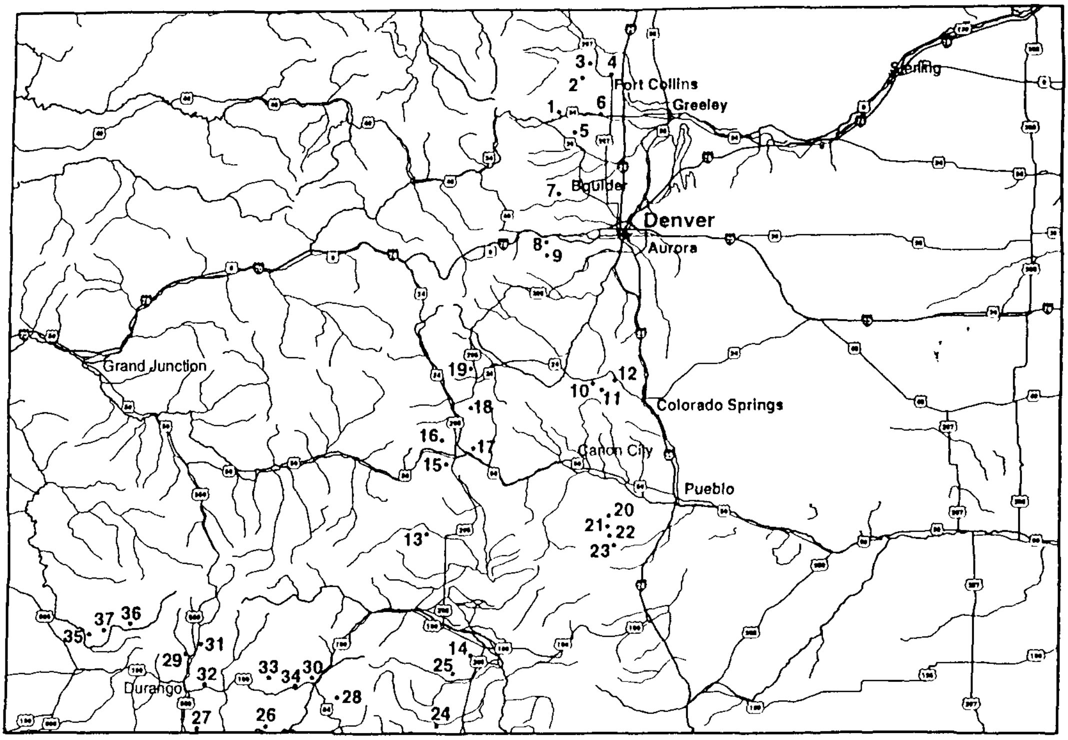

Fig. 1. Location of *Pinus ponderosa* dominated stands in the Front Range and Southwestern mountains of Colorado. Numbers refer to stand locations and descriptions available from the senior author.

stands were sampled throughout the *Pinus ponderosa* zone in the Front Range and Southwestern Mountains of Colorado (Fig. 1). Sampling occurred within the *Pinus ponderosa, Pseudotsuga menziesii* and *Picea pungens* series (complete legal descriptions of stand locations are available from the senior author). The Series is defined by the climax tree species of that habitat type. For example, a *Pseudotsuga menziesii* series may be dominated by *Pinus ponderosa* but the former is assumed to be the climax overstory on that site given its shade tolerance and reproductive success. Habitat types sampled supported mature or older stands of *Pinus ponderosa.* No attempt was made to sample all habitat types or to sample habitat types at a given intensity. We did not deliberately include stands previously classified as "old-growth" or restrict the sample to those sites suitable for timber production.

In many *Pinus ponderosa* dominated areas of Colorado, the mature or older condition is rare and the stands sampled were those that were healthy, available and representative of this condition on or adjacent to National Forests in the Front Range and in Southwestern Mountains. Much of the information leading to the selection of stands was provided by personnel from the U.S. Forest Service, Colorado State Forestry Division and landowners. Some stands were found while searching for others identified by the sources listed above. We believed this sampling strategy would provide a range of conditions allowing an assessment of the CWD and standing dead component of mature or older *Pinus ponderosa* stands in Colorado.

Selected stands had minimal human disturbance. Stands with > 25% of trees removed by logging or stands with extensive soil or ground layer vegetation disturbed by recreational vehicles or camping activities were not sampled. Also, stands with > 25% of the overstory with dwarf mistletoe, disease or insect infestations or mortality due to severe fire were excluded from sampling. Where stand size permitted, plots were replicated to evaluate stand variability. In those instances, plots were located along a transect with variable plot spacing to sample the mature or older components.

In this study, it became difficult to apply the stand concept to mature or older *Pinus ponderosa* stands. Older age classes of trees may occur in small clumps in some stands; in other stands, older age classes may occur over a considerable area. Thus, the "stand" varied from a small patch to a large area covering many hectares. Some stands were so small they represented only "pockets" of older *Pinus ponderosa* and were sampled with only one plot. This was essential considering the patchy nature of *Pinus ponderosa,* where clumps of older trees often occur within a matrix of younger individuals. In some stands, plot location was dictated by the diminutive nature of the patch of older trees. Areas dominated by young trees were not sampled. In this study a broad definition of a stand was used, including both small and large vegetation units of the mature or older condition.

A 0.1 ha (17.84 m radius) circular plot was used for sampling tree, standing dead and stump diameters, heights of living trees and for sampling coarse woody debris (CWD) and canopy coverage for all species. Diameters of living and standing dead trees $\geq$ 12.7 cm dbh (diameter breast high) were measured at dbh and tallied by species for basal area and density determinations. Increment cores were taken from four living individuals from the oldest cohort of canopy trees in each plot. Upon occasion, trees outside the 0.1 ha plot were cored when less than four acceptable trees occurred within the plot boundary. Trees comprising the oldest cohort were those canopy dominants which appeared to be the oldest and similar in height, crown characteristics and dbh. Cores were stored in paper straws and later mounted in grooved wooden holders for preparation and age determinations.

Coarse woody debris (CWD) is woody material not incorporated into the humus or mineral soil (Muller and Liu, 1991). Length and diameters at the ends of each piece (with the smallest diameter $\geq$ 10 cm) were measured in cm. Species was recorded when possible. Each CWD piece was placed into a decomposition class depending on the condition of the bark and wood. The decay classes were:

Class 1—Bark intact, some small twigs present, texture or wood structure intact, shape intact (round), wood original color, branches supporting trunk, wood sound;

Class 2—Bark intact to slightly sloughing, twigs absent, texture intact to sapwood with some decay, shape intact (round), log may be slightly sagging;

Class 3—Bark largely missing, twigs missing, texture showing some large sapwood pieces decayed, color faded, log strongly sagging;

Class 4—Bark missing, twigs missing, texture small blocky sapwood decayed and heartwood with some decay punky pieces, shape becoming oval or flattened, log on ground;

Class 5—Bark missing, twigs missing, texture soft and powdery sapwood missing or punky, heartwood decayed only knots remaining sound, shape oval to flattened, color faded to gray brown or yellowish, all of log on ground. Also, resin-laden "skeleton" wood (mostly heartwood) was included in this group.

In each 0.1 ha plot, estimates of canopy coverage of each species in all strata were made using the Daubenmire scale (Daubenmire 1959). Nomenclature followed Nelson (1992). The habitat type of each stand was determined following Hess and Alexander (1986) and De Velice et al. (1986). In some situations, habitat type was difficult to determine because 1) many herbaceous plants did not flower because of the dry year and 2) because the vegetation in some areas did not fit a predefined habitat type description. Consequently, habitat type names were given based on their similarity to other habitat types in Colorado and the Rocky Mountains following Alexander (1985, 1987, 1988).

Environmental measurements for each plot included aspect, slope percent, slope position, elevation (determined from USGS topographic maps), mesoscale landform index, a terrain shape index and lateral shape class. These environmental measurements were made to attempt to characterize site productivity. Aspect was the predominant plot azimuth and was linearly transformed using: $A' = \cos(A\text{-}45) + 1$ (Beers et al. 1966), where A' is the transformed aspect and A is the slope azimuth of the plot. Slope angle (%) of the plot was taken using a clinometer. The same two people took the slope measurement in each plot to keep the viewer's eye height consistent with a spot at equal height on the body of the person 20 m down or up slope from plot center. Slope position is a percentage relating the position of the plot on the slope to the length of the slope. For example, the crest of a ridge had zero slope position while the bottom of a slope or stream bottom had 100% slope position. The mesoscale landform index is the mean of eight measurements of the angle (a clinometer % value taken at eye-height) from plot center to the nearest topographic horizon (McNab 1993). The relative distance to the horizon being measured was also recorded as some horizons were only a few hundred meters away, while others were several kilometers. Horizons more than one kilometer away were considered to have minimal impact on the stand and were given a value of zero. Terrain shape index, a microscale landform index, was determined by estimating eight angle measurements from plot center to a 20 m radius with a clinometer (McNab 1989). The lateral shape class, as viewed from plot center, was assigned 1 for concavity, zero for flat terrain, and −1 for convex terrain (McNab 1989).

LABORATORY PROCEDURES AND DATA ANALYSIS. CWD volume was calculated as the frustum of a cone which is:

$$\text{Vol} = \left(\frac{H}{3}\right)\pi(RS^2 + RS*RL + RL^2),$$

where H is the height or length, RS is the small radius and RL is the large radius of the piece of CWD. Values were converted to m^3/ha. Height of dead trees was estimated using regression of height on the diameter of live trees. This estimated height and a 10 cm small diameter value and measured dbh for the larger diameter were used to calculate volume of standing dead trees. According to Harmon et al. (1986) some mass values reported in the literature may be overestimates due to high conversion factors, i.e., Brown (1974). Mass estimates for comparison with other studies made using conversion factors found in Harmon et al. (1986) and Harmon and Cromack (1987). Classes 1 and 2 CWD were converted to mass (Mg/ha) using 0.365, Class 3 using 0.343, Classes 4 using 0.180 and 5 using 0.178. Since decay class of standing dead trees was not determined in the field, all standing dead CWD was assumed to be in class 1.

Basal area (m^2/ha) and density (stems/ha) were calculated for live and dead trees. Plot data were summarized and analyzed using SAS (1990). A data matrix composed of canopy coverage values for thirty-two species most representative of the 15 habitat types was used for the Reciprocal Averaging ordination (Hill 1973) of these habitat types using ORDIFLEX (Gauch 1977). The same suite of species was used to ordinate stands using the Bray-Curtis polar technique with percent difference as the resemblance function and user-selected endpoints (Bray and Curtis 1957) through ORDIFLEX. These two ordinations were done to develop productivity gradients based on the vegetative composition of habitat types and stands.

Increment cores were sanded and ages determined in the laboratory using a dissecting microscope. Tree-ring chronologies from the two physiographic regions, Front Range and Southwestern Colorado, were obtained from the International Tree-Ring Data Bank and used to crossdate the cores. Ages of all cored trees were determined twice by different technicians to ensure accuracy. Recorded along with the age of the core was a correction factor estimating the age to center of the tree if the center were not included in the core. This was done by drawing a series of concentric rings simulating mean ring widths from cores with the center present and estimating the number of rings to the center. Also, a correction factor of 12 years (Peter Brown, pers. comm.) representing the number of years for the tree to reach dbh was included In data analysis. Increment cores that were broken, had fire scars, or otherwise had no curvature indicating proximity to the center were coded as missing and were omitted from the analyses. Cores from six plots were lost in transit. Therefore, age analyses on a plot basis had a n-size of 322.

A more detailed description of field and laboratory methods can be found in Hall (1995).

Results. COARSE WOODY DEBRIS. Coarse woody debris in the plots sampled in this study was highly variable. The mean CWD for all 328 plots was 15.9 ± 20.85 SD m^3/ha and a range of 0 to 238.7 m^3/ha (Table 1). This latter value was from the Lindner Ranch stand where a very large tree had fallen into the plot. Excluding this plot, the upper range value was 100.0 m^3/ha. Mass for the 328 plots averaged 3.4 ± 5.07 Mg/ha and ranged from 0 to 70.1 Mg/ha. Volume of standing dead CWD averaged 1.11 ± 2.28 m^3/ha or about 7.5% of the downed CWD. Mean standing dead mass was 0.41 ± 0.83 Mg/ha. Four plots had no measurable CWD. Sixty-three percent of the CWD measured was in class 4 followed by class 5 with 16% (Fig. 2). Eighty-eight % of the class 1 volume was standing dead CWD. However, class 1 comprised only about 8% of the total CWD. Several stands had some class 5 CWD which we called "skeleton" wood; that is, very old resin-laden, decay-resistant heartwood. Frequently, this skeleton wood had "charcoaled" surfaces.

Stand volume varied from less than one to > 50 m^3/ha (~10.3 Mg/ha). Coefficients of variation in volume (excluding the Lindner Ranch plot) ranged > 150% among the stands. CWD varied between the two physiographic areas sampled. The Front Range had an mean of 12.4

Table 1. Descriptive statistics of structural characteristics in mature or older *Pinus ponderosa* plots from the Front Range and Southwest Mountains of Colorado.

Variable	N	Mean	SD	Minimum	Maximum
Cover, %	328	63.59	16.77	7.70	99.50
Basal Area, Dead Trees, m^2/ha	328	1.25	2.34	0.00	13.50
Basal Area, Live Trees, m^2/ha	328	25.88	8.70	9.18	54.44
Density, Dead Trees, stems/ha	328	11.92	19.91	0.00	150.00
Density, Live Trees, stems/ha	328	240.95	106.82	40.00	810.00
Standing Dead Volume, m^3/ha	328	0.41	0.83	0.00	6.16
Downed Coarse Woody Debris, m^3/ha	328	14.82	19.77	0.00	221.76
Coarse woody debris, m^3/ha (Total)	328	15.93	20.85	0.00	238.65
Front Range CWD Volume	216	12.43	13.14	0.00	65.77
Southwestern Mountains CWD Volume	112	22.80	29.56	0.38	238.65
Age (All Trees)	1250	213.64	74.49	60.00	510.00
Age (Plot Average)	322	214.32	58.89	105.50	421.30

± 13.14 SD m^3/ha (2.6 ± 2.68 Mg/ha) while the Southwestern Mountains had 22.8 ± 29.56 m^3/ha (4.95 ± 7.62 Mg/ha) (Table 1). Most stands with CWD values less than 10 m^3/ha were dominated by an apparent cohort of similarly aged healthy trees that were not sufficiently old to be experiencing high levels of mortality.

CWD showed a slight relationship to a productivity gradient as suggested by the ordination of stands and habitat types. CWD increased with increasing mesicness of the stand ($\rho \leq 0.0026$, n=53) but the R^2 was low (0.15) (Fig. 3). Ordination of habitat types showed higher amounts of CWD in mesic stands ($R^2 = 0.30$, $\rho \leq 0.033$, n=15) (Fig. 4). CWD volume was not significantly correlated with any environmental variables measured in each plot or stand. Standing dead volume was significantly correlated ($r=0.22$, $\rho \leq 0.004$) with slope aspect when analyzed on a plot basis.

CWD varied among habitat types and series (Table 2). Values presented below exclude the Lindner Ranch plot with the downed tree. The Psme/Quga and the Pipo/Phmo habitat types had the highest mean volume of CWD with 22.38 and 22.05 m^3/ha, respectively (see Table 2 for habitat type abbreviations). The highest variability in CWD volume occurred in the Pipo/Quga and Psme/Fear habitat types. Six habitat types had coefficients of variation > 100%. The Pipo/Fear, Psme/Quga and Pipo/Quga had the highest standing dead volumes with 1.93, 1.75 and 1.62 m^3/ha, respectively. Consistent with the ordination results, mesic habitat types had higher volumes than those that were xeric (Table 2). However, when mean total volumes were averaged across series, the drier *Pinus ponderosa* se-

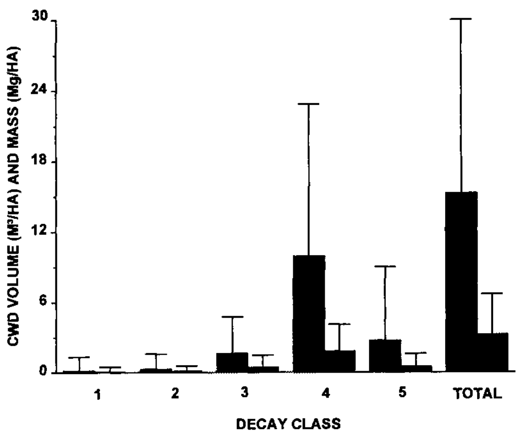

Fig. 2. Mean CWD for each decay class and for all decay classes from 328 samples from *Pinus ponderosa* dominated stands in the Front Range and Southwestern mountains of Colorado. Vertical bars represent the standard deviation.

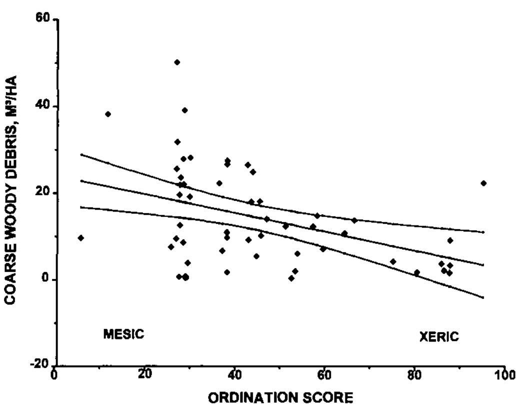

Fig. 3. Relationship between CWD volume and the Bray-Curtis polar ordination of *Pinus ponderosa* dominated stands along an implied topographic-moisture gradient. Upper and lower lines represent the 95% confidence limit for the regression (center line).

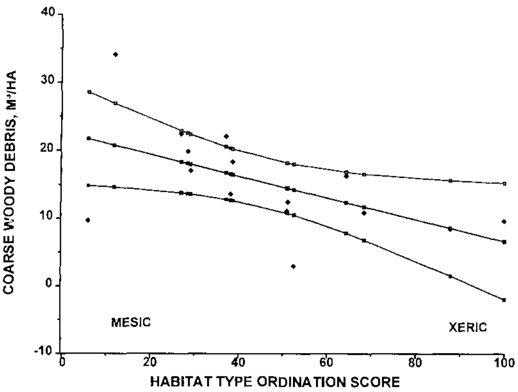

Fig. 4. Relationship between Reciprocal Averaging ordination of *Pinus ponderosa* dominated habitat types and CWD volume. Upper and lower lines represent the 95% confidence limit of the regression (center line).

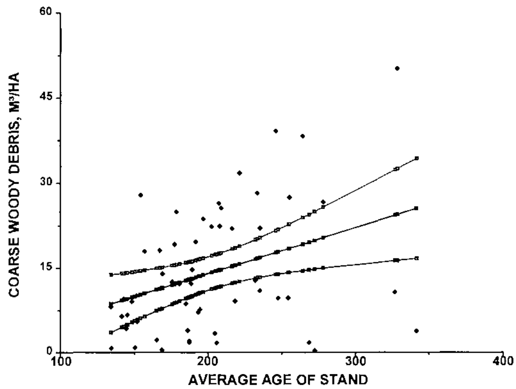

Fig. 5. Relationship between CWD and age of *Pinus ponderosa* stands in Colorado. Curved lines are 95% confidence limits of the regression (center line).

ries had about the same mean volume and mass as the presumably more mesic *Pseudotsuga menziesii* series. Standing dead volume was lowest in the Pipo series.

Mean age of the cored trees in the plots and stands was approximately 214 years (Table 1). CWD volume showed an increase with age of the dominant trees in the plot ($r = 0.20$, $\rho \leq 0.0004$, $n = 322$) and age of the stand ($r = 0.35$, $\rho \leq 0.009$, $n = 53$) (Fig. 5). Similarly, standing dead volume was correlated with mean age of the plots ($r = 0.19$, $\rho \leq 0.006$) and stands ($r =$

Table 2. Mean volume (m^3/ha), mass (Mg/ha) and standard deviations of total CWD and standing dead CWD by habitat type and series for *Pinus ponderosa* plots sampled from the Front Range and Southwest mountains of Colorado.

Habitat type	Plots	Mean total volume	Total volume SD	Mean total mass	Total mass SD	Standing dead volume	Standing dead SD	Standing dead mass	Standing dead mass SD
				Habitat type					
PIPO ARUV	4	2.91	3.13	0.66	0.62	0.68	1.15	0.25	0.42
PIPO CARO	13	12.40	8.95	2.84	2.14	0.30	0.48	0.11	0.18
PIPO CEMO	7	9.61	8.87	1.86	1.55	0.14	0.35	0.05	0.13
PIPO FEAR	11	16.25	18.86	3.03	3.45	0.24	0.43	0.09	0.16
PIPO MUMO	39	8.44	11.71	1.67	2.20	0.38	0.70	0.14	0.26
PIPO PUTR	6	10.82	8.79	3.12	2.85	1.53	2.43	0.56	0.89
PIPO QUGA	49	22.38	25.30	4.70	5.20	1.62	2.65	0.59	0.97
PIPU ARUV	2	9.68	10.02	1.81	1.73	0.37	0.39	0.14	0.14
PIPU FEAR	9	34.09	77.07	9.68	22.73	3.59	5.62	1.31	2.05
PIPU FEAR[1]	8	8.52	7.98	2.12	1.84	1.93	2.78	0.71	1.01
PSME ARUV	33	13.60	11.44	2.90	2.40	1.08	1.47	0.39	0.54
PSME CARO	25	18.33	16.44	3.81	3.24	1.13	2.22	0.41	0.81
PSME FEAR	28	19.83	19.68	3.91	4.06	0.89	1.22	0.33	0.45
PSME PHMO	18	22.05	18.03	4.60	3.38	1.03	1.82	0.38	0.67
PSME PUTR	50	11.04	11.21	2.39	2.50	1.02	2.48	0.37	0.91
PSME QUGA	34	17.03	16.64	3.67	3.70	1.75	3.19	0.64	1.17
				Series					
PIPO	129	14.81	19.10	3.11	3.90	0.89	1.87	0.32	0.68
PIPU	11	29.66	69.71	8.25	20.59	3.01	5.20	1.10	1.90
PIPU[1]	10	8.75	7.80	2.06	1.73	1.62	2.54	0.59	0.93
PSME	188	15.91	15.45	3.34	3.22	1.16	2.24	0.42	0.81

[1] Plot with big downed tree removed. For habitat types, the acronyms are as follows: for Series, Pipo = *Pinus ponderosa,* Psme = *Pseudostuga menziesii* and Pipu = *Picea pungens.* For habitat type indicator species, Aruv = *Arctostaphylos uva-ursi,* Caro = *Carex rossii,* Cemo = *Cercocarpus montanus,* Fear = *Festuca arizonica,* Mumo = *Muehlenbergia montana,* Phmo = *Physocarpus monogynous,* Putr = *Purshia tridentata* and Quga = *Quercus gambellii.*

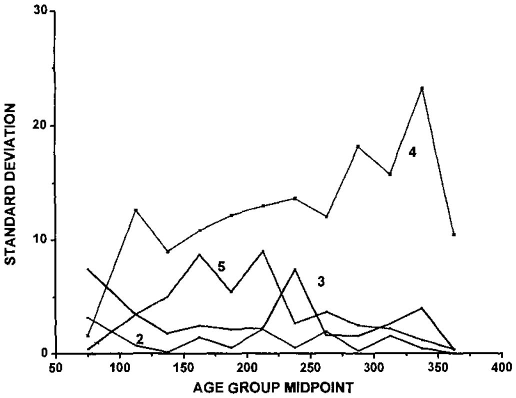

Fig. 6. Relationship between age and variability of CWD decay classes 2 through 5 in *Pinus ponderosa* dominated stands from Colorado.

Table 3. Mean and Standard Deviation (SD) for standing dead density (stems/ha) and basal area (m^3/ha) in *Pinus ponderosa* dominated habitat types in the Front Range and Southwestern mountains of Colorado.

Habitat type	Plot	Density	SD	Basal area	SD
Pipo Aruv	4	2.50	5.00	0.72	1.45
Pipo Caro	13	15.38	24.70	0.42	0.71
Pipo Cemo	7	2.85	7.55	0.19	0.51
Pipo Fear	11	4.54	8.20	0.29	0.63
Pipo Mumo	39	6.15	10.66	0.47	0.92
Pipo Putr	6	15.00	23.45	2.01	3.22
Pipo Quga	49	11.02	14.17	1.65	2.47
Pipu Aruv	2	5.00	7.07	0.46	0.66
Pipu Fear	9	15.55	17.40	3.05	4.42
Psme Aruv	33	14.24	17.85	1.42	2.01
Psme Caro	25	16.00	25.33	1.45	2.83
Psme Fear	28	11.07	16.17	1.08	1.42
Psme Phmo	18	12.22	15.92	1.27	1.92
Psme Putr	50	15.40	31.50	1.31	2.97
Psme Quga	34	12.94	18.99	1.64	2.77
Average	328	11.92	19.91	1.25	2.33

0.30, $\rho \leq 0.027$). After about 150 years, variability of CWD with age increases markedly (Fig. 6). When this relationship was examined by decay class, only class 4 showed a significant relationship ($r = 0.343$, $\rho \leq 0.012$, $n = 53$) to mean age of the trees in the stand. Variability across all decay classes did not respond similarly with age (Fig. 6). Decay class 5 displayed decreasing variability after about 150 years with increasing age, while decay classes 2 and 3 or standing dead volume showed no discernable variability pattern with respect to age.

Pinus ponderosa contributed > 92% of the total CWD volume while decay class 4 *Pinus ponderosa* contributed > 62%. *Populus tremuloides* contributed the next highest total with just over 4% of the total. *Pseudotsuga menziesii* contributed nearly 2% and the remaining species were all < 1% of the total. Three species, *Abies concolor, Juniperus osteosperma* and *Quercus gambellii* showed the maximum contribution of CWD in class 3 while all other species had the highest contribution in class 4. The total volume of CWD in the unknown category was < 1% of the total.

STANDING DEAD CHARACTERISTICS. Only 156 (48%) of the plots had standing dead trees; 122 plots had standing dead *Pinus ponderosa. Pseudotsuga menziesii* occurred in 28 plots, mostly in the Front Range. Nine species plus an unknown category of standing dead occurred in the plots. Diameters of the dead trees ranged from 12.7 (the minimum tree size) to 98.1 cm with mean of 34.6 ± 17.36 SD. Standing dead density averaged 11.9 ± 19.9 SD stems/ha and basal area averaged 1.25 ± 2.33 m^2/ha. Variation for these structural variables was generally high with coefficients of variation often exceeding 400%. Lowest densities of standing dead trees occurred in stands that were accessible in both physiographic areas. For most stands, densities < 20 stems/ha were typical while 31 stands had densities of 10 or fewer stems/ha. Seventy-seven percent of the standing dead was < 40 cm dbh and 62% were < 30 cm dbh. Only 2.3% of the standing dead trees were above 67 cm dbh. About half the stands (25) had standing dead > 60 cm dbh. Eight, six and three stands had standing dead greater than 70, 80 and 90 cm dbh, respectively. Stands with standing dead > 90 cm dbh were in the mountains of Southwestern Colorado. Generally, basal area of standing dead was low for all stands.

Standing dead density and basal area varied with habitat type (Table 3). Density was consistently between 11 and 15 stems/ha for all but four of the 15 habitat types studied. These four, most of which were on drier sites, had lower density values. Basal area was quite variable with the highest value in the Pipo/Fear and the lowest in the Pipo/Cemo habitat types (Table 3). Number of standing dead was generally greater in the *Pseudotsuga menziesii* Series with 66.6% of the total while 28.5% occurred in the *Pinus ponderosa* Series. Most of the standing dead was *Pinus ponderosa* followed by *Pseudotsuga menziesii.* Only in the Psme/Phmo habitat type did the density of *Pseudotsuga menziesii* exceed the density of dead *Pinus ponderosa.* No pattern of

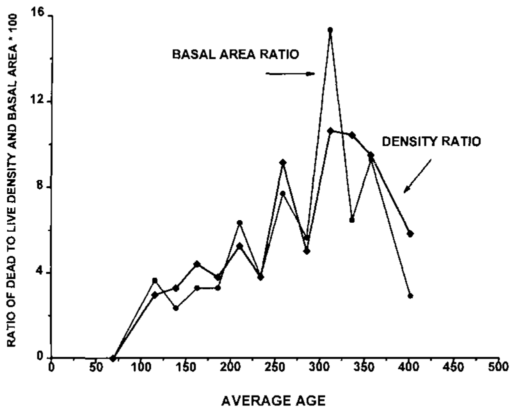

Fig. 7. Ratio of dead-to-live density and basal area in relation to average age for *Pinus ponderosa* stands in Colorado.

standing dead existed in relation to a productivity gradient based on the habitat type ordination.

Ratios (%) of dead to live density and basal area increased from < 3% to almost 16% (Fig. 7). Both structural values increase similarly followed by a leveling off or decline. The last age-group contains only 4 plots and should be interpreted cautiously. It appears about five to 10% of the standing trees are dead in stands > 250 years old.

Pinus ponderosa had the highest density and basal area followed by *Pseudotsuga menziesii* and *Populus tremuloides*. *Pinus ponderosa* had the lowest coefficient of variation with 183%. Standing dead volume and mass comprised 7.5% and 13.6% of the total CWD, respectively. *Pinus ponderosa* and *Pseudotsuga menziesii* comprised 76 and 20% of the total standing dead volume and mass, respectively. The remaining species each made up < 1% of the total standing dead volume or mass.

Discussion. Values of CWD from this study are much lower than for other coniferous forest stands in the western United States (Huff 1984; Grier and Logan 1977; Spies et al. 1988) and the eastern United States (Harmon et al. 1986; MacMillan 1981; Muller and Liu 1991; Tyrrell and Crow 1994; McCarthy and Bailey 1994) and have high variability (Table 4). Spies et al. (1988) reported values more than 72 Mg/ha for Douglas-Fir forests of western Washington and Oregon. These values are almost greater than the maximum values reported for plots in this study and considerably above the mean value per plot or stand.

Mass values in this study are below the mean range of 9–23 Mg/ha in *Pinus ponderosa* stands on the east and west sides of the continental divide in the northern Rockies (Brown and See 1981). Brown and See (1981) suggest less than 22–34 Mg/ha should remain to promote ecosystem function and minimize fire hazards in managed stands. Sackett (1979) reported 18 Mg/ha (> 7.6 cm diameter) for 62 relatively undisturbed *Pinus ponderosa* stands from the Southwest. In the mixed conifer type, CWD averaged 41.7 Mg/ha (Sackett 1979). Since these stands were sampled in the mid 1970's, the fuel loadings might be considered "natural" in a highly managed fire regime but atypical of presettlement fire regimes. Sackett (1980) found an undisturbed *Pinus ponderosa* stand near the San Francisco peaks in Arizona had 16.0 Mg/ha of CWD while another stand 96 km to the southeast on limestone derived soils supported 37.1 Mg/ha. Fire reduced CWD 30.7% and 56%, respectively, in these two areas. Fule and Covington (1994b) reported 8.6 Mg/ha (> 7.6 cm diameter) for *Pinus ponderosa* stands on the North Rim of the Grand Canyon on sedimentary soils and 7.4 Mg/ha for stands on basalt soils in the Coconino National Forest. These values are higher than those we found in Colorado. Fule and Covington (1994a) reported 12 and 7 Mg/ha for two pine-oak forest stands in the Sierra Madre Occidental mountains in Mexico. The latter stand had burned five times more frequently since 1945 than the first stand, resulting in decreased CWD.

The pattern of large amounts of CWD in decay classes 4 and 5 in this study was also found in managed stands in the central Appalachians by McCarthy and Bailey (1994). However, this pattern has not been observed in studies of other forest types (Spies et al. 1988; Tyrrell and Crow 1994). The difference may be due to various combinations of 1) drier conditions that result in slower decomposition rates (Hinds et al. 1965), 2) fire suppression, 3) an input pulse from an older woody cohort that synchronously reached the end of its life cycle in the past and 4) the death of large trees due to mountain pine beetle (*Dendroctonus ponderosae*) infestations. Most stands did not have multiple decay classes of similar-sized trees seen in other forest types in Colorado, e.g., the *Picea-Abies* forest at Bowen Gulch in Colorado (pers. obs.). This would suggest fire (or perhaps humans) removed the older component of large CWD or that the stand is not sufficiently old to produce multiple aged components of CWD. The presence of char-

Table 4. Volume (m^3/ha) and biomass (Mg/ha) of downed coarse woody debris for selected forest types of North America. Bold values are those reported in the literature, non-bolded values were estimated using wood density values from the literature. Mass volume conversions for eastern species are from MacMillan (1981).

Forest type	Location	Volume	Mass	Sources
Douglas Fir	PNW-West Cascades	309–1421	77–355	Grier and Logan 1977, Harmon et al. 1986, Spies and Franklin 1988
Mixed Mesophytic Deciduous Oak-Beech	Cumberland Plateau	66.3	21.8	Muller and Liu 1991
Mixed Mesophytic Deciduous Oak	Indiana	39.8	16.5	MacMillan 1981
Southern Maple	Tennessee	44	14 (32 yrs)	Onega and Eickmeier, 1991
Central Appalachians (Managed)	Maryland	96 (2 yrs) 40 (25 yrs) 52 (80 yrs) 50 (>100 yrs)	55 (2 yrs) 17 (25 yrs) 19 (80 yrs) 33 (>100 yrs)	McCarthy and Bailey, 1994
Hemlock-hardwood	North Central Lake States	54	16	Tyrell and Crow 1994
Northern Hardwoods (Stands > 100 yr old)	New Hampshire	70–100	21–30	Gore and Patterson 1986
Boreal Forest (Stand of various ages)	Newfoundland	15–78	4–22	Sturtevant et al. 1997
Aspen (Boreal) (Stands of various ages)	Alberta, Canada	61–101	15–25	Lee 1997
Spruce-fir	Central-Southern Rocky Mountains	189	52	Arthur and Fahey 1990
Mixed Conifer	Southwest	42	18	Sackett 1979
Ponderosa Pine	Southwest	28	7.8	Fule and Covington, 1994b
Ponderosa Pine	Northern Rocky Mountains	30–77	9–23	Brown and See 1981
Pine Oak	Sierra Madre Occidental	24–42	7–12	Fule and Covington 1994a
Ponderosa Pine (Mature)	Front Range Colorado	12	3	This study
Ponderosa Pine (Mature)	Southwestern Colorado	23	5	This study

coaled "skeletonized" class 5 CWD indicates fire has likely removed some CWD and *Pinus ponderosa* has occupied the site for some time. Covington and Moore (1994b) reported stumps and down logs of *Pinus ponderosa* may persist at least 100 years in Arizona. Some CWD at Cheesman Reservoir in the Front Range dates 400–500 years B.P. (Peter Brown, pers. comm.). A dendrochronological analysis of CWD would help elucidate the dynamics and longevity of CWD in *Pinus ponderosa* stands.

We propose past disturbance, e.g., fire, disease, insect infestation and human intervention, in these stands affects the various CWD attributes significantly. The lack of strength between CWD and site productivity, as shown by the ordination analyses, and the general lack of significant relationships with individual environmental factors support this. Brown and See (1981) found a similar lack of environment-CWD relationships in the northern Rockies as did Spies et al. (1988) in the Pacific Northwest. Tyrrell (1991) found little evidence habitat type or slope affected patterns of CWD in old-growth hemlock-hardwood forests in Wisconsin. Some of these differences might be explained by the presumed higher fire frequency in the drier environments. Brown and See (1981) and Swetnam and Baisan (1996) suggest higher CWD loadings are often found on sites with lower fire frequencies. The relationship between standing dead volume and aspect suggests drier conditions slow decay and allow trees to remain standing longer. Lack of difference in CWD between the *Pinus ponderosa* and *Pseudotsuga menziesii* series is because both productive and unproductive habitat types were included in the samples. It is likely, given the relatively high disturbance frequency in the *Pinus ponderosa* type, that few relationships between CWD and environmental variables would be found. We that suggest the more frequent the disturbance, the weaker the relationship between CWD and physical characteristics or productivity of the site.

The high variability in CWD with age of the stand (see Fig. 6) also appears to be related to disturbance. For example, several stands had CWD volumes less than 5 m^3/ha and averaged more than 286 years old and all showed evidence of some timber removal. Several inaccessible stands had CWD volumes greater than 25 m^3/ha (~7–8 Mg/ha) and averaged more than 240 years of age. Complicating this relationship is that many extant older stands often are on harsher sites and perhaps have experienced less human impact due to their lower productivity. Brown and See (1981) found no relationship between CWD and stand age in the northern Rocky Mountains. Basing stand age on the age of the canopy dominants does not reveal how long the stand has occupied the site, it only indicates how long the canopy dominants have been present. Sampling a full range of stand ages might have revealed a stronger relationship between CWD and age (see Spies et al. 1988). McCarthy and Bailey (1994) found that CWD was greatest following clear-cutting and decreased to minimal amounts in stands about 25 years of age. Subsequently, CWD increased to about 50 m^3/ha in stands that were mature (~75 years) or old (>100 years). Perhaps recently severely disturbed *Pinus ponderosa* stands would show high CWD followed by a decrease to values similar to those reported here for mature stands. Our prediction is that without biomass removing disturbance, there will be a substantial increase in CWD when the dominant cohort in these stands reaches the end of its life-span.

Decreasing variability of class 5 CWD with age suggests the amount of this class of CWD may become a somewhat consistent component of old stands. Perhaps the oldest category of CWD represents an equilibrium amount of CWD in a stand balanced by decay and fire vs. input, given the current fire regime. Decay-resistant "skeleton" wood may persist because of its slow decay rate and may remain in the system through several fire cycles in spite of its resin-laden nature. Further studies should separate this type of CWD into a separate decay class. It likely has a very different role in the system than decayed, punky class 5 CWD.

Lack of recent fire in some stands (Touchan et al. 1996) may partially explain the relatively high contribution of *Populus tremuloides* to the CWD total. In the Rocky Mountains, *Populus tremuloides* has a maximum life span of about 200 years but most do not live that long (Fowells 1965). Jones and DeByle (1985) point out because of reduced fire frequencies, *P. tremuloides* stands in the western United States are predominantly old and commonly being replaced by conifers.

Densities and basal areas of standing dead CWD in this study are lower than for many other coniferous forest types (Tyrrell and Crow 1994) possibly due to the lower productivity of low-elevation *Pinus ponderosa* dominated sites. Roovers and Rebertus (1993) found 142 stems/

ha and 13.2 m^3/ha for density and basal area, respectively in an old growth *Picea-Abies* forest in Colorado. In the Front Range, mean standing dead density in old-growth *Pinus contorta* and *Picea-Abies* stands was about 80 stems/ha (Robertson 1992). The greater densities in these higher elevation forests may lead to more self-thinning mortality, which results in greater amounts of standing dead CWD. In this study most standing dead trees were small, which indicates there is not a great volume or mass available for dead and down CWD. These small trees may reflect self-thinning in stands where density has increased due to fire suppression (Covington and Moore 1994b).

Much of the standing dead *Pseudotsuga menziesii* in the Front Range, e.g., Missouri Gulch near the Manitou Experimental Forest, results from the twofold effect of epidemic spruce budworm (*Choritoneura occidentalis*) during the late 1970's and early 1980's followed by an attack on the weakened trees by the Douglas fir beetle (*Dendroctonus pseudotsugae*) (David Leatherman, pèrs. comm., Colorado State Dept. of Forestry). About 25–40% of the mortality was due to spruce budworm while the remaining mortality was due to the fir beetle. The expectation is standing dead *Pseudotsuga menziesii* will contribute a pulse of CWD to the forest floor as they decay and fall. Lack of fire increases stand density which may increase the likelihood of pine beetle infestations (Larsson et al. 1983; Covington and Moore 1994a, b; Covington et al. 1994) and, therefore, will increase CWD in the future. Apparently, the dynamics of the standing dead component are different in insect infested stands from those that are not infested.

The proportion (~ 10%) of dead trees in the stand should maintain suitable habitat for species requiring snags and should result in a consistent contribution of CWD to the forest floor. Stands lacking standing dead trees will not have an immediate source of CWD. In this case, should much of the downed CWD be consumed by fire, a lag will occur before new trees fall from the standing dead component. Harrington (1996b) reports about 75% of fire-killed trees will fall within 10 years after the burn, which replaces CWD removed by fire. Avery et al. (1976) report the mean yearly input of CWD is about 0.25 Mg/ha/yr in Arizona. If this is a characteristic rate, it would require about 10–20 years to accumulate the mean CWD mass reported for stands in this study, assuming no loss from decay or export.

CONCLUSIONS. Mature or older *Pinus ponderosa* stands in Colorado support lower CWD loadings than other *Pinus ponderosa* forests and other coniferous forest types elsewhere in North America. The relationships among CWD, environment and stand age are obscured by the effects of past disturbance influences unknown to us. It is difficult to understand CWD dynamics without a clear understanding of the effects of fire and other disturbances on this stand characteristic. In healthy, mature stands, a relatively small proportion of the total CWD is standing dead. This proportion will likely change as the oldest cohort begins to become senescent and die.

Management of old-growth *Pinus ponderosa* forests should be directed toward creating some desired future condition. If the desired future condition is that of presettlement times, then we must recognize these forests had a structure and composition quite different from the *Pinus ponderosa* forests of today (Cooper 1960; White 1985; Harrington and Sackett 1992; Covington and Moore 1994a; Covington and Moore 1994b; Covington et al. 1994). These forests apparently had less CWD than the present forests (Harrington 1996a). Unknown, unfortunately, are the typical loadings of CWD in presettlement forests. If the presettlement forest structure is the desired future condition, future research should work toward this goal.

The current old-growth definition for *Pinus ponderosa* in Colorado does not require a specific amount of CWD (Mehl 1992). Clearly, given the amount of disturbance in the stands sampled, it is difficult to determine threshold levels of CWD typical of mature or old-growth forests. Additional research, including dendrochronological studies, should be undertaken to understand more fully the nature of CWD in this forest type.

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