STRUCTURE OF DOWNED WOODY AND VEGETATIVE DETRITUS IN OLD-GROWTH *SEQUOIA SEMPERVIRENS* FORESTS

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ABSTRACT

STRUCTURE OF DOWNED WOODY AND VEGETATIVE DETRITUS IN OLD-GROWTH *SEQUOIA SEMPERVIRENS* FORESTS

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Structural properties of downed woody and vegetative detritus populations in unmanaged old-growth forests provide evidence of the reference conditions from which the impact of natural and anthropogenic disturbances may be evaluated. The structure of downed detritus populations in five old-growth *Sequoia sempervirens* (coast redwood) stands along the north coast of California was assessed using data collected from an intensive network of line intersect sampling transects. Total mass of woody and vegetative detritus ranged between 252 and 619 Mg ha^{-1} among sites, and volume between 540 and 1400 m^3 ha^{-1}. Eighty six percent of DWD mass consisted of logs > 7.6 cm diameter, four percent consisted of particles ≤ 7.6 cm diameter, and ten percent of DWD mass was litter (O_i) and duff (O_e and O_a). Forest floor bulk density ranged between 4.9 and 6.3 Mg ha^{-1} cm^{-1} and depth between 7.4 and 10.9 cm among sites. Average surface fuel heights ranged between 26.2 and 46.4 cm among sites. These values are among the greatest recorded in any forest ecosystem.

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INTRODUCTION

Old-growth forest ecosystems of the Pacific Northwest harbor many of the world's grandest accumulations of living and dead trees, yet surprisingly, little is known about the structure and function of the downed woody detritus. Old-growth forests play a major role in sustaining terrestrial biodiversity (Mosseler et al. 2003, Houde et al. 2007), provide essential habitat for many vertebrates and invertebrates (Thomas et al. 1993), represent reference conditions for degraded or managed forests (Frelich et al. 2005), and are valued for their capacity to store large amounts of above- and below-ground carbon (Harmon et al. 1990, Smithwick et al. 2002, Homann et al. 2004, Fredeen et al. 2005).

Dynamic processes in forest ecosystems, including forest succession, and natural and human-caused disturbances, manipulate the forest structure to varying degrees depending on the stage of stand development, and the type, magnitude, spatial pattern, and frequency of the disturbance. Structural characteristics of downed woody detritus (DWD), an important component of old-growth forests, are strongly correlated with natural and human-caused disturbance regimes, environmental and topographic characteristics, ecosystem processes, and stand dynamics (e.g., Franklin et al. 1987, Ohmann and Waddell 2002, Steed and Wagner 2002, Kennedy et al. 2008). The rate of input and the spatial arrangement of DWD are influenced by forest productivity, stage of forest succession, and disturbance characteristics (Harmon et al. 1986). Decomposition rate is a primary regulator of DWD turnover time and is affected by environmental characteristics, local disturbance regimes, water and gravity, physical damage caused by wildlife, microbial respiration and metabolization, and quality of the substrate (Harmon et al. 1986, Zhang et al. 2008).

Initial and secondary stages of stand development generally contribute to the increase of small diameter DWD to the forest floor. Throughout these initial stages, the canopy of the young cohort closes and increasing competitive pressures cause natural pruning of lower tree branches and density-dependent mortality (Peet and Christensen 1987). During the maturation stage of stand development, living trees attain their maximum height and crown spread (Franklin et al. 2002) while the mass of DWD typically reaches a minimum relative to the other developmental stages due to decomposition of the small diameter detritus accumulated during initial stages and other legacy DWD from previous cohorts (Maser et al. 1988, Spies et al. 1988). Upper limits of DWD loading generally occur during the final stages of stand development (i.e. old-growth), as large, decadent trees die and are recruited to the forest floor (Ohmann and Waddell 2002).

Accumulations of DWD may be altered throughout stand development as a result of natural and human-caused disturbances (Oliver and Larson 1996). With substantial variation in frequency and magnitude, wind uproots and breaks trees and branches resulting in DWD recruitment (White 1979, Sollins 1982). Fire may both reduce DWD accumulations through consumption and increase accumulations through mortality of overstory and understory trees (Agee et al. 1978). Insects and diseases contribute to tree mortality, resulting in additional inputs to standing and downed woody detritus pools (Harmon et al. 1986). Structural characteristics of DWD and the effects that disturbances and successional dynamics have on patterns of DWD in old-growth forest ecosystems are not well understood but deserve attention, considering these forests may define the upper limits of terrestrial ecosystem DWD mass and volume.

Among terrestrial forest ecosystems, old-growth *Sequoia sempervirens* (coast redwood) forests contain the tallest tree species currently recorded. Coast redwood forests naturally occur on 878,000 ha within a belt 725 km long and 10 to 48 km wide along the Pacific Coast between Monterey County, California and Curry County, Oregon, USA, of which ten percent (84,174 ha) is old-growth (Fox 1996, Ornduff 1998). Common conifer and hardwood forest associates of coast redwood are *Pseudotsuga menziesii* (Douglas-fir), *Tsuga heterophylla* (western hemlock), *Lithocarpus densiflorus* (tanoak), *Abies grandis* (grand fir), *Picea sitchensis* (Sitka spruce), and *Arbutus menziesii* (Pacific madrone) (Lenihan 1990, Mahony and Stuart 2000). Coast redwood is a long-lived species that may exceed 1,000 years, with the oldest known individual estimated to be 2,200 years old (Ornduff 1998). Maximum height of old-growth coast redwood trees range between 60 m in the southern portion (Henson and Usner 1993) to upwards of 115 m in the northern portion of its range (Sillett 2008, personal communication), and although rare, tree diameters can be as much as 700 cm (Sawyer et al. 2000a, Sillett and Van Pelt 2007). Density of coast redwood in old-growth forests may be as much as 160 stems ha^{-1} (Hunter and Parker 1993, Busing and Fujimori 2002, Giusti 2007, Dagley 2008), with basal area of approximately 360 m^2 ha^{-1} (Busing and Fujimori 2002, Busing and Fujimori 2005, Sillett and Van Pelt 2007). Trees in old-growth coast redwood forests exhibit both random and clumped spatial distributions (Dagley 2008). Standing woody biomass in old-growth coast redwood forests may be as much as 3,500 Mg ha^{-1}, with volumes as much as 10,000 m^3 ha^{-1} (Sawyer et al. 2000b, Busing and Fujimori 2005).

The primary disturbance agents in old-growth coast redwood forests are fire, wind, flood, terrestrial vertebrates, invertebrates, and disease (Roy 1966, Sawyer et al. 2000a). The fire regime in the coast redwood region is of moderate severity (Agee 1993) with tremendous variation in estimated historical fire frequency from as short as two years up to 500 years between successive events (Veirs 1982, Stuart 1987, Finney and Martin 1989, Brown and Swetnam 1994, Brown et al.1999, Stephens and Fry 2005), and the extent of fires also vary throughout the region (Oneal et al. 2006). Wind uproots and breaks stems and branches of single or large groups of coast redwood trees recruiting DWD to the forest floor, though the frequency of events and the magnitude of effects are not well understood (Harmon et al. 1986, Sawyer et al. 2000b). Major flood events can uproot large coast redwood trees, damage and kill residual standing trees, carry away forest floor DWD, and deposit suspended detritus from upstream areas (Stone and Vasey 1968, Becking 1968, Marden 1993, Zinke et al. 1996). Invertebrate and terrestrial vertebrate (e.g., *Ursus americanus*) disturbances generally are clumped and scattered throughout coast redwood forests, affecting younger and smaller trees, as well as the dead, weakened, or dying trees (Sawyer et al. 2000a, Johnson and Lyon 1991, Sinclair and Lyon 2005). Diseases (e.g., *Fomitopsis pinicola* and *Armillaria* sp.) play a minor role in redwood mortality, typically attacking weakened, or dead trees in clumped and scattered spatial distributions, altering accumulations of DWD by predisposing trees to susceptibility of secondary disturbances such as wind and insects, and through decomposition of DWD (Olson et al. 1990, Sawyer et al. 2000a, Sinclair and Lyon 2005).

Downed woody and vegetative detritus consists of dead whole and fragmented trees and shrubs, stems, branches, and twigs, sloughed bark, fallen needles, leaves, seed cones and other debris in various stages of decomposition that occupies the forest floor (Harmon et al. 1986, Caza 1993, Woldendorp et al. 2002). Stumps, snags, and below-ground woody detritus (fine and coarse dead roots) also contribute to the amount of total woody detritus in forest ecosystems, but are not discussed here. Among the important functions of DWD, the structural properties of populations in unmanaged old-growth forests provide evidence of the reference conditions from which the impact of natural and anthropogenic disturbances may be evaluated (e.g., Maser et al. 1979, Harmon et al. 1986, Harmon and Franklin 1989, Smithwick et al. 2002, Frelich et al. 2005). Lastly, DWD comprises the primary fuel in fire-prone ecosystems and its mass is important to the intensity and effects of fire (Agee 1993).

Size categories are often used to classify DWD, based on the minimum functional size when used for examining and discussing DWD-associated ecological processes (e.g., 10 cm diameter; Enrong et al. 2006), or based upon “timelag” categories, which are useful for estimating forest fuel mass, changes in moisture content, and for predicting fire behavior and effects (Deeming et al. 1977). Fire ecologists often quantitatively describe DWD in terms of mass (Mg ha^{-1}) to estimate fire behavior and effects, while forest ecologists generally use volume (m^3 ha^{-1}), mass, and proportion of area covered to evaluate DWD properties relative to ecological processes.

To date, six studies have quantified DWD characteristics in old-growth coast redwood forests. Two of these studies occurred over the same area in the Upper Bull Creek (alluvial) Flats, Humboldt Redwoods State Park, California (Sugihara 1992, Busing and Fujimori 2005), one of which found 299.2 Mg ha^{-1} of logs > 10 cm diameter (Sugihara 1992) while the other found 242.0 Mg ha^{-1} of logs > 10 cm diameter (Busing and Fujimori 2005). An additional study completed in a 6 ha area within the sloped old-growth coast redwood-Douglas-fir forest overlooking the Upper Bull Creek Flats in Humboldt Redwoods State Park found only 58.9 Mg ha^{-1} of logs >7.6 cm diameter (Stuart 1985). Two studies completed in the same sloped, upland old-growth coast redwood stand in Prairie Creek Redwoods State Park, California found 200 Mg ha^{-1} (Bingham and Sawyer 1988) and 353 Mg ha^{-1} of logs ≥ 25 cm diameter and ≥ 4 m length (Porter 2002). Porter (2002) studied a sloped, lowland site in the Yurok Research Natural Area, California, where 525.6 Mg ha^{-1} of logs ≥ 25 cm diameter and ≥ 4 m long was found. Each of the six DWD studies in old-growth coast redwood forests used a form of line intersect sampling, though they differed in specific methodology (Table 1).

Based on review of the divergent methodologies and widely ranging results (an order of magnitude difference among studies), it is clear that our current understanding of the structural characteristics of DWD in old-growth coast redwood forests is hindered by the lack of consistent and comparable sampling methods. The objectives of this study were to describe the structure of DWD populations in five old-growth coast redwood stands, and to investigate error using measured parameter estimator input values specific to each site.

Table 1. *Sequoia sempervirens* downed woody detritus study comparison. Attributes not described in the studies denoted by *NS* (not stated).

	Bingham (1984) and Bingham and Sawyer (1988)	Stuart (1985)	Sugihara (1992)	Porter (2002) and Porter and Sawyer (2007)	Porter (2002) and Porter and Sawyer (2007)	Busing and Fujimori (2005)
Site	Prairie Creek Redwoods State Park	Humboldt Redwoods State Park	Humboldt Redwoods State Park	Prairie Creek Redwoods State Park	Yurok Research Natural Area	Humboldt Redwoods State Park
Sample area (ha)	80	6	50	291	74	8
Sample method	LIS*	LIS*	LIS*	LIS*	LIS*	LIS*
Plot location	Systematic[†]	Systematic	Random	Systematic[‡]	Systematic[‡]	Constrained
Transect length (m)	60	15	50	30	30	100
Transect orientation	*NS*	*NS*	Random[§]	Random[ǀ]	Random[ǀ]	Systematic[¶]
Transect arrangement	Radial	Radial	Radial	Radial	Radial	Radial
Transects plot^{-1}	1	1	1	1	1	1
Total transects	60	90	20	*NS*	*NS*	8
Total transect length (m)	3600	1370	1000	*NS*	*NS*	800
Minimum diameter (cm)	25	None	10	25	25	None
Volume estimator	Van Wagner 1968	N/A	N/A	Van Wagner 1968	Van Wagner 1968	Van Wagner 1968
Mass estimator	Brown 1974	Brown 1974	Brown 1974	Brown 1974	Brown 1974	Brown 1974
Quadratic mean diameter squared (d^2)	N/A	Brown 1974	N/A	N/A	N/A	Brown 1974
Specific gravity (s)	USFS 1955; Brown 1974	Brown 1974	Bingham 1988	USFS 1955; Brown 1974	USFS 1955; Brown 1974	**
Nonhorizontal particle angle (a)	Brown 1974	Brown 1974	Brown 1974	Brown 1974	Brown 1974	Brown 1974
Slope correction factor (c)	1.088	Brown 1974	None	*NS*	*NS*	None
Decay categories	3	2	3	3	3	5

[*]Line intersect sampling (LIS)

[†]120 m x 120 m grid

[‡]60 m x 120 m grid

[§]Random selection of one of four cardinal directions

[ǀ]Random selection of azimuth

[¶]Four transects oriented north to south and four transects oriented east to west

[**]s of particles ≤ 7.6 cm diameter taken from Brown (1974); s of particles > 7.6 cm diameter determined from laboratory analysis of samples collected on site (value not stated)

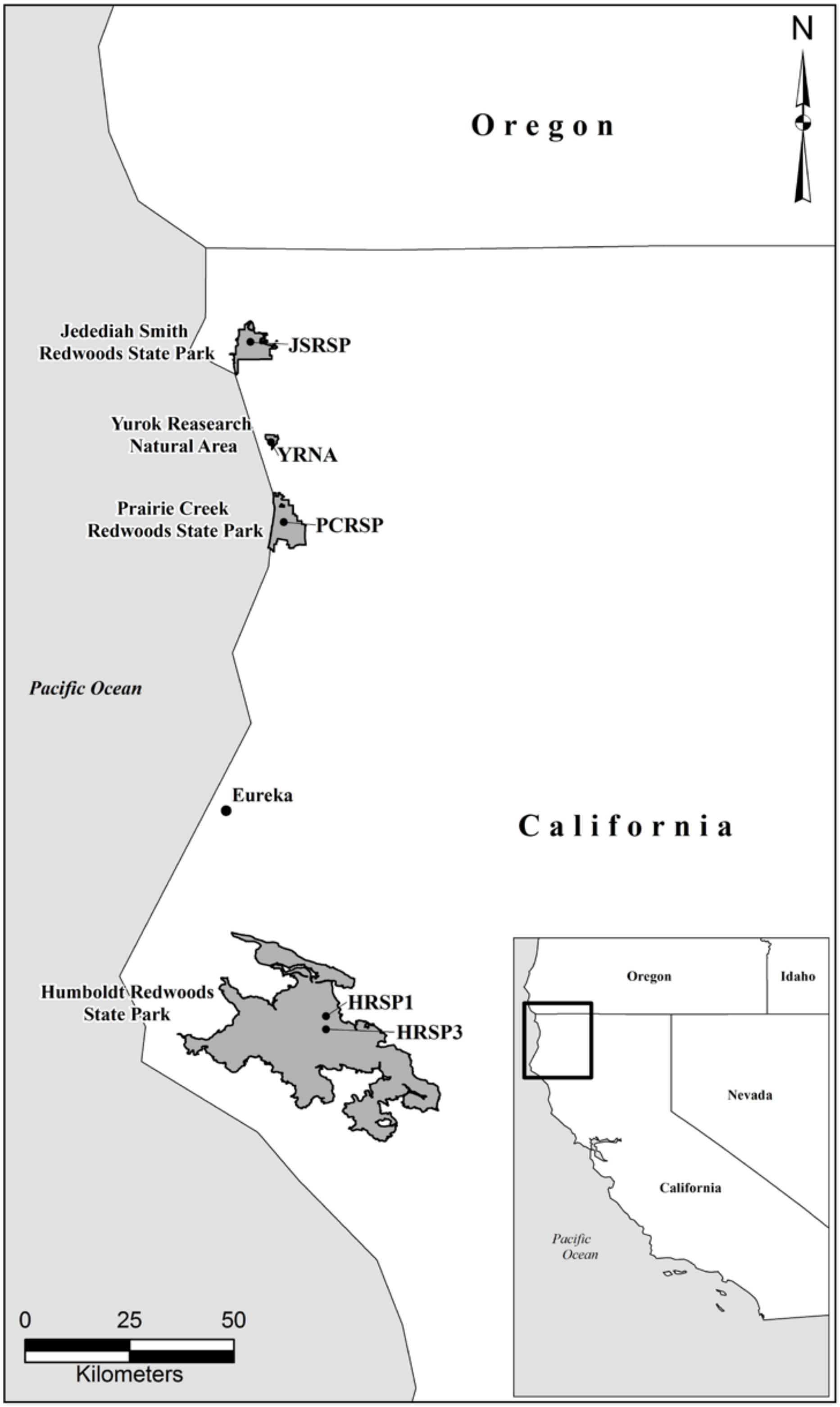
STUDY SITES

I selected five sites to estimate mass of surface and ground woody and vegetative detritus within old-growth coast redwood forests in the northern sub-region (Sawyer et al. 2000b) of the coast redwood range. Sites were located on alluvial flats (slope < 10%), and on low and mid-slope positions (slope < 30%), with overstory coast redwood canopy cover exceeding 50 percent. The five sites span a 180 km latitudinal gradient (40°14’01” N to 41°49’20” N), and a 30 km width (123°46’39” W to 124°04’52” W; Figure 1).

The Franciscan Assemblage is the principle geologic formation underlying the northern sub-region of the coast redwood’s range (Blake and Jones 1981) and has the greatest influence on the region’s soils (Cooper 1975). The sedimentary rocks that make up this portion of the Franciscan Assemblage are composed of arkosic sandstones, andesitic graywackes, and quartzofeldspathic graywackes interbedded with radiolarian chert (Blake and Jones 1981). Soils of the study sites generally are very deep and well-drained fine and coarse loams formed in alluvium, residuum, or colluvium from mixed sedimentary sources (NRCS 2008).

The climate of the study region is described as mesothermal and Mediterranean with warm, dry summers and cool, wet winters. Mean annual precipitation ranges between 1,524 mm and 2,034 mm among sites (Horn 1966, WRCC 2008). Rainfall is the dominant form of precipitation throughout the region with 95 percent typically occurring between October and May (Horn 1966). Summer fog drip may input as much as 450 mm of water annually (Azevedo and Morgan 1974, Dawson 1998). Average annual

Figure 1. Northwestern California study region and site locations.



temperature ranges between 11.0°C and 12.6°C among the five sites (WRCC 2008). Relative humidity is typically around 90 percent during the winter months, with mid-summer means around 50 percent at inland locations and 90 percent near the coast; periodic offshore winds may substantially reduce these values (Elford and McDonough 1974). Wind speeds are typically light throughout the study region with expected speeds between 65 and 80 km hr^{-1} once every two years and 130 to 145 km hr^{-1} approximately once every 100 years. Prevailing wind direction between November and March is typically from the southeast while winds from April through October are generally from the north or northwest (Elford and McDonough 1974).

Humboldt Redwoods State Park (HRSP), Humboldt County, California, was the southernmost study area, located ca. 35 km inland, encompassing 21,450 ha, of which 6,880 ha is old-growth coast redwood forest. Average annual temperatures at HRSP range from a low of 8.0°C to a high of 17.1°C (WRCC 2008), and mean annual precipitation is 1,524 mm (Horn 1966, WRCC 2008). Two study sites were located at HRSP: HRSP1 and HRSP3. HRSP1 was a 50 ha area within the Upper Bull Creek Flats, an alluvial flat old-growth stand adjacent to the north bank of Bull Creek, with average slope of two percent and elevation of 50 m (Table 2). Soils were very deep, moderately well-drained coarse-silty and coarse-loamy Aquic and Oxyaquic Udifluvents of the Eelriver and Cottoneva series (NRCS 2008). Vegetation throughout HRSP1 was of the SESE-POMU type (Mahony and Stuart 2000) with 75 percent canopy cover and 137.2 m^2 ha^{-1} of overstory basal area (Table 3). HRSP3 was a 40 ha old-growth stand upslope from the south bank of Bull Creek, < 1 km from the southwestern boundary of HRSP1, with a

Table 2. Physical and geographical attributes of five old-growth *Sequoia sempervirens* stands in northwestern California, USA.

Site name	Site abbreviation	Topographic position	Latitude range	Longitude range	Elevation (m)	Aspect	Slope (%)	Area (ha)
Humboldt Redwoods State Park	HRSP1	Lowland alluvial flat	40°20'43.4"N - 40°21'11.5"N	123°57'09.4"W - 123°58'34.3"W	50	SE	0-6	50
Humboldt Redwoods State Park	HRSP3	Upland sloped	40°20'40.2"N - 40°20'53.1"N	123°58'53.8"W - 123°59'24.1"W	50-200	NNE	10-35	40
Jedediah Smith Redwoods State Park	JSRSP	Lowland alluvial flat	41°46'00.2"N - 41°46'20.7"N	124°06'17.5"W - 124°07'07.7"W	70	S	0-3	40
Prairie Creek Redwoods State Park	PCRSP	Lowland alluvial flat	41°22'31.0"N - 41°24'29.5"N	124°00'44.2"W - 124°01'46.6"W	90	SW	0-7	50
Yurok Research Natural Area	YRNA	Lowland sloped	41°34'41.1"N - 41°34'56.5"N	124°03'49.5"W - 124°04'09.3"W	20-110	SE	5-25	20

Table 3. Structure and composition in five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Frequency based on the percent of plots where the species were present. Nomenclature according to Hickman (1993). Dashed lines indicate species absence.

Species	HRSP 1	HRSP 3	JSRSP	PCRSP	YRNA
Abies grandis (Douglas) Lindley (grand fir; ABGR)					
Basal Area ($m^2\ ha^{-1}$)	0.3	1.4	--	--	--
Midstory Cover (%)	0.4	0.7	--	--	--
Understory Cover (%)	0.2	0.1	--	--	--
Frequency (%)	22.2	40.0	--	--	--
Acer circinatum Pursh (vine maple; ACCI)					
Understory Cover (%)	--	--	0.1	--	--
Frequency (%)	--	--	20.0	--	--
Arbutus menziesii Pursh (Pacific madrone; ARME)					
Basal Area ($m^2\ ha^{-1}$)	--	1.4	--	--	--
Midstory Cover (%)	--	1.1	--	--	--
Understory Cover (%)	--	--	--	--	--
Frequency (%)	--	30.0	--	--	--
Blechnum spicant (L.) Smith (deer fern; BLSP)					
Understory Cover (%)	--	--	22.2	1.0	10.8
Frequency (%)	--	--	100.0	75.0	87.5
Corylus cornuta Marsh. var. *californica* (A. DC.) W. Sharp (California hazelnut; COCO)					
Basal Area ($m^2\ ha^{-1}$)	0.3	--	--	--	--
Midstory Cover (%)	4.8	--	--	--	--
Understory Cover (%)	< 0.1	2.4	7.6	--	0.1
Frequency (%)	55.6	40.0	40.0	--	12.5
Gaultheria shallon Pursh (salal; GASH)					
Understory Cover (%)	< 0.1	0.3	6.7	6.3	0.4
Frequency (%)	3.7	40.0	100.0	37.5	25.0
Lithocarpus densiflorus (Hook. & Arn.) Rehder (tanoak; LIDE)					
Basal Area ($m^2\ ha^{-1}$)	0.3	8.7	1.8	--	--
Midstory Cover (%)	9.1	32.0	2.6	0.1	--
Understory Cover (%)	2.2	25.2	2.2	--	--
Frequency (%)	96.3	100.0	80.0	12.5	--
Oxalis oregana Nutt. (redwood sorrel; OXOR)					
Understory Cover (%)	9.5	0.2	9.8	45.3	20.6
Frequency (%)	100.0	70.0	100.0	100.0	100.0
Picea sitchensis (Bong.) Carrière (Sitka spruce; PISI)					
Basal Area ($m^2\ ha^{-1}$)	--	--	--	1.7	--
Overstory Cover (%)	--	--	--	0.4	--
Midstory Cover (%)	--	--	--	0.1	--
Understory Cover (%)	--	--	--	--	0.1
Frequency (%)	--	--	--	12.5	12.5
Polystichum munitum (Kaulf.) C. Presl (western sword fern; POMU)					
Understory Cover (%)	14.2	0.5	62.0	87.5	68.8
Frequency (%)	100.0	60.0	100.0	100.0	100.0

Table 3. Structure and composition in five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Frequency based on the percent of plots where the species were present. Nomenclature according to Hickman (1993). Dashed lines indicate species absence. (continued)

	Site				
Species	HRSP 1	HRSP 3	JSRSP	PCRSP	YRNA
Pseudotsuga menziesii (Mirbel) Franco var. *menziesii* (Douglas-fir; PSME)					
Basal Area ($m^2 ha^{-1}$)	0.2	13.3	--	6.3	--
Overstory Cover (%)	--	15.1	--	4.1	--
Midstory Cover (%)	0.1	1.8	--	0.1	--
Understory Cover (%)	--	--	--	--	--
Frequency (%)	3.7	100.0	--	50.0	--
Rhamnus purshiana DC. (cascara; RHPU)					
Understory Cover (%)	--	--	8.1	0.4	< 0.1
Frequency (%)	--	--	40.0	25.0	12.5
Rhododendron macrophyllum D. Don ex G. Don (Pacific rhododendron; RHMA)					
Understory Cover (%)	--	--	--	--	0.6
Frequency (%)	--	--	--	--	50.0
Rubus spectabilis Pursh (salmonberry; RUSP)					
Understory Cover (%)	< 0.1	--	1.3	3.8	1.3
Frequency (%)	3.7	--	60.0	37.5	37.5
Sequoia sempervirens (D. Don) Endl. (coast redwood; SESE)					
Basal Area ($m^2 ha^{-1}$)	135.2	113.0	135.0	163.6	217.0
Overstory Cover (%)	74.8	59.8	47.0	71.9	65.6
Midstory Cover (%)	6.3	12.0	3.3	11.8	13.9
Understory Cover (%)	0.6	0.5	0.2	0.6	1.9
Frequency (%)	100.0	100.0	100.0	100.0	100.0
Tsuga heterophylla (Raf.) Sarg. (western hemlock; TSHE)					
Basal Area ($m^2 ha^{-1}$)	--	--	9.2	1.7	1.7
Overstory Cover (%)	--	--	7.5	0.4	--
Midstory Cover (%)	--	--	26.6	1.5	6.1
Understory Cover (%)	--	--	0.2	0.1	--
Frequency (%)	--	--	100.0	50.0	50.0
Umbellularia californica (Hook. & Arn.) Nutt. (California bay; UMCA)					
Basal Area ($m^2 ha^{-1}$)	0.9	--	--	--	--
Midstory Cover (%)	4.5	--	--	--	--
Understory Cover (%)	--	--	--	< 0.1	--
Frequency (%)	63.0	10.0	--	12.5	--
Vaccinium ovatum Pursh (evergreen huckleberry; VAOV)					
Understory Cover (%)	0.9	52.1	30.1	6.6	19.5
Frequency (%)	51.9	100.0	100.0	75.0	100.0
Vaccinium parvifolium Smith (red huckleberry; VAPA)					
Understory Cover (%)	0.1	0.1	3.9	5.0	6.6
Frequency (%)	3.7	10.0	100.0	87.5	87.5

north-northeast-facing 25 percent average slope and elevation between 50 and 200 m (Table 2). Soils were very deep, well-drained fine-loamy and loamy-skeletal Typic and Ultic Hapludalfs and Dystric Eutrudepts of the Redwoodhouse, Yager Creek, and Mailridge series (NRCS 2008). Vegetation throughout HRSP3 was of the SESE-PSME/VAOV type (Mahony and Stuart 2000) with 75 percent canopy cover and 126.3 m^2 ha^{-1} of overstory basal area (Table 3).

Jedediah Smith Redwoods State Park (JSRSP), the northernmost study area, is located 10 km inland, near Crescent City, California, and contains 4,050 ha of old-growth coast redwood forest. Average annual temperatures at JSRSP range from a low of 7.1°C to a high of 16.1°C (WRCC 2008), and mean annual precipitation is 1,795 mm (WRCC 2008). The JSRSP site covered 40 ha of alluvial flat old-growth coast redwood forest on the north side of Mill Creek, with average slope < 1 percent and elevation of 70 m (Table 2). Soils were very deep, well-drained, fine-loamy Andic Dystrudepts and coarse-loamy Oxyaquic Eutrudepts of the Bigtree and Mystery series (NRCS 2008). Vegetation throughout JSRSP was of the SESE-TSHE/RUSP type (Mahony and Stuart 2000) with 50 percent canopy cover and 146.0 m^2 ha^{-1} of overstory basal area (Table 3).

Prairie Creek Redwoods State Park (PCRSP), located in the central portion of the study region, < 5 km from the Pacific Ocean, contains ca. 6,000 ha of old-growth coast redwood forest. Average annual temperatures at PCRSP range from a low of 5.7°C to a high of 16.3°C (WRCC 2008), and mean annual precipitation is 1,711 mm (WRCC 2008). The PCRSP study site covered ca. 50 ha of alluvial old-growth forest along the eastern bank of Prairie Creek, with average slope of three percent and elevation of 90 m

(Table 2). Soils were very deep, well-drained fine-loamy Andic Dystrudepts and coarse-loamy Oxyaquic Eutrudepts of the Bigtree and Mystery series (NRCS 2008). Vegetation throughout PCRSP was of the SESE-TSHE/RUSP type (Mahony and Stuart 2000) with 75 percent canopy cover and 173.3 m^2 ha^{-1} of overstory basal area (Table 3).

Approximately 20 km north of PCRSP is the Redwood Experimental Forest, which contains the Yurok Research Natural Area (YRNA). The YRNA study site is 3 km east of the Pacific Ocean along the north bank of High Prairie Creek. Average annual temperatures at YRNA range from a low of 7.0°C to a high of 16.0°C (WRCC 2008), and mean annual precipitation is 2,034 mm (WRCC 2008). The YRNA study area covered 20 ha of old-growth coast redwood forest, with a southeast-facing 17 percent average slope between 20 and 110 m elevation (Table 2). Soils were very deep, well-drained fine-loamy and loamy-skeletal Typic Palehumults and Typic Haplohumults of the Sasquatch, Yeti, and Footstep series (NRCS 2008). Vegetation throughout YRNA was of the SESE-TSHE/RUSP type (Mahony and Stuart 2000) with 65 percent canopy cover and 218.7 m^2 ha^{-1} of overstory basal area (Table 3).

Based on review of the California FRAP (2003) database and studies completed by Stuart (1987) and Brown and Swetnam (1994), no fire has occurred within the perimeters of any of the five study sites since at least 1950. HRSP1 was affected, however, by the 1955 and 1964 Eel River floods (Becking 1968, Stone and Vasey 1968). I observed isolated occurrences of cut logs at HRSP1 and evidence of a historic homestead suggesting that humans have also influenced detritus mass there, though the magnitude is unknown.

MATERIALS AND METHODS

Field Measurements

Field data were collected between July 2006 and December 2007. Sample plots within HRSP1 (n = 27), HRSP3 (n = 10), and YRNA (n = 8) were systematically located 100 m apart following a square grid pattern (Figure 2), originating from a randomly selected initial point. Sample plots within PCRSP (n = 8) and JSRSP (n = 5) were randomly located due to limits created by the sample area configurations. All plots were located with a GPS, and slope and aspect were measured.

Surface woody detritus and forest floor data were collected using line intersect sampling (LIS) methods (Van Wagner 1968, Brown 1974). According to convention, snags and belowground woody detritus were not sampled. LIS plots at each sample point consisted of three randomly oriented 50 m transects radiating in a Y-shaped arrangement (Figure 2). Random orientation of transects ensured that each sample did not violate the LIS assumption of random particle orientation (Van Wagner 1968, Brown 1974, Marshall *et al*. 2000). Orientation of the initial sample transect (T1) was randomly selected from a defined, uniform distribution ($\theta_T \sim U\ [0, 360°]$); bearings of sample transects two (T2) and three (T3) were determined by adding 120° and 240° to θ_{T1}, respectively. Length of sample transects was 50 m at all sites except YRNA, where transects were reduced to 25 m to fit within the smaller area.

Fine and coarse woody detritus sample methods were based upon standard techniques (Brown 1971, Brown 1974, Brown and Roussopoulos 1974). Data were

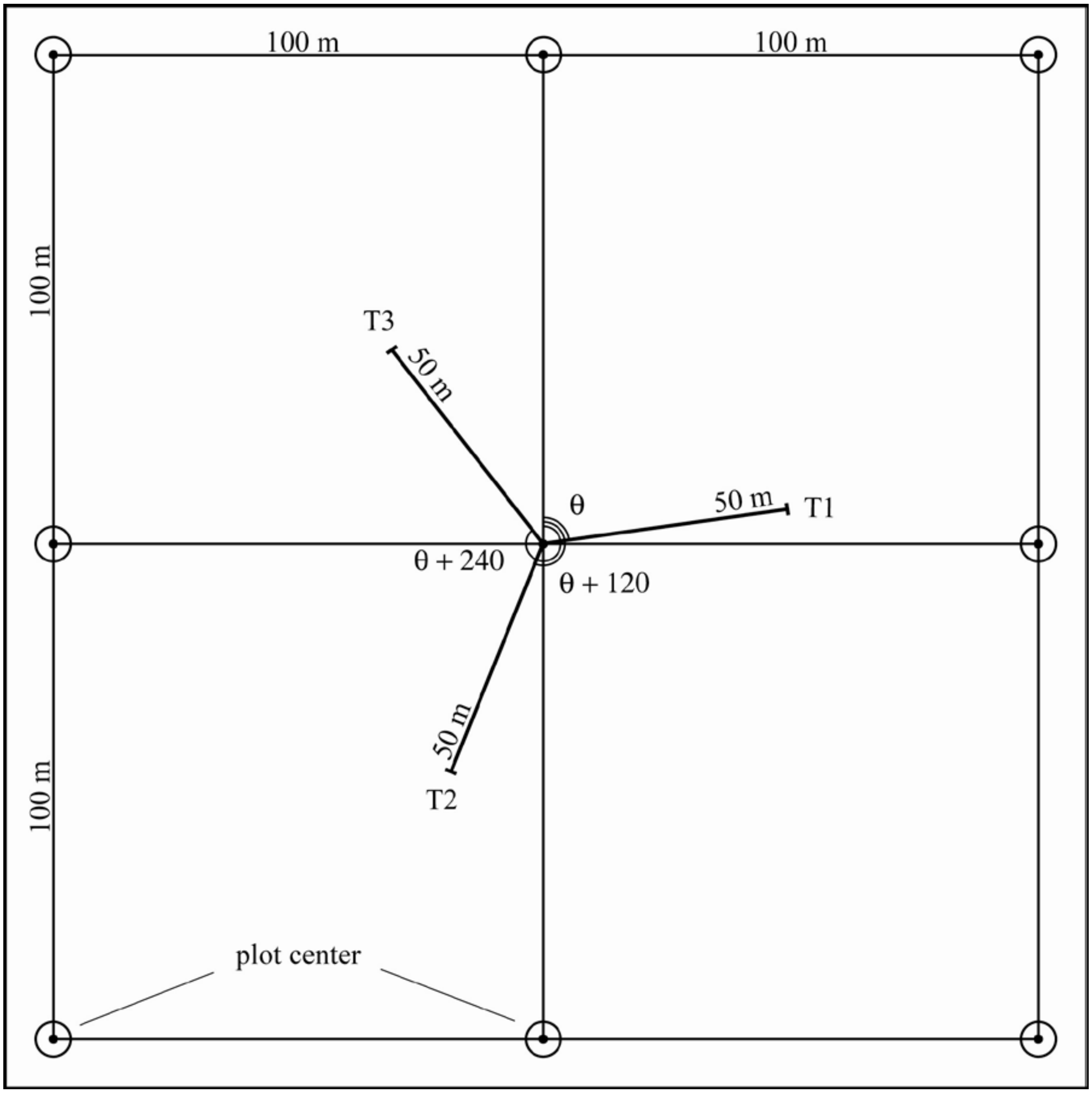


Figure 2. Systematic location of sample plots used to sample downed woody detritus populations in five old-growth *Sequoia sempervirens* stands in northwestern California, USA; radial (Y-shaped) transect arrangement used to collect downed woody detritus data at all plot locations.

collected corresponding to individual particle timelag category (Deeming *et al*. 1977): 1-hr < 0.6 cm; 10-hr 0.6-2.5 cm; 100-hr 2.51-7.6 cm; and 1000-hr + > 7.6 cm diameter.

All particles ≤ 7.6 cm in diameter (i.e. 1-, 10-, and 100-hr) were sampled along designated intervals initiating at the end of each sample transect opposite plot center to prevent trampling of samples and to ensure a wider spatial arrangement of sample points. All woody particles whose central axis intersected the transect within 2 m above the ground were sampled (Brown 1974, Brown and Roussopoulos 1974). The number of intersections of 1-hr and 10-hr particles were tallied by category along the first 3 m of each sample transect, and 100-hr particles were tallied along the first 5 m (Figure 3). The proportion (*P*) of tallies contributed by each species present was estimated to the nearest 5 percent for each timelag category. Additionally, tallies of 1-hr and 10-hr particles were further categorized as either woody (W) or leafy (L); woody particles (1-hr W and 10-hr W) had the appearance of typical branches or twigs, while leafy particles (1-hr L and 10-hr L) were branch-like in appearance with leaves retained in scale-like or awl-like arrangements, or as sprays of alternating 2-ranked linear leaves (Figure 4). Tally data for 1-, 10-, and 100-hr particles were recorded in 0.5 m increments along the sample transect length to allow for flexibility in calculating mass estimates using various transect lengths (Figure 3).

Coarse particles (1000-hr +) were surveyed along the total length of each sample transect (Figure 3). All woody particles > 7.6 cm in diameter with a central axis that intersected the sample transect within a plane extending 3 m above the ground surface were sampled. Species, diameter, category of decay, and orientation (i.e. the angle of the

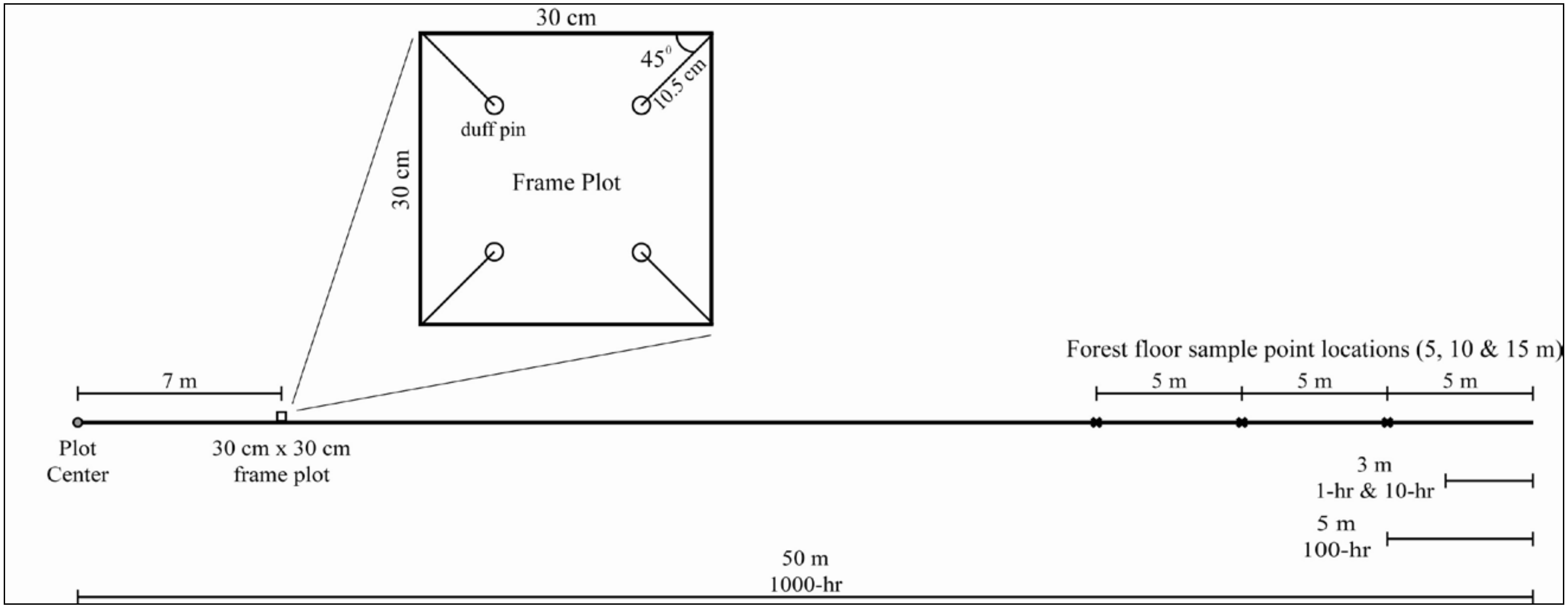


Figure 3. Plan view of transect and frame plot used for sampling downed woody detritus in five old-growth *Sequoia sempervirens* stands in northwestern California, USA.

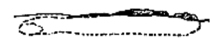
Figure 4. Woody-leafy gradient (a-f) of 1-hr particles (< 0.6 cm) within *Sequoia sempervirens* stands in northwestern California, USA. Example of a 1-hr woody particle (a) is visible on the far left. 1-hr leafy particle examples (b) and (c) show leaves in scale-like and awl-like arrangements. Leafy particles (d-f) show sprays of alternating 2-ranked linear leaves. Particle (e) provides a view of the top surface of the branch and leaves and particle (f) shows the bottom surface.

particle away from horizontal) of all intersecting particles were determined. Intersections involving the vertex of the radial transects were excluded from the sample (Affleck et al. 2005). The distance along the sample transect at the point of particle intersection was also recorded in order to allow for the analysis of mass estimates under various transect length scenarios.

Due to the large dimensions of downed logs (max. diameter = 484.8 cm), diameter measurement of large logs in the sample required the use of a caliper consisting of multiple 1.22 m range poles joined together, a 2 m length of straight, rigid 5 x 40 mm aluminum fastened to one end of the range poles, and a plumb-bob suspended by a string on the opposing end. The string and aluminum were positioned flush against opposing sides of the log and the cross-sectional distance between them (the particle diameter) was measured. When feasible, diameter of logs > 7.6 cm was measured using a diameter tape. Classification of decay was based on a five category system developed by Sollins (1982) for use with Douglas-fir logs (Table 4) since no protocol for decay classification of coast redwood logs existed.

Three surface fuel height, litter depth, and duff depth measurements were made at 5, 10, and 15 m along each transect. Forest floor (i.e. litter and duff) samples were collected at each sample point from a 30 cm x 30 cm frame placed 7 m from plot center adjacent to the left side of one randomly selected transect (Figure 3). Prior to sample removal, 20 cm long steel nails were placed in each of the four quadrants in the sampling frame so that the head of each nail was flush with the surface of the litter at that point.

Table 4. Attribute characteristics for each category of decay used to classify intersected 1000-hr + particles (> 7.6 cm). System of categorization adapted from Fogel et al. (1973), Maser et al. (1979), and Sollins (1982) for use with *Pseudotsuga menziesii* boles.

	Log Decay Category				
Particle Attribute	1	2	3	4	5
					
Bark	Intact	Intact	Sloughing or absent	Detached or absent	Detached or absent
Twigs, 3 cm	Present	Absent	Absent	Absent	Absent
Texture	Intact	Intact to partly soft	Hard, large pieces	Small, soft blocky pieces	Soft and powdery
Shape	Round	Round	Round	Round to oval	Oval
Color of wood	Original color	Original color	Original color to faded	Light brown to reddish brown	Red brown to dark brown
Portion of log on ground	Tree elevated on support points	Tree elevated on suuport points but sagging slightly	Tree is sagging near ground	All of tree on ground	All of tree on ground
Invading roots	Absent	Absent	Sapwood only	Throughout	Throughout

Nails were positioned by orienting a 10.5 cm line at a 45° angle from each corner of the frame; nail location was at the terminus of each line (Figure 3). Woody and vegetative detritus within the frame were collected by strata: woody debris, litter (O_i), fermentation (O_e), and humus (O_a). Depth of each stratum was estimated by measuring the length of the nail exposed by excavation.

Site-specific measurements of average diameter, specific gravity, and nonhorizontal angle values were used in the calculation of downed woody detritus mass estimates (Brown 1974). Woody particles (n = 50) from each timelag category and from each species contributing ≥ 5 percent of the species present were randomly collected at each site. Grab samples were collected and transported to the lab for specific gravity (s) analysis. Samples of logs > 7.6 cm were opportunistically collected for each species in order to equally represent the five categories of decay. The average diameter of particles ≤ 7.6 cm for each species and timelag category was determined from perpendicular diameter measurements taken at a random point along the length of each particle. Nonhorizontal angles (a; the particle angle deviation from horizontal) of particles (n = 50) in each timelag category were measured along a randomly located transect within each study area using a protractor for the smallest particles and a hand-held clinometer for the larger particles.

Vegetation composition and structure were surveyed at each sample plot. Percent cover of all species occupying each overstory (> 25 m), midstory (5–25 m) and understory (< 5 m) stratum was estimated using relevé sampling (Sawyer and Keeler-Wolf 1995). Basal area of all overstory species was estimated at each plot using 20 or 60 basal area factor (BAF) wedge prisms; data were collected in English units and converted to metric.

Laboratory Measurements

All field samples were dried in convection ovens to a constant mass. Litter and duff samples were dried at 65°C for 72 hours then removed and weighed. Mineral soil captured in duff samples was removed by floating the samples in water. Organic matter was skimmed from the water surface then re-dried, weighed, and used to correct the original mass measurement.

Woody particles were dried at 75°C to a constant mass. Specific gravity of the woody particles was determined following methods described in ASTM D 2395-02 and Illston (1994). After drying, particles were removed from the oven, then peeled, shaved, and sawed to 3 cm lengths. Particles were then oven-dried at 75°C to remove any moisture adsorbed during preparation and then weighed. Each particle was submerged in a 400 ml water-filled beaker on a tared balance and the mass of the volume of water displaced was recorded. For each particle, the oven-dry mass was divided by the mass of the water displaced; the resulting quotient was the particle’s specific gravity. Mean specific gravity was estimated by species and timelag category at all sites. When multiple species were represented in a timelag category the composite estimate was calculated using methods in Brown (1974).

Data Analysis

Mass and volume of ground and surface downed woody and vegetative detritus, fuel bed depth, and surface fuel height were calculated for each transect in the Y-shaped arrangement then averaged to derive plot estimates (Brown 1974). Site estimates were derived by calculating the mean of all plot estimates at each site. Mass of all particles ≤ 7.6 cm diameter ($M_{\leq 7.6}$) was estimated by timelag category; 1-hr particle mass was further partitioned into woody and leafy categories. Mass of particles > 7.6 cm diameter ($M_{>7.6}$) was estimated by species and category of decay.

Mass (Mg ha^{-1}) of woody particles ≤ 7.6 cm diameter ($M_{\leq 7.6}$; 1-hr, 10-hr, and 100-hr) was determined using Equation 1, adapted from Brown (1974), along with site-specific estimator input values in Table 5.

$$M_{\leq 7.6} = \frac{knd^2 s_{oc} ac}{Nl} \tag{1}$$

where k is an equation constant that allows for the use of specific gravity in place of density in the mass equation and equals 1.234 (Van Wagner 1982); n is the number of particle intersections in each timelag category; and, d^2 is the square of the quadratic mean diameter (cm) of particles representing each timelag category, calculated using Equation 2.

$$d^2 = \left(\sqrt{\frac{\sum_{i=1}^{n} diameter_i^2}{n}} \right)^2 \tag{2}$$

Where, *diameter*^{2} is the square of the diameter (cm) measurement. If multiple species each contributed ≥ 5 percent to the composition of particles tallied (P), those species were included in the calculation of a composite quadratic mean diameter using Equation 3.

Table 5. Estimator input values used to calculate mass of downed woody detritus in five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Mass estimator and variable definitions adapted from Brown (1974).

Fuel size category	Input variable	Site: HRSP1	HRSP3	JSRSP	PCRSP	YRNA
All	k	1.234	1.234	1.234	1.234	1.234
1-hr woody	d^2 (cm)	0.46	0.46	0.43	0.52	0.47
< 0.6 cm	s	0.63	0.63	0.51	0.61	0.57
	a	1.01	1.01	1.01	1.01	1.01
1-hr leafy	d^2 (cm)	0.43	0.43	0.44	0.44	0.43
< 0.6 cm	s	0.68	0.68	0.65	0.63	0.61
	a	1.01	1.01	1.01	1.01	1.01
10-hr woody	d^2 (cm)	1.50	1.45	1.46	1.43	1.11
0.6 - 2.5 cm	s	0.55	0.53	0.54	0.52	0.53
	a	1.01	1.01	1.01	1.01	1.01
10-hr leafy	d^2 (cm)	0.82	0.82	0.89	0.83	0.77
0.6 - 2.5 cm	s	0.60	0.60	0.55	0.59	0.58
	a	1.01	1.01	1.01	1.01	1.01
100-hr	d^2 (cm)	4.48	4.48	4.35	4.16	4.87
2.51 - 7.6 cm	s	0.50	0.50	0.49	0.54	0.50
	a	1.01	1.01	1.01	1.01	1.01
1000-hr	s	0.38	0.38	0.39	0.41	0.40
> 7.6 cm	a	1.00	1.00	1.00	1.00	1.00

$$d_c^2 = \frac{\sum_{i=1}^{n}(P_i \times d_i^2)}{\sum_{i=1}^{n} P_i} \tag{3}$$

where d_c^2 is the composite quadratic mean diameter, P_i (%) is the contribution made by each species to the total particle count, and d^2 is the quadratic mean diameter of each corresponding species.

With respect to Equation 1, s_{oc} is the mean composite specific gravity value of oven-dry particles in each timelag category. Specific gravity of oven-dry particles (s_o) was calculated using Equation 4 (Illston 1994).

$$s_o = \frac{m_o}{V_o \rho_w} \tag{4}$$

where m_o is the oven-dry mass (g) of the particle, V_o is the volume (cm^3) of the particle at oven-dry moisture content, and ρ_w is the density (g cm^{-3}) of water. By multiplying V_o and ρ_w, the mass of a displaced volume of water can be calculated (m_{dw}, g; Equation 5).

$$m_{dw} = V_o \rho_w \tag{5}$$

Using methods described in the laboratory measurements section, above, the mass of water displaced (m_{dw}) by oven-dry particles was measured. Substitution of m_{dw} into Equation 4 yields the following equation for calculation of the oven-dry specific gravity of a particle (s_o):

$$s_o = \frac{m_o}{m_{dw}} \tag{6}$$

Substituting the species-specific estimates of s_o into Equation 3 for all species with particle counts ≥ 5 percent of the total particle counts, allowed for the calculation of the composite specific gravity (Equation 7).

$$s_{oc} = \frac{\sum_{i=1}^{n}(P_i \times s_{o,i})}{\sum_{i=1}^{n} P_i} \tag{7}$$

where s_{oc} is the composite oven-dry specific gravity value, P_i is the percent of particle counts, and s_o is the specific gravity of each corresponding species. Mean composite nonhorizontal angle correction factor, *a*, was estimated using the methods described in the field measurements section above. Slope correction factor, *c*, was calculated using Equation 8.

$$c = \sqrt{1 + (\frac{\text{percent slope}}{100})^2} \tag{8}$$

Nl used in Equation 1 represents the total transect length (m).

Mass (Mg ha^{-1}) of woody particles > 7.6 cm diameter ($M_{>7.6}$; 1000-hr +) was determined using Equation 9, adapted from Brown (1974).

$$M_{>7.6} = \frac{k(\sum d^2) s_{oc} ac}{Nl} \tag{9}$$

where *k* is an equation constant and equal to 1.234 (Van Wagner 1982), Σd^2 is the sum of squared diameters (cm) of all particles > 7.6 cm intersecting the sample transect, s_{oc} is the composite specific gravity value according to the rules and analytic procedures described above, a is the nonhorizontal angle correction factor, c is the slope correction factor, and Nl is the total transect length (m).

Mass estimates of particles > 7.6 cm were converted to dry volume (m^3 ha^{-1}) using methods described by Brown (1974). Prior to calculation, SI mass measurements were converted to the English equivalent in order to use with Equation 10.

$$V_{>7.6} = \frac{32.05 \times M_{>7.6}}{s_{oc}} \tag{10}$$

Where, $M_{>7.6}$ is the mass of particles > 7.6 cm (ton ac^{-1}), and s_{oc} is the composite oven-dry specific gravity value. Following calculation of $V_{>.7.6}$, English estimates were back-converted to their SI equivalent.

Surface and ground detrital mass, bulk density, height, and depth data were compared individually among sites by timelag category, species, category of decay, and forest floor horizon using one-way analyses of variance (ANOVA; Sokal and Rohlf 1995; $\alpha = 0.05$). Potential outlying data points were identified through investigation of box plots and confirmed by calculating the Z-score of each candidate (Triola 2005). Data points with a Z-score < -2 or > 2 were evaluated further to determine if they were the result of collection or entry errors and to determine whether the data could be justifiably removed from the set. Homogeneity of variance among sites was assessed through side-by-side comparison of box plots and tested using Levene's test for relative variation (Schultz 1985; $\alpha = 0.05$). Normality of the data was assessed through the investigation of normal probability plots and tested using the Shapiro-Wilk W-test (Zar 1999; $\alpha = 0.05$). Data that failed to meet any of the previous assumptions of parametric ANOVA were transformed using log and square root functions then reanalyzed (Sokal and Rohlf 1995). When ANOVA detected significant differences among site means, post-hoc Tukey-Kramer HSD tests were used to identify different and similar sites (Sokal and Rohlf 1995). Statistical analyses were completed using the NCSS software (Hintze 2007).

RESULTS

I sampled 8,100 m of transects across the five study sites (Table 6). Since plot estimates were based on the mean of three transects per plot, sample size (i.e. total number of plots) across the five sites was 58 (n = 174 transects). Mass of 1-hr woody and leafy particles ranged between 2.6 and 3.9 Mg ha^{-1} and varied significantly across the five sites (F = 7.21; P < 0.001; Table 7). Volume of 1-hr woody and leafy particles ranged between 2.4 and 7.1 m^3 ha^{-1} among the five sites (Table 7). Relative to the total mass of downed woody detritus, the mass of 1-hr particles represent < 2 percent across all sites (Table 8). Woody 1-hr particles comprised 42.1 to 64.1 percent of the total 1-hr mass among the five sites (coefficient of variation = V < 25%), while leafy 1-hr particles made up 35.9 to 57.9 percent of the total 1-hr mass (18.2% ≤ V ≤ 27.3%). Significant differences in 1-hr woody mass (F = 10.37; P < 0.001; Table 9) and 1-hr leafy mass (F = 14.08; P < 0.001; Table 9) were detected among sites. Significant differences between 1-hr woody and 1-hr leafy mass estimates were found at all sites except PCRSP (Table 9). Of all sites with a difference between 1-hr woody and leafy particles, HRSP1 stood alone as the only site to have more leafy than woody mass (57.9% of 1-hr mass; P < 0.01; Table 9).

Mass of 10-hr particles ranged between 3.2 and 6.1 Mg ha^{-1}, and differed among sites (F = 2.78; P = 0.036; Table 7). Within the five sites, 10-hr mass variation ranged between 36.4 and 44.3 percent of the site means. Volume of 10-hr particles ranged between 6.0 and 12.0 m^3 ha^{-1} among the five sites (Table 7). Less than three percent of

Table 6. Number of plots (*n*) and length of sample transect (individual and total) used for collecting field data within study sites.

Site	*n*	Transects plot^{-1}	Transect length (m)	Total transect length (m)
HRSP1	27	3	50	4050
HRSP3	10	3	50	1500
JSRSP	5	3	50	750
PCRSP	8	3	50	1200
YRNA	8	3	25	600
Total				8100

Table 7. Surface particle mass (± SD) and volume estimates by timelag category among five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Estimates of 1000-hr + particles partitioned by decay category (“DC;” Sollins 1982). Significantly different within-category mass estimates among sites determined from one-way ANOVA ($\alpha = 0.05$) and Tukey-Kramer post hoc tests. Mass estimate superscripts identify significantly different sites.

Category		HRSP1	HRSP3	JSRSP	PCRSP	YRNA	P-value
		($Mg\ ha^{-1}$)					
1-hr	Woody	1.6 (0.4)^{a}	2.2 (0.4)^{b}	2.5 (0.4)^{b}	1.6 (0.4)^{a}	1.5 (0.3)^{a}	< 0.001
	Leafy	2.2 (0.6)^{a}	1.4 (0.3)^{b}	1.4 (0.3)^{b}	1.5 (0.3)^{b}	1.1 (0.2)^{b}	< 0.001
10-hr		6.1 (2.7)^{a}	5.5 (2.0)^{ab}	5.2 (1.9)^{ab}	4.3 (1.7)^{ab}	3.2 (1.3)^{b}	0.04
100-hr		8.8 (4.5)	9.0 (3.9)	5.3 (1.6)	7.7 (2.8)	9.2 (4.2)	0.39
1000-hr +	DC 1	12.8 (38.6)	2.2 (2.3)	0.2 (0.3)	1.8 (2.3)	0.2 (0.6)	0.40
	DC 2	53.9 (81.0)	22.6 (25.4)	8.3 (15.0)	23.6 (19.6)	13.3 (19.4)	0.50
	DC 3	149.8 (115.7)^{a}	88.0 (87.4)^{a}	298.7 (143.6)^{ab}	398.2 (292.6)^{b}	169.6 (165.9)^{ab}	< 0.01
	DC 4	100.2 (108.4)	49.1 (44.9)	53.1 (57.5)	107.6 (89.1)	122.8 (154.7)	0.48
	DC 5	12.8 (23.7)	30.5 (32.1)	25.6 (50.4)	31.4 (37.7)	77.1 (122.6)	0.37
1000-hr + Total		329.5 (208.6)^{ab}	192.3 (173.7)^{a}	385.9 (117.5)^{ab}	562.6 (367.6)^{b}	383.0 (312.0)^{ab}	0.03
Total woody		348.2 (210.9)^{ab}	210.4 (126.3)^{a}	400.3 (118.5)^{ab}	577.7 (366.9)^{b}	398.0 (312.7)^{ab}	0.04
		HRSP1	HRSP3	JSRSP	PCRSP	YRNA	
Category		($m^3\ ha^{-1}$)					
1-hr	Woody	2.5	3.5	4.9	2.6	2.6	--
	Leafy	3.2	2.1	2.2	2.4	1.8	--
10-hr		12.0	10.4	9.6	8.3	6.0	--
100-hr		17.6	17.9	10.8	14.3	18.4	--
1000-hr +	DC 1	33.7	5.8	0.5	4.4	0.5	--
	DC 2	141.9	59.5	21.3	57.6	33.3	--
	DC 3	394.4	231.6	766.2	971.6	424.2	--
	DC 4	263.8	129.2	136.2	262.5	307.1	--
	DC 5	33.7	80.3	65.7	76.6	192.8	--
1000-hr + Total		867.4	506.4	989.9	1372.7	957.9	--
Total woody		902.8	540.3	1017.4	1400.3	986.8	--

Table 8. Composition of downed woody detritus mass by timelag category within five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Offset italicized values represent the amount of 1000-hr + logs partitioned by category of decay; categories adapted from Sollins (1982).

	Site					Study
	HRSP1	HRSP3	JSRSP	PCRSP	YRNA	average
Timelag category	(%)					
1-hr	1.9	1.7	1.0	0.5	0.8	1.2
10-hr	2.9	2.6	1.3	0.8	1.1	1.7
100-hr	3.9	4.3	1.3	1.3	1.9	2.5
1000-hr +	91.3	91.4	96.4	97.4	96.2	94.6
DC 1	*3.9*	*1.2*	*0.1*	*0.3*	*0.1*	*1.1*
DC 2	*16.4*	*11.7*	*2.1*	*4.2*	*3.5*	*7.6*
DC 3	*45.4*	*45.7*	*77.4*	*70.8*	*44.2*	*56.7*
DC 4	*30.4*	*25.5*	*13.8*	*19.1*	*32.1*	*24.2*
DC 5	*3.9*	*15.9*	*6.6*	*5.6*	*20.1*	*10.4*

Table 9. Mass estimates (± SD) of 1-hr particles among five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Within-site differences between 1-hr woody and leafy mass estimates determined from two-sample T-test ($\alpha = 0.05$). Woody mass and leafy mass differences among sites determined from one-way ANOVA ($\alpha = 0.05$) and Tukey-Kramer post hoc tests. Estimate superscripts identify groupings of significantly different sites.

Site	Woody	Leafy	P-value
	------------ (Mg ha^{-1})	------------	
HRSP1	1.6 (0.4)^{a}	2.2 (0.6)^{a}	< 0.001
HRSP3	2.2 (0.4)^{b}	1.4 (0.3)^{b}	< 0.001
JSRSP	2.5 (0.4)^{b}	1.4 (0.3)^{b}	< 0.001
PCRSP	1.6 (0.4)^{a}	1.5 (0.3)^{b}	0.65
YRNA	1.5 (0.3)^{a}	1.1 (0.2)^{b}	< 0.01
P-value	< 0.001	< 0.001	

the total downed woody mass within all sites consisted of 10-hr particles (Table 8). Relative to woody and leafy particle characteristics, woody 10-hr particles made up 97.7 to 100.0 percent of the total 10-hr mass among all sites. Mass of 10-hr leafy particles was negligible at all sites ($\leq$ 0.1 Mg ha^{-1}) and hence, the combined woody and leafy estimate was used in all analyses.

Mass of 100-hr particles across the five sites ranged between 5.3 Mg ha^{-1} at JSRSP and 9.2 Mg ha^{-1} at YRNA (Table 7). Plot estimates varied between 30.2 and 51.1 percent of the mean across all sites. No significant differences were detected in the mass estimates of 100-hr particles among sites ($F = 1.05$; $P = 0.39$; Table 7). Volume of 100-hr particles ranged between 9.4 and 18.4 m^3 ha^{-1} among the five sites (Table 7). 100-hr particles represented between 1.3 and 4.3 percent of total mass across the five sites (Table 8).

Particles > 7.6 cm (i.e. 1000-hr +) contributed the overwhelming majority (mean = 94.6 percent) of mass of downed woody detritus in all study sites (Table 8). Mass estimates of 1000-hr + particles varied tremendously, with estimates ranging between 192.4 and 562.6 Mg ha^{-1} among sites (Table 7). Within the sites, plot estimates ranged between 30.4 and 81.5 percent of the site means. Mass distributions of 1000-hr + particles among plots within each site appear to be approximately normal (Appendix A), supported by the results of the Shapiro-Wilk W-test (Zar 1999), except when partitioned by category of decay (Appendices B - F). The minimum mass of 1000-hr + particles occurred at HRSP3 and the maximum at PCRSP; both sites differed from each other and from the remaining three similar sites (F = 2.86; P = 0.03). Volume of 1000-hr + particles ranged between 506.4 (HRSP3) and 1,372.7 m^3 ha^{-1} (PCRSP) across the five sites (Table 7).

With the exception of one site (HRSP3), particles > 7.6 cm consisted of at least 94 percent coast redwood. Douglas-fir logs at HRSP3 replaced nearly one quarter the mass of coast redwood logs found at HRSP1. Large hardwood logs (Pacific madrone, tanoak, and California bay) were found only at Humboldt Redwoods State Park, the southernmost site. The greatest diversity (species richness) of conifer logs occurred at PCRSP; species included Sitka spruce, Douglas-fir, coast redwood, and western hemlock.

Between nearly one-half and three-quarters of the total 1000-hr + mass among sites was concentrated in particles of intermediate decay (DC 3; Table 8). Across the five decay categories, recently dead logs (DC 1) contributed least to the total mass of 1000-hr logs and ranged between 0.2 and 12.8 Mg ha^{-1} among sites (Table 7). More than 50 percent of decay category one logs were < 20.0 cm diameter across the five sites (Figure 5). Comparison of diameter class distributions among all decay categories revealed that the majority (58.3%) of logs ≥ 200.0 cm diameter were in decay category 3 (Figure 5). Mass estimates were similar across all decay categories among sites with the exception of category three: PCRSP had significantly more mass within decay category three than all other sites (F = 5.72; P = 0.001; Table 7).

Approximately 1,700 logs > 7.6 cm were sampled across the five sites. The mean number of log intersections was 10.8 per 50 m transect across all study sites. Logs > 7.6

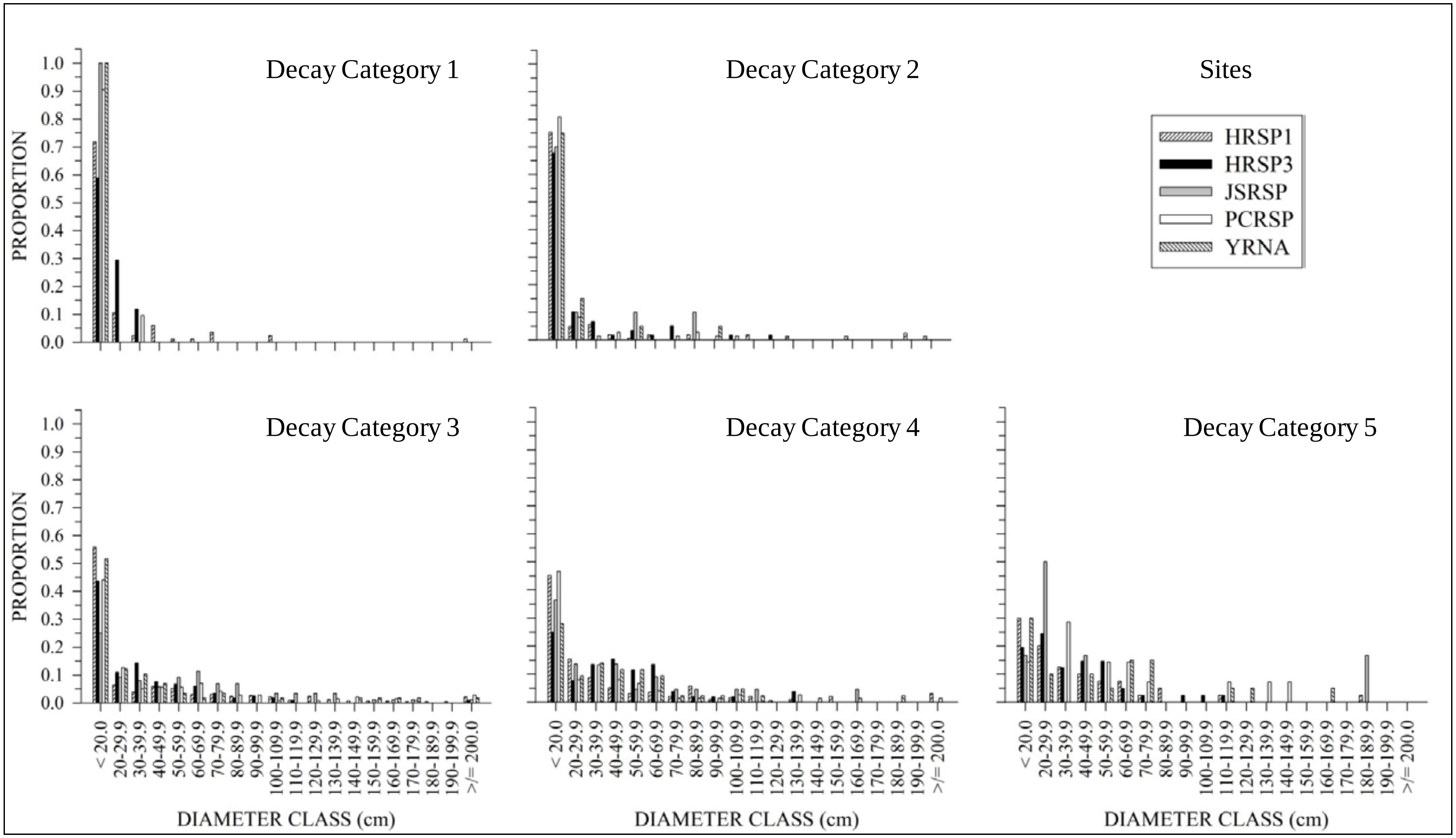


Figure 5. Diameter distribution of large downed logs (> 7.6 cm) in five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Relative frequency histograms given for logs in each of the five categories of decay.

cm followed a negative exponential (reverse J-shaped) diameter class distribution (Figure 6); as the size of the log increased, its total contribution decreased. The spike in the quantity of logs in the largest class (i.e. ≥ 200.0 cm) occurs only as a result of truncation. The largest log sampled during the study was at PCRSP and measured 484.8 cm in diameter at the point of transect intersection. Overall, the greatest amount of 1000-hr + logs across all sites were within the < 20.0 cm diameter class (Figure 6).

Total mass of downed woody detritus was significantly greater at PCRSP (total DWD mass = 577.7 Mg ha^{-1}) than any of the other old-growth stands ($F = 2.77$; $P = 0.037$; Table 7). Total mass ranged between 210.4 and 577.7 Mg ha^{-1} across all sites (Table 7) with variability within sites between 29.6 and 78.6 percent of the mean.

Mass of the litter horizon ranged between 9.6 and 16.7 Mg ha^{-1}; no significant differences were found among sites ($F = 1.77$; $P = 0.154$; Table 10). Bulk density of the litter horizon ranged between 3.6 and 5.6 Mg ha^{-1} cm^{-1} (Table 10) and showed substantial within-site variation between 18.6 and 91.7 percent of the mean estimates (Table 10). No differences in litter bulk density estimates among sites were found ($F = 0.84$; $P = 0.508$; Table 10).

Mass of the duff horizons (fermentation + humus) across the five sites ranged between 9.2 and 33.8 Mg ha^{-1} (Table 10), and showed substantial within-site variation between 53.8 and 129.7 percent of the mean. No significant differences in duff mass were found among study sites ($F = 1.03$; $P = 0.404$; Table 10). Estimates of duff horizon bulk density did not differ and were between 4.1 and 7.5 Mg ha^{-1} cm^{-1} across sites. Within-

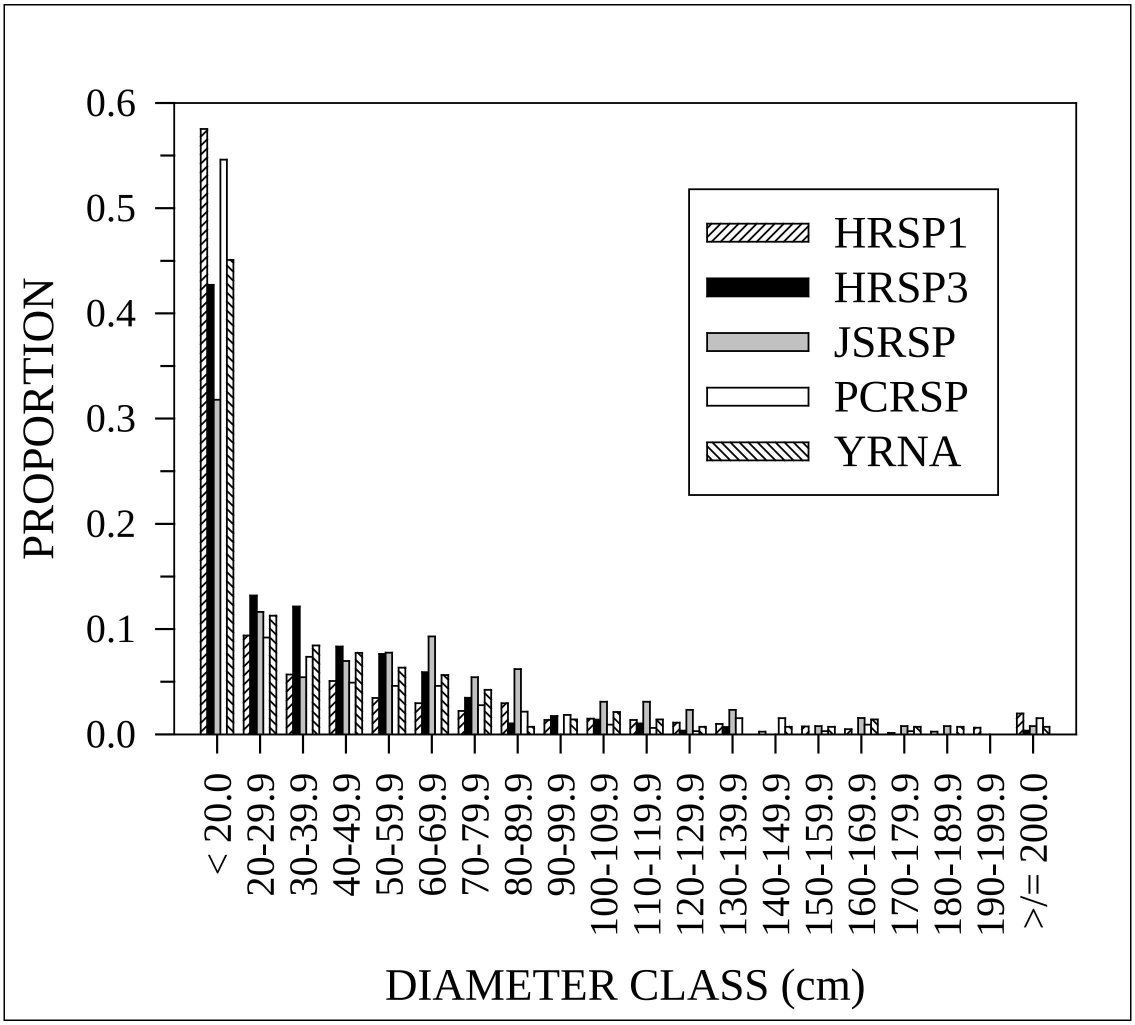


Figure 6. Diameter class distribution of 1000-hr + particles within five old-growth *Sequoia sempervirens* stands. Proportion based on counts of particle intersections. The smallest class (< 20.0 cm) includes particles 7.61 – 19.99 cm. The largest class includes all particles ≥ 200.0 cm.

Table 10. Surface fuel height (± SD), and forest floor depth (± SD), mass (± SD) and bulk density (± SD) estimates in five old-growth *Sequoia sempervirens* stands in northwestern California, USA. Sample intensity (*n*) and collection dates also included. Significantly different within-category estimates among sites determined from one-way ANOVA ($\alpha = 0.05$) and Tukey-Kramer post hoc tests. Estimate superscripts identify groupings of significantly different sites.

	HRSP1	HRSP3	JSRSP	PCRSP	YRNA	P-value
Sample date	09/2006	08/2007	12/2006	01/2007	03/2007	
			Height (cm)			
n	243	90	45	72	72	
Surface fuel	32.3 (21.3)	46.4 (23.7)	41.3 (13.1)	31.2 (12.3)	26.2 (4.5)	0.16
			Depth (cm)			
n	243	90	45	72	72	
Litter	6.6 (1.5)^{a}	5.5 (0.9)^{a}	5.9 (1.4)^{a}	5.0 (1.0)^{a}	9.6 (2.3)^{b}	< 0.001
Duff	3.3 (2.8)^{ab}	5.2 (2.1)^{a}	1.7 (1.0)^{b}	2.4 (0.6)^{ab}	1.3 (1.4)^{b}	< 0.01
Forest floor	9.9 (3.4)	10.8 (2.5)	7.6 (1.3)	7.4 (0.9)	10.9 (3.4)	0.05
			Mass (Mg ha^{-1})			
n	14	10	6	8	8	
Litter	11.5 (4.9)	9.9 (4.8)	13.3 (4.7)	9.6 (10.2)	16.7 (6.1)	0.15
Duff	33.8 (27.4)	32.0 (41.5)	9.2 (9.8)	31.4 (16.9)	20.9 (25.7)	0.40
Forest floor	45.3 (30.2)	41.9 (42.9)	22.5 (9.3)	41.0 (18.0)	37.6 (26.2)	0.62
			Bulk density (Mg ha^{-1} cm^{-1})			
n	14	10	6	8	8	
Litter	4.1 (1.6)	4.8 (2.7)	4.3 (0.8)	3.6 (3.3)	5.6 (3.1)	0.51
Duff	7.1 (2.6)	7.5 (2.9)	4.1 (3.8)	7.0 (1.8)	4.2 (3.9)	0.06
Forest floor	5.7 (2.1)	6.3 (2.5)	4.9 (1.0)	5.8 (1.5)	6.3 (2.9)	0.72
			Bulk density (kg m^{-3})			
n	14	10	6	8	8	
Litter	41.4 (15.8)	48.4 (27.2)	43.3 (7.5)	35.8 (33.0)	56.2 (31.0)	0.51
Duff	70.5 (26.3)	75.3 (29.0)	41.3 (37.7)	69.8 (17.9)	42.4 (39.0)	0.06
Forest floor	57.2 (20.8)	63.0 (25.3)	49.1 (10.1)	57.5 (14.5)	63.1 (28.6)	0.74

site variation in duff bulk density was between 25.7 and 92.7 percent of the mean.

Forest floor mass did not differ across sites and was between 22.5 and 45.3 Mg ha^{-1} (Table 10). Mass of the litter horizon accounted for 23.4 to 59.1 percent of the forest floor mass among sites, while duff contributed 40.9 to 76.6 percent of floor mass. The combined mass of forest floor and surface woody detritus ranged from a low of 252.3 Mg ha^{-1} at HRSP3 to the maximum mass of 618.7 Mg ha^{-1} at PCRSP with litter and duff together accounting for as little as 5.3 to 16.6 percent of the total mass. Bulk density of the forest floors were similar among all sites (F = 0.52; P = 0.732; Table 10) and ranged between 4.9 and 6.3 Mg ha^{-1} cm^{-1}; within-site variation was between 20.4 and 46.0 percent of the mean.

More than 500 surface fuel height and forest floor depth measurements were made across the five sites. The total sample size was reduced (n = 58), however, because plot estimates were based on the mean of three transect estimates per plot, and each transect estimate was based on the mean of three measurements. Surface fuel heights were similar among all sites (F = 1.73; P = 0.16; Table 10), with means ranging between 26.2 and 46.4 cm (Table 10), varying within-site between 17.2 and 65 percent of the mean. Surface fuel heights were greatest at HRSP3 and least at YRNA, the two upland sites under investigation. Depth of the litter horizon was significantly greater at YRNA than at any other site (F = 12.51; P < 0.001; Table 10). Average litter depth ranged between 5.0 and 6.6 cm at the four similar sites, and reached a maximum mean depth of 9.6 cm at YRNA (Table 10). There was minor within-site variation in litter depth across all sites ($16.4\% \le V \le 24.0\%$). Duff depths differed among sites, with the greatest depth at HRSP3 ($F = 4.33$; $P = 0.004$; Table 10). Duff depth averaged between 1.3 and 5.2 cm across sites (Table 10), with a range of within-site variation between 25.0 and 107.7 percent of the mean. Total depth of the forest floor ranged between 7.4 and 10.9 cm and did not differ significantly among sites ($F = 2.56$; $P = 0.05$; Table 10).

DISCUSSION

The mass and volume estimates of downed woody particles > 7.6 cm diameter reported in this study exceed the range of values reported in other studies for Pacific Northwest old-growth forests (Table 11). Across the 8,100 m of transect sampled, 1000-hr + logs contributed the most to the mass of DWD across all sites, ranging from 76 to 91 percent of total DWD mass (Appendix G). Mass of 1000-hr + logs ranged between 192.3 and 562.6 Mg ha^{-1} and volume between 506.4 and 1372.7 m^3 ha^{-1} (Table 7). Because the minimum size requirements of large downed logs are defined inconsistently among studies (e.g., > 7.6, > 10, or ≥ 25 cm diameter), comparisons of mass estimates among studies may be misleading. Data were reanalyzed here to assess the magnitude of difference in mass estimates using various minimum particle diameters. Mass of 1000-hr + logs at PCRSP was estimated using a 25 cm minimum diameter with the result of 548.8 Mg ha^{-1}, a reduction of 2.4 percent relative to the original mass estimated using a 7.6 cm minimum diameter. Mass of 1000-hr + logs ≥ 25 cm at JSRSP decreased 6.6 percent (360.4 Mg ha^{-1}) relative to the original estimate based on a 7.6 cm minimum diameter. The slight reduction in mass estimates from using a larger minimum diameter may be negligible when comparing studies employing diameters between 7.6 and 25 cm.

Though minor, the average mass of 1000-hr + particles at HRSP1 was greater than the values reported in Sugihara (1992) and Busing and Fujimori (2005), likely resulting from differences in the sampling protocols, including differences in the minimum particle diameter defined for each study, and from differences in the mass

Table 11. Mass of downed woody and forest floor detritus reported for various forest types and stand successional stages.

Forest type	Location	Stand successional stage	1-hr	10-hr	100-hr	1000-hr	Litter	Duff	Forest floor	Source
			Mass (Mg ha^{-1})							
Abies concolor	Tulare County, CA, USA	Mature	--	--	--	--	23.9	28.2	52.1	Agee *et al.* (1978)
Abies lasiocarpa	Olympic NP, WA, USA	Mature	1.0	3.8	3.1	19.2[*]	--	--	--	Taylor and Fonda (1990)
Fagus sp.	Maruia Valley, New Zealand	Old-growth	--	--	--	119.4[§]	--	--	--	Stewart and Burrows (1994)
Mixed-conifer	Sequoia NP, CA, USA	Old-growth	--	--	--	67.1[‡]	--	--	--	Harmon *et al.* (1987)
Mixed-oak	Appalachian Range, USA	None stated	0.2	1.5	5.7	4.4[*]	6.3	11.6	17.9	Chojnacky and Schuler (2004)
Pinus jeffreyi	Sequoia NP, CA, USA	Old-growth	--	--	--	28.0[‡]	--	--	--	Harmon *et al.* (1987)
Pinus lambertiana	Tulare County, CA, USA	Mature	--	--	--	--	16.7	27.6	44.4	Agee *et al.* (1978)
Pinus lambertiana	Sequoia NP, CA, USA	Old-growth	--	--	--	32.6[‡]	--	--	--	Harmon *et al.* (1987)
Pinus ponderosa	Tulare County, CA, USA	Mature	--	--	--	--	17.3	31.9	49.2	Agee *et al.* (1978)
Pinus ponderosa	Pinecrest, CA, USA	Mature	--	--	--	--	--	--	49.7	Kittredge (1955)
Pinus ponderosa	Cascade Range, WA, USA	Mature	0.1	2.1	1.7	6.6[*]	--	--	--	Taylor and Fonda (1990)
Pseudotsuga menziesii	Berkeley, CA, USA	Young-growth	--	--	--	--	--	--	30.9	Kittredge (1940)
Pseudotsuga menziesii	H. J. Andrews, Exp. Forest, OR, USA	Old-growth				190.0[‡]	--	--	--	Grier and Logan (1977)
Pseudotsuga menziesii	H. J. Andrews, Exp. Forest, OR, USA	Old-growth	--	--	--	143.0[‡]	--	--	--	Sollins *et al.* (1987)
Sequoia sempervirens	Berkeley, CA, USA	Young-growth	--	--	--	--	--	--	27.7	Kittredge (1940)
Sequoia sempervirens	Humboldt Redwoods SP, CA, USA	Old-growth	1.1	4.3	4.3	58.9[*]	23.3	26.0	49.3	Stuart (1985)
Sequoia sempervirens	Prairie Creek SP, CA, USA	Old-growth	--	--	--	200.0[‖]	--	--	--	Bingham and Sawyer (1988)
Sequoia sempervirens	Humboldt Redwoods SP, CA, USA	Old-growth	--	--	--	299.2[†]	--	--	--	Sugihara (1992)
Sequoia sempervirens	Humboldt Redwoods SP, CA, USA	Old-growth	--	--	--	--	30.0	--	--	Pillers and Stuart (1993)
Sequoia sempervirens	Prairie Creek SP, CA, USA	Old-growth	--	--	--	--	17.7	--	--	Pillers and Stuart (1993)
Sequoia sempervirens	Humboldt Redwoods SP, CA, USA	Old-growth	0.1	1.0	2.0	244.0[*]	--	--	--	Busing and Fujimori (2005)
Sequoia sempervirens	Prairie Creek SP, CA, USA	Old-growth	--	--	--	353.0[‖]	--	--	--	Porter and Sawyer (2007)
Sequoia sempervirens	Yurok RNA, CA, USA	Old-growth	--	--	--	525.6[‖]	--	--	--	Porter and Sawyer (2007)
Sequoiadendron giganteum	Tulare County, CA, USA	Young-growth	--	--	--	--	15.6	15.0	30.6	Agee *et al.* (1978)
Sequoiadendron giganteum	Sequoia NP, CA, USA	Old-growth	--	--	--	--	--	--	64.5	Kittredge (1955)
Sequoiadendron giganteum	Sequoia NP, CA, USA	Old-growth	--	--	--	383.0[‡]	--	--	--	Harmon *et al.* (1987)
Thuja plicata	Western Forest Products, BC, Canada	Old-growth	--	--	--	275.3[‡]	4.3	109.4	113.7	Keenan *et al.* (1993)
Tsuga heterophylla	Western Forest Products, BC, Canada	Young-growth	--	--	--	188.2[‡]	4.1	73.1	77.2	Keenan *et al.* (1993)
Tsuga heterophylla	Olympic NP, WA, USA	Mature	2.2	1.2	0.9	126.6[*]	5.6	10.5	16.1	Agee and Huff (1987)
Tsuga heterophylla	Siuslaw National Forest, OR, USA	Mature	--	--	--	46.6[¶]	--	--	--	Kennedy and Spies (2007)
Tsuga heterophylla	Olympic NP, WA, USA	Old-growth	--	--	--	94.0[†]	--	--	--	Graham and Cromack (1982)
Tsuga heterophylla	Olympic NP, WA, USA	Old-growth	--	--	--	121.0[†]	--	--	--	Graham and Cromack (1982)
Tsuga heterophylla	Olympic NP, WA, USA	Old-growth	2.9	1.1	2.1	452.9[*]	10.5	87.8	98.3	Agee and Huff (1987)

[*]Minimum particle diameter = 7.6 cm
[†]Minimum particle diameter = 10.0 cm
[‡]Minimum particle diameter = 15.0 cm
[§]Minimum particle diameter = 20.0 cm
[‖]Minimum particle diameter = 25.0 cm
[¶]Minimum particle diameter = 30.0 cm

estimators and input values used (Table 11). The slight difference in volume of 1000-hr + particles between this study (volume = 867 m^3 ha^{-1}) and Busing and Fujimori (2005; volume = 797 m^3 ha^{-1}) was also likely related to differences in protocols between studies. The lower mass reported in Stuart (1985), describing a more xeric, upland coast redwood-Douglas-fir stand at HRSP, which most closely resembles HRSP3, was likely the result of productivity and stand structure differences, dissimilar microsite environmental characteristics, and disparate disturbance histories between the two sites. Mass and volume of 1000-hr + particles at PCRSP described by Bingham (1984; volume = 957 m^3 ha^{-1}) for upland old-growth coast redwood stands were also less than the values reported in this study, likely resulting from differences in stand productivity, structure and composition, environmental characteristics, and disturbance history. Compared to a similar alluvial site at PCRSP, Sillett and Van Pelt (2007) found 1,258 m^3 ha^{-1}, 9.1 percent less than the volume reported in this study (Table 7). The average mass and volume of 1000-hr + particles at YRNA reported in this study were less than the values reported for the same area by Porter and Sawyer (2007), likely resulting from differences in protocols and the parameter estimators and input values used.

Compared to other forest types, the productivity, favorable environmental conditions, and the age that coast redwoods attain all contribute to the development of the superlative coast redwood groves and the massive accumulations of DWD therein (Roy 1966, Fujimori 1972, Zinke 1988, Sawyer et al. 2000*a*). The structure and longevity of the living and dead woody components of old-growth coast redwood forests are influenced by both the presence and the exclusion of fire, as well as infrequent high magnitude flood and wind events. The resistance of redwood to decay also contributes to the greater accumulations of DWD in old-growth coast redwood forests compared to other forest types (Clark and Scheffer 1983). Specific to this study, three of the five study sites were located on alluvial flats adjacent to perennial streams, which favor development of the most massive coast redwood stands due to the higher concentrations of soil nutrients and moisture, and tempered disturbance regimes.

Mass of DWD differed between HRSP3 and PCRSP ($F = 2.77$; $P = 0.04$), where the minimum and maximum DWD masses were observed, respectively. HRSP3 was expected to have the minimum mass among sites since this site receives the least annual precipitation, has soils of the driest moisture regimes, spans the highest elevations, and has the least basal area among sites. YRNA, the other upland site, more closely resembles the three alluvial sites in DWD mass and site characteristics. Woody loading was greatest at PCRSP, driven primarily by the substantial mass of 1000-hr + particles of intermediate decay (i.e. DC 3). The largest log was also found at PCRSP (484.8 cm diameter). Though the mass of DWD did not differ significantly among the three alluvial sites ($F = 2.74$; $P = 0.08$), the disparities likely reflect the minor differences in site and environmental characteristics, divergent disturbance histories, and differences in the sampling protocol and estimator input values specific to each site (e.g., specific gravity).

The large quantities of live tree biomass and volume in old-growth coast redwood forests are primary indicators of the potential of DWD accumulations in these forests. Total standing biomass of trees in HRSP1 was between 3,350 and 4,995 Mg ha^{-1} (Busing and Fujimori 2005); the volume of overstory coast redwood trees was 9,272 m^3 ha^{-1}

(Dagley 2008). In a one-ha study area at PCRSP, 4,283 Mg and 10,448 m^3 of aboveground biomass was found, among the greatest values ever reported (Sillett and Van Pelt 2007). The DWD mass estimate at PCRSP, the maximum reported in this study, and exceeding other comparable studies (Table 11), reflects the exceptional live tree biomass reported by Sillett and Van Pelt (2007). Productivity of coast redwood stems at HRSP1 was estimated between 4 and 5 Mg ha^{-1} yr^{-1}, with total tree productivity across all species between 7 and 10 Mg ha^{-1} yr^{-1} (Busing and Fujimori 2005).

The coefficient of dispersion (*CD*; Sokal and Rohlf 1995) was used to describe the spatial distribution of 1000-hr + logs: when $CD < 1$, 1000-hr + particles are distributed uniformly throughout the site; when $CD = 1$, particles are distributed randomly (Poisson distribution); when $CD > 1$, particles are spatially aggregated. The *CD* of 1000-hr + particles ranged among sites between 35.8 and 254.1 (Appendix H), suggesting that DWD > 7.6 cm diameter are clumped across all sites, a common feature of other forest types (e.g., Harmon et al. 1986, Grove 2001, Böhl and Brändli 2007).

Spatial distributions of 1000-hr + particles are dependent upon the spatial structure of the contributing overstory, and patterns of input, such as from aggregated wind mortality, localized insect outbreak and spread of pathogens (Harmon et al. 1986). Since the structural characteristics of DWD populations tend to reflect the structural characteristics of the living forest (Spies et al. 1988), the spatial distribution of trees in these sites should indicate the spatial characteristics of DWD. Overstory trees of all sizes were distributed uniformly throughout HRSP1 (Dagley 2008) and lacked spatial variation at YRNA (Taylor 1982). The uniform spatial distribution of overstory trees is also reflected in the nearly uniform distribution of particles ≤ 7.6 cm diameter across all sites. Large logs were clumped at each site ($35.8 \leq CD \leq 254.1$), indicating that small-scale, patchy disturbances affecting individual or small groups of trees regulates the spatial distribution of large DWD in old-growth coast redwood forests. The lack of clumping of 1000-hr + decay category 1 logs in all sites other than HRSP1 indicated by the coefficient of dispersion (Appendix H) may be misleading as a result of error introduced by the small sample sizes.

In comparison to all species identified, coast redwood logs contributed the majority of the 1000-hr + log mass, ranging between 75 and 100 percent among sites (Appendix I). Three studies have reported similar findings for the species composition of 1000-hr + logs, ranging between 84 and 90 percent coast redwood (Bingham 1984, Porter 2002, Sillett and Van Pelt 2007).

The composition of 1000-hr + particle mass mirrored the overstory basal area (Appendices I and J). The most substantial disproportionate basal area-1000-hr + mass relationship was associated with Douglas-fir at HRSP3, where it made up only 9.7 percent of the overstory basal area, but comprised 21.6 percent of the 1000-hr + mass. The substantial difference between these two compositional values, relative to the minor differences among all other species and site comparisons, suggests that the presence of Douglas-fir in the overstory is being reduced in this stand (i.e. Douglas-fir mortality and log recruitment rates are greater than the regeneration rate of this species).

Coast redwood was the only species contributing 1000-hr + logs > 110 cm diameter, although Douglas-fir logs were as large as 110 cm diameter (Appendix K).

Other than coast redwood and Douglas-fir, 1000-hr + logs contributed by all other species were less than 50 cm in diameter (Appendix K). Diameters of 1000-hr + logs exhibited a negative exponential (reverse J-shaped) distribution across all sites, with the majority of particles between 7.6 and 20.0 cm diameter, ranging between 32 and 58 percent of the total number of intersections (Figure 6; Appendix L). The negative exponential, positively skewed diameter distribution of logs has also been found in other old-growth forests, and is likely a reflection of overstory structure (Harmon et al. 1986, Oliver and Larson 1996, Grove 2001, Feller 2003, Rahman et al. 2008). As expected, the diameter distribution of overstory trees at HRSP1, reproduced from Sugihara (1992), reflects the reverse J-shaped distribution of 1000-hr + logs, with the majority concentrated in the < 30 cm diameter class while larger classes contained successively fewer individuals. The average diameter of all 1000-hr + coast redwood logs at HRSP1 was only 38.1 cm, substantially less than the average diameter of overstory trees (240.4 cm DBH) reported by Fujimori (1977), suggesting that the majority of 1000-hr + particles at HRSP1 consists of dead small trees, as well as fallen limbs, branches, and reiterated trunks from the large trees in the canopy (Sillett and Van Pelt 2007).

Small-scale disturbances prevent steady state conditions and create structural heterogeneity within DWD (Spies et al. 1988, Stewart and Burrows 1994). Disturbances (wind, fire, and flood) and decay-causing organisms in old-growth forests regulate DWD dynamics (Harmon et al. 1986, Busing and Fujimori 2005). Since the mid 1900’s, however, fire has been essentially removed from coast redwood forests (e.g., Stuart 1987, Brown and Swetnam 1994, Brown and Baxter 2003), shifting the burden of regulating

DWD to decay-causing organisms. As a result, one should expect greater accumulations of DWD in today's old-growth coast redwood forests relative to pre-suppression forests.

Of the species comprising 1000-hr + particles across sites, no *Abies grandis* (grand fir) logs in advanced decay stages (DC 4 and 5) were found; 63 percent of *Arbutus menziesii* (Pacific madrone) showed no signs of decay (DC 1), and nearly 50 percent of particle intersections of the other species present were decay category 3 (Appendix M). The majority of 1000-hr + particles were of intermediate decay, ranging between 44.3 and 77.4 percent of the total mass among sites (Table 7, Appendix N). Bingham and Sawyer (1988) and Porter (2002) also reported the greatest quantity of log mass at PCRSP and YRNA consisted of particles of intermediate decay, akin to other studies in Pacific Northwest forests (e.g., Harmon et al. 1986, Spies et al. 1988, Feller 2003). Comparing conifer regeneration on logs of all decay categories, seedling density is greatest on category 3 logs (Porter 2007), which were the most abundant logs across all sites reported here, influencing the structural characteristics of regenerating stands by providing a source for recruitment of young trees into the overstory canopy (Bingham 1984, Porter 2002). The exclusion of fire in coast redwood ecosystems may have increased the importance of DWD and nurse logs for seedling recruitment. Indeed, western hemlock and other fire-intolerant species dominate redwood nurse logs (Porter 2002); these species would otherwise struggle to persist in a fire regime characterized by surface fires at intervals reported in the region's forests (Stuart 1987, Brown and Swetnam 1994, Brown et al. 1999, Brown and Baxter 2003, Stephens and Fry 2005).

Across sites, large log mass was normally distributed among decay categories [Shapiro-Wilk W-test ($\alpha = 0.05$): $0.12 \leq P \leq 0.42$; Appendices B - F], with the majority concentrated in decay category 3 (Appendix N). The normal distribution of 1000-hr + particles suggests that the residence time of large DWD in old-growth coast redwood forests increases geometrically with successive categories (Harmon et al. 1986). Since coast redwood comprises the majority of 1000-hr + logs in old-growth coast redwood forests, residence time is expected to be long due to the natural decay resistance of coast redwood heartwood (Clark and Scheffer 1983).

Decay category one 1000-hr + logs were scarce at all sites (0.1 to 1.1% of 1000-hr + mass), except HRSP1 where 12.8 Mg ha^{-1} (3.9% of 1000-hr + mass) were found. The mass at HRSP1 was driven by four plots that contained relatively large quantities (> 20 Mg ha^{-1}) of 1000-hr + decay category 1 particles; two of these plots had > 80 Mg ha^{-1}. HRSP1 plot 10 contained the greatest load of 1000-hr + decay category 1 particles (mass = 188 Mg ha^{-1}), generated by the uprooting and recruitment of one large (216 cm diameter at point of intersection) coast redwood tree (Figure 7). Overturned trees are common in old-growth coast redwood forests, especially in alluvial areas such as HRSP1, where wind is frequent and the soil is perennially moist (Boe 1966, Roy 1966, Busing and Fujimori 2005). The second greatest plot mass of 1000-hr + decay category 1 logs (mass = 81 Mg ha^{-1}) was plot 27 at HRSP1, where a large diameter old-growth coast redwood tree had broken 3 m up the stem and fallen, likely the result of a combination of fire effects and wind or mechanical imbalance (Finney 1991). Across all sites, the other 1000-hr + decay category 1 logs consisted of small diameter stems and branches likely

Figure 7. A large downed 1000-hr + decay category 1 log at HRSP1 Plot 10; the massive root wad is visible on the left.

abscised from the stems and crowns of living and standing dead overstory and midstory trees, or from recently dead and recruited understory and midstory trees.

The quantity of 1000-hr + decay category 5 particles was greatest at the two upland sites (HRSP3 and YRNA; Table 10; Appendix N). Site and environmental characteristic differences, and composition of DWD-contributing species (i.e. more tanoak and Douglas-fir) are the likely causes of the greater presence of decay category 5 particles in the upland sites.

Particles of decay categories 1 through 4 followed a negative exponential diameter distribution across all sites (Figure 5). The least decayed 1000-hr + particles across sites were also the smallest particles in the 1000-hr + timelag category, and recently fallen large trees were rare (Figure 5 and Appendix O). The majority of 1000-hr + decay category 5 particles across sites were < 80.0 cm, and no particles > 200.0 cm were found in this most advanced stage of decay, the only category with the latter observation (Figure 5).

The mode and rate of mortality control the input rate of DWD in coast redwood forests. Busing and Fujimori (2002) estimated that the annual rate of mortality of coast redwood trees ≥ 10 cm DBH in HRSP1 was 0.41 stems ha^{-1}, of which 76 percent was recruited to the forest floor (i.e. treefalls), the remainder died standing. Average annual input of 1000-hr + particles over a 29 year period in HRSP1 ranged between 5.7 and 6.9 Mg ha^{-1}; total input over the study period was between 166 and 199 Mg ha^{-1} (Busing and Fujimori 2005). The recruitment rate of 1000-hr + particles at HRSP1 was substantially greater than other forests in the Pacific Northwest (between 1.5 and 4.5 Mg ha^{-1} yr^{-1};

Grier 1978, Sollins 1982). The rarity of recently dead and downed (DC 1 or 2), large old-growth coast redwood trees throughout the study sites provides evidence for infrequent and isolated mortality of overstory trees, and the infrequent recruitment of recently dead trees to the forest floor. Relative to the amount of 1000-hr + log mass concentrated in decay categories 2 through 4, the absence of decay category 1 particles is obvious (Appendix N). The large coefficients of variation (V = 302%; Appendix P) and dispersion (CD = 116.4) of decay category 1 particles at HRSP1 strongly suggests that these logs were infrequent and spatially aggregated. The diameter distribution of 1000-hr + decay category 1 logs indicates that the least decayed particles across sites were also the smallest particles in the 1000-hr + timelag category, and recently dead and downed large trees (i.e. > 100 cm diameter) were rare (Figure 5; Appendix O).

If there is greater mortality in the stand than inferred from the negligible amount of decay category 1 logs on the forest floor, the dead individuals must be standing, which suggests that the agents of mortality of large old-growth coast redwood trees must kill them standing, where they persist in the overstory progressing through the first one or two stages of decay, and are then recruited to the floor by stochastic events (e.g., wind, fire, or structural failure). Similarly, mortality in old-growth Douglas-fir forests of the Pacific Northwest may be such that trees commonly die standing, followed by recruitment of DWD of moderate to advanced stages of decay (Spies et al. 1988). Long-term study of old-growth coast redwood forests is needed in order to confirm the dynamics of individual tree mortality and DWD recruitment mechanisms.

Fine woody detritus (FWD), downed woody particles $\leq$ 7.6 cm diameter, contributed a minor amount to the total DWD accumulations in the sites reported here, ranging between only 2.4 and 7.2 percent (Appendix G). The greater diversity and frequency of understory and midstory trees at HRSP1 and HRSP3 relative to the northern sites (Table 3) likely contributed to the greater amount of FWD in these sites. 1-hr particles accounted for 17.3 to 27.1 percent, 10-hr particles between 21.3 and 36.1 percent, and 100-hr particles between 36.8 and 61.3 percent of the total FWD mass among sites (Appendix G). Combined with the mass of forest floor detritus (i.e. litter and duff), FWD accounted for 26.9 to 39.0 percent of the total mass across sites (Appendix G), highlighting the magnitude of forest floor detritus accumulations in old-growth coast redwood forests.

The mass of FWD was normally distributed across sites (Shapiro-Wilk W-test; $\alpha = 0.05$; Appendices B - F; Figure 8) and size classes, except for 10-hr particles at HRSP1, and 1-hr leafy particles at HRSP3 and JSRSP, suggesting little variation in the mass of these particles among plots within each site. Other than 10-hr particles at HRSP1, which were distributed randomly ($CD = 1.20$), 1-hr and 10-hr particles were distributed uniformly across sites ($0.04 \leq CD \leq 0.73$; Appendix H). The variation of 1-hr and 10-hr particle masses among plots was mild across sites ($16.2\% \leq V \leq 44.8\%$; Appendix P); the greatest variation was associated with 10-hr particles at HRSP1, where 10-hr mass was also greatest. There was moderate evidence that 100-hr particles were clumped at HRSP1 ($CD = 2.3$), HRSP3 ($CD = 1.7$), and YRNA ($CD = 1.9$), strong evidence of a random

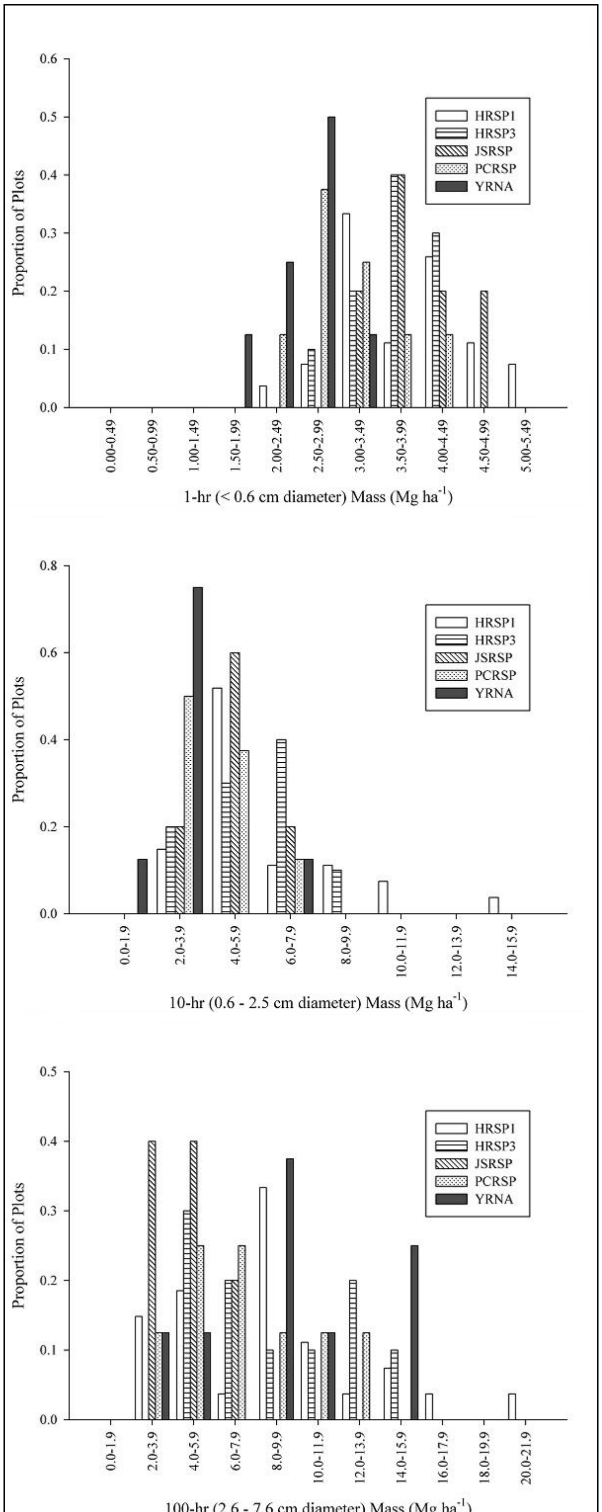


Figure 8. Frequency of FWD mass (Mg ha^{-1}) estimates among sample plots in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California.

distribution at PCRSP (*CD* = 1.0), and strong evidence of a uniform distribution at JSRSP (*CD* = 0.5).

Mass estimates of FWD are limited for old-growth coast redwood forests; of those that exist, both were completed at Humboldt Redwoods State Park. Near HRSP1, Busing and Fujimori (2005) found 3.1 Mg ha^{-1} of FWD, substantially less than the values reported in this study for the same site. Estimate differences are likely the result of the small sample size (total transect length = 800 m) used by Busing and Fujimori (2005), as well as the relatively smaller size of their sample area, and their use of default specific gravity and quadratic mean diameter values (Brown 1974) to estimate volume and mass. Stuart (1985) found 9.7 Mg ha^{-1} of FWD in an upland site most closely resembling HRSP3, where 18.1 Mg ha^{-1} of FWD was found. The difference between these two studies was driven by the greater mass of 100-hr particles found at HRSP3, likely the result of differences in the vegetation composition between the two sites. Relative to estimates of FWD in other forest types outside the redwood region, the mass estimates reported in this study tend to be greater across all timelag categories, especially 100-hr particles (Table 11).

The increasing availability of light along a vertical gradient from the bottom of the crown to the top gives rise to foliar morphological variation and the development of awl-like leaf arrangements, characteristics of leafy particles, in the upper crowns of old-growth redwoods (Jennings 2002, Mullin 2008), giving rise to mass accumulations of 1-hr leafy particles between 1.1 and 2.2 Mg ha^{-1} among sites (Table 7). HRSP1 was the only site where the mass of 1-hr leafy particles was statistically greater than the mass of

1-hr woody particles (Table 9); the ratio of 1-hr woody mass to 1-hr leafy mass was 0.73. At all other sites, except PCRSP, where there was no difference, mass of 1-hr leafy particles was less than the mass of 1-hr woody particles; the ratio of 1-hr woody mass to 1-hr leafy mass ranged between 1.07 at PCRSP to 1.79 at JSRSP. The greater specific gravity of 1-hr leafy particles relative to woody particles (Table 5) and the greater quadratic mean diameter of 1-hr woody particles relative to leafy particles (Table 5), likely resulted in a combined effect that reconciled the mass estimate differences between the two particle types. The large accumulation of leafy particles at HRSP1 and HRSP3 may be a reflection of differences in light availability between the sunny southern sites and the foggy northern sites that are nearer to the coast. The effect that the two 1-hr particle types have on fire behavior and fire effects in old-growth coast redwood forests deserves investigation, particularly considering the substantial quantities and variation reported here and the importance of 1-hr fuels to fire spread (Rothermel 1983).

Mass of the forest floor ranged between 22.5 and 45.3 Mg ha^{-1} across sites while bulk density ranged between 4.9 and 6.3 Mg ha^{-1} cm^{-1} (Table 10). There was strong evidence that mass and bulk density of the forest floor, whether partitioned by stratum or combined, did not differ among sites (Table 10). Forest floor mass and bulk density estimates were similar to previous estimates of old-growth coast redwood stands (Stuart 1985, Finney and Martin 1993), and other forests (Table 11).

Litter and duff accounted for the majority of FWD and forest floor mass across sites (Appendix G). Duff accounted for 74.6 to 76.6 percent of the forest floor mass at HRSP1, HRSP3, and PCRSP, while only accounting for 40.9 percent at JSRSP and 55.6

percent at YRNA. Substantial duff accumulations were found at HRSP1 and HRSP3, which comprised 8.6 and 12.7 percent of the total DWD mass at each site, respectively. Duff mass varied the most among plots within sites (53.8% $\leq V \leq$ 129.7%), relative to other forest floor mass and bulk density estimates (12.2% $\leq V \leq$ 107.7%). Forest floor mass, especially duff mass (9.1 $\leq CD \leq$ 53.8), was aggregated within each site, with areas of similar mass characteristics clumped together. Considering that the presettlement fire return interval at HRSP is approximately 25 years (Stuart 1987), and fire has been excluded from the forest since at least 1950, large quantities of duff at HRSP1 and HRSP3 may indicate that the southern sites are not within their historical fire return interval. The northern sites, which are wetter and closer to the coast, may have fire return intervals as long as 500 years (Veirs 1982), and therefore the effects of fire exclusion on DWD may not yet be realized.

Surface fuel height ranged between 26.2 and 46.4 cm among sites (Table 10). Similar to forest floor depth, the tallest and shortest heights of surface fuels were at the two upland sites. Within each site, areas of similar surface fuel height appear to be spatially clustered (4.2 $\leq CD \leq$ 14.0), except at YRNA where surface fuel heights were nearly random among sample plots (CD = 0.8).

Aside from the site, structural, environmental, and disturbance characteristics that give rise to DWD in coast redwood forests, error associated with the sampling protocol may contribute to differences among site estimates in this study as well as the differences among previous studies that overlap the sites reported here. Deviations in the sample method (e.g., LIS and fixed area plots) and design (e.g., single or radial transect arrangements, transect length, and plot location strategy) influence variation in the sample data and the potential for committing a Type I or Type II error. Application of an appropriate sampling protocol is fundamental to increase estimate precision of DWD structural characteristics in old-growth coast redwood forests.

According to Brown (1974), LIS mass estimate accuracy can be improved by employing a LIS design that guarantees at least one 1000-hr + particle is intersected by more than three-fourths of the sample transects and at least 35 to 50 intersections over an entire sampled area. Across all sites, except YRNA, the mean count of 1000-hr + particle intersections along each 50 m sample transect ranged between 8.6 and 13.6 and total number of intersections between 129 and 810, exceeding Brown's (1974) minimum precision requirements, which suggests that the LIS design used during this study was sufficient (Appendix Q). The mean number of 1000-hr + intersections was 5.9 and total intersections was 142 at YRNA where 25 m sample transects were used. Among all sites, there was no significant difference in the mean number of 1000-hr + particle intersections ($F = 1.72$; $P = 0.16$; Appendix Q).

Accuracy of the estimates and appropriateness of the sampling protocol used during this study was assessed through the percent error (i.e. the ratio of the standard error to the mean estimate expressed as a percent). Brown (1974) suggests that percent sampling error < 20 is sufficient for most fire-ecology applications but should be reduced 5 or 10 percent for other purposes requiring greater estimate precision. The percent error of 1-, 10-, and 100-hr estimates was ≤ 16.9 percent across sites, inferring that the sample design employed (i.e. length, arrangement, intensity, and distribution of sample transects) met the minimum precision requirements (Appendix R). The percent error associated with 1000-hr + logs at HRSP1, HRSP3, and JSRSP was ≤ 20.1 percent, but increased to 23.1 percent at PCRSP, and 28.8 percent at YRNA (Appendix R). The increased percent error at PCRSP may be a result of the method used to locate sample points; at YRNA, the increase is likely the result of the shorter transect length only (25 m). When 1000-hr + logs were partitioned by decay category, the percent error was substantially increased for categories one, two, four, and five, not surprising considering these particles were less common than decay category 3 logs (Appendix R). All other design attributes remaining constant, estimate accuracy can be improved for 1000-hr + logs in old-growth coast redwood forests by employing longer sample transects in order to reduce the variation between plots.

Error may be introduced to DWD estimates from the parameter estimator employed (e.g., Van Wagner 1968, Brown 1974) and the use of default or site-specific input values. Accuracy of mass estimates using Brown (1974) will be improved through the measurement of site-specific correction factors for particle specific gravity, transect slope, deviation of particles away from the horizontal plane that they are assumed to lie within, and with the use of quadratic mean diameter instead of the arithmetic mean diameter of sample particles (Kane et al., in press). Alternatively, users of Brown (1974) are offered default estimator input values to use in lieu of site-specific values. The volume estimator given in Van Wagner (1968), commonly used in DWD studies, requires the measurement of diameter and transect length, which are part of the basic sample protocol for any LIS method, but lack correction factors for nonhorizontal particles, and uses the arithmetic mean instead of the quadratic mean diameter. Mass estimates using Van Wagner (1968) are calculated by multiplying volume by the particle specific gravity. Depending on the estimator used, and the choice to use default or site-specific input values, the magnitude of error may contribute to differences among site estimates in this study as well as the differences among previous studies that overlap the sites reported here.

Correction factors for slope (*c*) are required for estimates using Brown (1974), but squared quadratic mean diameter (d^2), specific gravity (*s*), and nonhorizontal particle angle (*a*) may be measured (Table 5) or based on given default values (Table 12). Mass estimates for DWD in HRSP1 using default input values and using measured input values were compared using a two sample T-test (Sokal and Rohlf 1995; $\alpha = 0.05$). Site-specific inputs resulted in significantly greater mass estimates of 1-hr woody and leafy, and 100-hr particles when compared to estimates using default values, ranging between 32 and 162 percent (Table 12). There was strong evidence that 1000-hr + mass estimates did not differ ($T = 0.48$; $P = 0.64$) when either default or site-specific input values were used (Table 12). Because mass was calculated for all 1000-hr + particles, and not partitioned by category of decay, the default input value used was 0.35, the mean of the sound (0.40) and rotten (0.30) specific gravity values provided. This value approximated the mean composite specific gravity value measured at HRSP1 (0.38; Table 5), which represented an average for particles in all decay categories.

Table 12. Default downed woody detritus mass estimator input values (Brown 1974), and site-specific arithmetic average diameter and specific gravity (*s*) of coast redwood (*Sequoia sempervirens*) DWD by timelag category in five old-growth stands in northwestern California, U.S.A. Significantly different estimates among sites determined from one-way ANOVA ($\alpha = 0.05$) and Tukey-Kramer post hoc tests. Results of two-sample T-tests ($\alpha = 0.05$) comparing mass (Mg ha^{-1}) estimate differences at HRSP1 using measured (site-specific; this study) vs. default estimator input values are also given.

	1-hr woody	1-hr leafy	10-hr woody	10-hr leafy	100-hr	1000-hr +
Default inputs (Brown 1974)						
d^2 (cm)	0.097	0.097	1.865	1.865	17.806	--
s	0.48	0.48	0.48	0.48	0.40	0.30-0.40
a	1.13	1.13	1.13	1.13	1.13	1.00
SESE specific gravity ANOVA						
HRSP	0.63 [a]	0.68 [a]	0.51	0.60 [b]	0.50 [ab]	0.38
JSRSP	0.61 [ab]	0.65 [ab]	0.53	0.55 [a]	0.49 [a]	0.39
PCRSP	0.61 [ab]	0.63 [bc]	0.52	0.59 [bc]	0.54 [b]	0.41
YRNA	0.59 [b]	0.61 [c]	0.53	0.58 [c]	0.50 [ab]	0.42
P-value	0.06	< 0.01	0.55	< 0.01	0.02	0.57
SESE average diameter ANOVA						
HRSP (cm)	0.45 [a]	0.42	1.40 [a]	0.81 [ab]	4.27	38.09 [a]
JSRSP (cm)	0.47 [ab]	0.43	1.39 [a]	0.87 [a]	4.34	52.72 [b]
PCRSP (cm)	0.51 [b]	0.43	1.30 [ab]	0.82 [ab]	4.01	38.01 [a]
YRNA (cm)	0.47 [ab]	0.41	1.04 [b]	0.77 [b]	4.63	40.05 [ab]
P-value	0.02	0.66	< 0.01	0.01	0.14	0.01
HRSP1 T-test for mass estimate differences generated from site-specific and default input values						
Site-specific (Mg ha^{-1})	1.57	2.17	6.06	0.03	8.79	329.49
Default (Mg ha^{-1})	0.60	0.88	5.03	0.07	6.65	303.48
P-value	< 0.01	< 0.01	0.07	0.03	0.03	0.64
Percent change	161.7	146.6	20.5	(57.1)	32.2	8.6
HRSP1 T-test for mass estimate differences generated from min/max nonhoriz. angle corr. factors						
a = 1.00	1.56	2.15	6.07	0.03	8.71	--
a = 1.13	1.76	2.43	6.86	0.03	9.84	--
P-value	0.10	0.15	0.27	0.78	0.42	--
HRSP3 T-test for mass estimate differences generated from min/max nonhoriz. angle corr. factors						
a = 1.00	2.24	1.39	5.65	--	8.67	--
a = 1.13	2.53	1.57	6.39	--	9.80	--
P-value	0.17	0.29	0.41	--	0.53	--
JSRSP T-test for mass estimate differences generated from min/max nonhoriz. angle corr. factors						
a = 1.00	3.72	1.34	5.20	0.10	5.55	--
a = 1.13	4.20	1.51	5.88	0.11	6.27	--
P-value	0.41	0.44	0.62	0.87	0.71	--
PCRSP T-test for mass estimate differences generated from min/max nonhoriz. angle corr. factors						
a = 1.00	1.56	1.48	4.24	0.06	7.59	--
a = 1.13	1.77	1.67	4.80	0.06	8.57	--
P-value	0.37	0.47	0.54	0.85	0.63	--
YRNA T-test for mass estimate differences generated from min/max nonhoriz. angle corr. factors						
a = 1.00	1.58	1.05	3.20	0.01	9.07	--
a = 1.13	1.79	1.18	3.62	0.01	10.25	--
P-value	0.41	0.32	0.55	0.93	0.65	--

Values of coast redwood specific gravity differed among all sites for 1-hr woody, 1-hr leafy, 10-hr leafy, and 100-hr particles (Table 12), suggesting the need to estimate these values specifically for each site under investigation. Results suggest that the use of measured, default, or the complete exclusion of the nonhorizontal angle correction factor from mass estimates does not produce significantly different results (Table 12). Though it may not be necessary to measure the nonhorizontal angle in old-growth coast redwood DWD populations, it is necessary to measure specific gravity and quadratic mean diameter for all species and size categories in order to reduce the potential for under or overestimating mass and volume.

CONCLUSIONS

The mass of DWD averaged 425 Mg ha^{-1} across the five study sites, and reached a maximum of 618.7 Mg ha^{-1} at PCRSP, 11 percent greater than any previously published DWD mass estimate (Table 11). Forest floor mass averaged 37.7 Mg ha^{-1} among sites, 9.7 percent of DWD mass. Duff accounted for 75.5 percent of the forest floor mass at HRSP1 and HRSP3, perhaps reflecting that these stands are outside of their historical fire return interval. Mass of fine woody detritus, also greater than any previously published estimates (Table 11), averaged 4.2 percent of the DWD loading among sites, of which 50.8 percent consisted of uniformly distributed 1-hr and 10-hr particles, providing a homogeneous fuelbed able to sustain surface fire given the necessary environmental conditions. Clusters of big logs contributed an average of 86.0 percent of DWD mass across sites, 75 to 100 percent of which consisted of coast redwood logs. Clustering of large logs across study sites likely reflects the small scale, patchy disturbance regime affecting individual or small groups of trees in old-growth coast redwood forests.

Though large logs drove the massive accumulations of DWD in the study stands, up to 58 percent of the 1000-hr + intersections were < 20 cm diameter. The mean diameter of 1000-hr + logs among sites was 40.4 cm, within the range of mean diameters for understory and midstory trees (Sugihara 1992), indication that 1000-hr + logs were mostly small diameter, and that the largest logs (i.e. > 200 cm diameter) were infrequent across sites. Large woody particles followed a negative exponential diameter distribution across all sites and decay categories other than DC 5, further illustration of the predominance of small diameter logs. These distributions also highlighted the minor presence of particles in early decay stages (i.e. DC 1 and 2), of which approximately 50 percent were < 20 cm diameter. The rarity of particles in early decay stages, which also tended to be clustered within each site, further indicates that mortality of large overstory trees in the study stands is infrequent and isolated. If mortality is greater than what can be inferred from the few undecayed logs sampled, dead trees must be standing, where they progress through the preliminary stages of decay (i.e. DC 1 and 2) and are eventually recruited to the forest floor in decay category 3 or later.

Because coast redwood trees are long-lived, any investigation of the dynamics of forest processes, such as mortality and log recruitment, will require long term study achieved through the creation and monitoring of permanent plots. Ecological studies are needed in coast redwood forests to balance the tradeoffs between the mass and volume of DWD necessary for maintaining ecosystem processes (Harmon 2001, Harmon 2002) with fuel-related fire hazard concerns (Lehmkuhl et al. 2007) in order to converge the two, often opposing perspectives (Mount 2002). DWD accumulations need to be investigated among environmental and topographic gradients, for all stand ages, throughout the range of coast redwood in order to complete our understanding of DWD structure and dynamics. The first step in achieving a complete and accurate survey of coast redwood DWD will require determination of an appropriate sample protocol that can be repeated among studies. Once the structure of coast redwood DWD has been described, investigation will be needed to determine the dynamics of the large and small particles (e.g., diurnal and seasonal moisture dynamics, input and decay rates, and changes in physical properties as decay progresses) in order to understand and predict disturbances and associated effects (e.g., fire effects) in these forests. With a clear understanding of the structure and dynamics of DWD in coast redwood forests, fire managers and researchers, ecologists, and natural resource managers will have the tools necessary to implement precision protocols for the management of detritus populations and forest disturbances, including both wild and prescribed fire, in order to achieve a diversity of ecosystem management and monitoring objectives.

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PERSONAL COMMUNICATIONS

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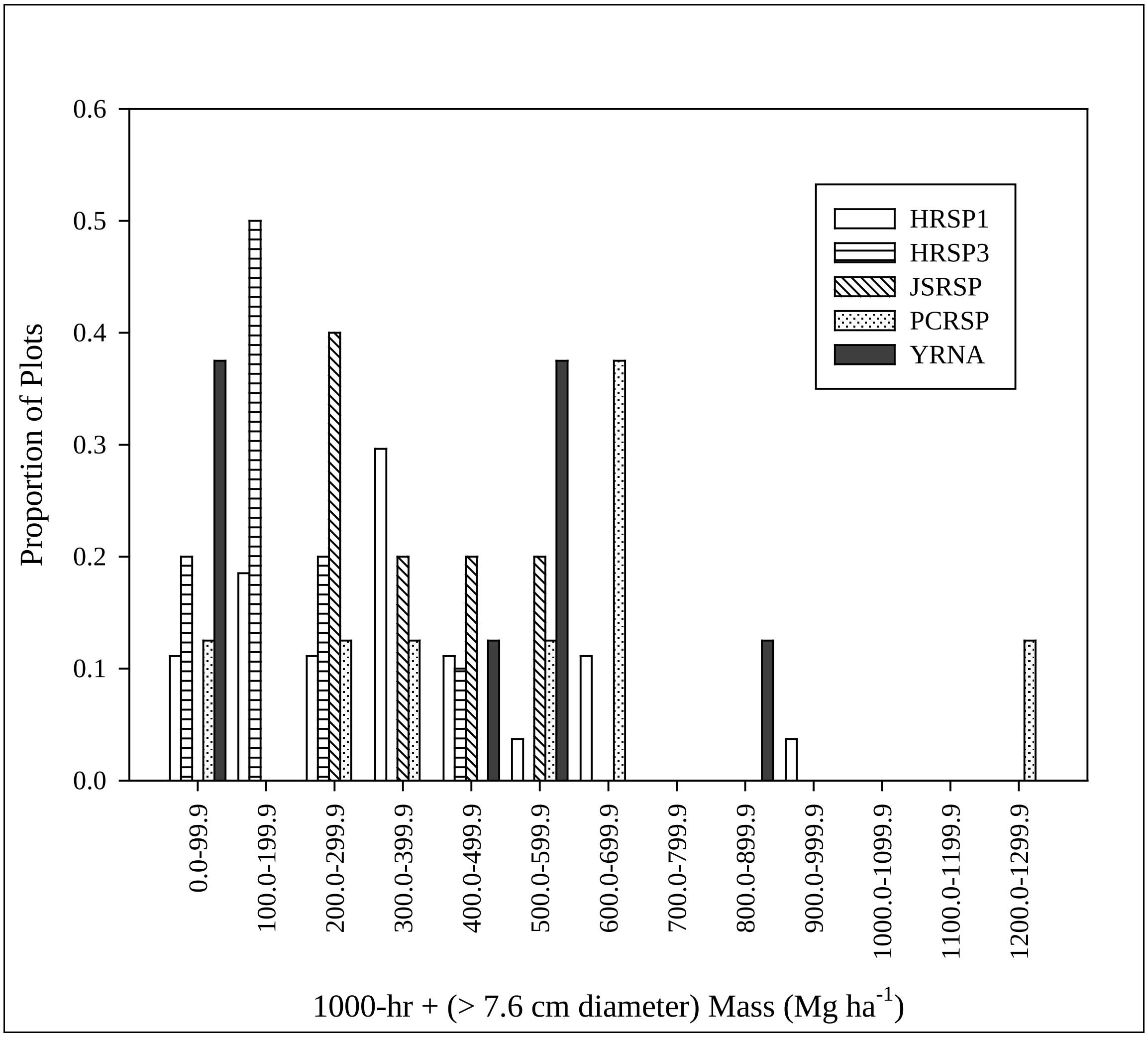
APPENDICES



Appendix A. Distribution of 1000-hr + particle mass estimates among plots in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Appendix B. HRSP1 downed woody and forest floor detritus summary statistics. Mass estimates are means of three (50 m transect) estimates per plot. Depth and height estimates are means of three plot estimates, which are each means of three measurements per transect.

Variable	n	$\bar{x}$	s	SE	Min.	Max.	----- 95% CI ----- Lower	Upper	V (%)	Shapiro-Wilk P
1-hr W (Mg ha^{-1})	27	1.6	0.4	0.1	0.9	2.4	1.4	1.7	27.2	0.174
1-hr L (Mg ha^{-1})	27	2.2	0.6	0.1	1.2	3.1	2.0	2.4	25.8	0.230
1-hr total (Mg ha^{-1})	27	3.7	0.7	0.1	2.4	5.3	3.5	4.0	19.9	0.614
10-hr W (Mg ha^{-1})	27	6.1	2.7	0.5	2.7	14.0	5.0	7.1	44.8	**0.002**
10-hr L (Mg ha^{-1})	27	0.0	0.0	0.0	0.0	0.1	0.0	0.0	142.4	< **0.001**
10-hr total (Mg ha^{-1})	27	6.1	2.7	0.5	2.7	14.0	5.0	7.2	44.8	**0.002**
100-hr (Mg ha^{-1})	27	8.8	4.5	0.9	3.3	20.0	7.0	10.6	50.6	0.052
1000-hr DC 1 (Mg ha^{-1})	27	12.8	38.6	7.4	0.0	188.0	-2.5	28.0	302.1	< **0.001**
1000-hr DC 2 (Mg ha^{-1})	27	53.9	81.0	15.6	0.0	339.9	21.9	86.0	150.3	< **0.001**
1000-hr DC 3 (Mg ha^{-1})	27	149.8	115.7	22.3	1.8	514.6	104.0	195.6	77.3	**0.025**
1000-hr DC 4 (Mg ha^{-1})	27	100.2	108.4	20.9	0.0	388.5	57.3	143.1	108.2	< **0.001**
1000-hr DC 5 (Mg ha^{-1})	27	12.8	23.7	4.6	0.0	111.9	3.4	22.1	185.1	< **0.001**
1000-hr total (Mg ha^{-1})	27	329.5	208.6	40.1	28.4	891.6	247.0	412.0	63.3	0.125
DWD total (Mg ha^{-1})	27	348.1	210.9	40.6	49.5	926.7	264.7	431.5	60.6	0.105
Surface fuel height (cm)	27	32.3	21.3	4.1	8.1	94.7	23.8	40.6	65.9	< **0.001**
Litter depth (cm)	27	6.6	1.5	0.3	3.7	9.5	6.0	7.1	22.2	0.965
Litter bulk density (Mg ha^{-1} cm^{-1})	14	4.1	1.6	0.4	1.7	6.6	3.2	5.1	38.1	0.531
Litter mass (Mg ha^{-1})	14	11.5	4.9	1.3	3.7	20.5	8.6	14.4	43.0	0.788
Duff depth (cm)	27	3.3	2.8	0.5	0.5	14.0	2.2	4.5	83.9	< **0.001**
Duff bulk density (Mg ha^{-1} cm^{-1})	14	7.1	2.6	0.7	2.1	11.0	5.6	8.6	37.0	0.827
Duff mass (Mg ha^{-1})	14	33.8	27.4	7.3	6.7	105.7	17.9	49.6	81.2	**0.013**
Forest floor depth (cm)	27	9.9	3.4	0.7	4.9	22.2	8.6	11.3	34.6	**0.003**
Forest floor bulk density (Mg ha^{-1} cm^{-1})	14	5.7	2.1	0.6	2.2	9.7	4.5	6.9	36.3	0.389
Forest floor mass (Mg ha^{-1})	14	45.3	30.2	8.1	13.8	126.1	27.8	62.7	66.7	**0.018**
Slope (%)	27	3.7	3.3	0.6	1.0	12.0	2.4	5.0	90.4	< **0.001**
Basal area (m^2 ha^{-1})	27	137.2	31.2	6.0	82.7	220.4	124.9	149.6	22.8	0.119

Appendix C. HRSP3 downed woody and forest floor detritus summary statistics. Mass estimates are means of three (50 m transect) estimates per plot. Depth and height estimates are means of three plot estimates, which are each means of three measurements per transect.

Variable	*n*	$\bar{x}$	*s*	SE	Min.	Max.	----- 95% CI ----- Lower	Upper	*V* (%)	Shapiro-Wilk P
1-hr W (Mg ha^{-1})	10	2.2	0.4	0.1	1.6	2.7	1.9	2.5	18.2	0.385
1-hr L (Mg ha^{-1})	10	1.4	0.3	0.1	0.6	1.8	1.2	1.6	23.2	**0.015**
1-hr total (Mg ha^{-1})	10	3.6	0.5	0.2	2.5	4.2	3.3	4.0	14.3	0.203
10-hr W (Mg ha^{-1})	10	5.5	2.0	0.7	2.4	8.2	4.1	7.0	37.0	0.418
10-hr L (Mg ha^{-1})	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	--
10-hr total (Mg ha^{-1})	10	5.5	2.0	0.7	2.4	8.2	4.1	7.0	37.0	0.418
100-hr (Mg ha^{-1})	10	9.0	3.9	1.2	5.3	15.6	6.2	11.8	43.6	0.066
1000-hr DC 1 (Mg ha^{-1})	10	2.2	2.3	0.7	0.0	5.7	0.6	3.9	104.1	**0.021**
1000-hr DC 2 (Mg ha^{-1})	10	22.6	25.4	8.0	0.6	75.4	4.4	40.7	112.3	**0.035**
1000-hr DC 3 (Mg ha^{-1})	10	88.0	87.4	27.6	22.4	315.3	25.4	150.5	99.4	**0.002**
1000-hr DC 4 (Mg ha^{-1})	10	49.1	44.9	14.2	0.3	153.9	17.0	81.2	91.4	0.119
1000-hr DC 5 (Mg ha^{-1})	10	30.5	32.1	10.2	0.3	76.8	7.6	53.5	105.2	**0.010**
1000-hr total (Mg ha^{-1})	10	192.4	122.2	38.6	31.3	466.6	105.0	279.8	63.5	0.387
DWD total (Mg ha^{-1})	10	210.5	126.3	39.9	43.3	490.4	120.2	300.8	60.0	0.436
Surface fuel height (cm)	10	46.4	23.7	7.5	15.8	88.7	29.5	63.3	51.0	0.450
Litter depth (cm)	10	5.5	0.9	0.3	3.9	7.1	4.9	6.2	16.4	0.971
Litter bulk density (Mg ha^{-1} cm^{-1})	10	4.8	2.7	0.9	1.8	10.3	2.9	6.8	56.4	0.168
Litter mass (Mg ha^{-1})	10	9.9	4.8	1.5	3.7	17.3	6.5	13.3	48.6	0.500
Duff depth (cm)	10	5.2	2.1	0.7	2.5	9.2	3.7	6.7	39.9	0.221
Duff bulk density (Mg ha^{-1} cm^{-1})	10	7.5	2.9	0.9	4.3	12.8	5.4	9.6	38.7	0.110
Duff mass (Mg ha^{-1})	10	32.0	41.5	13.1	2.3	146.3	2.4	61.7	129.5	< **0.001**
Forest floor depth (cm)	10	10.8	2.5	0.8	7.2	14.8	9.0	12.5	23.1	0.578
Forest floor bulk density (Mg ha^{-1} cm^{-1})	10	6.3	2.5	0.8	3.4	11.4	4.5	8.1	40.3	0.106
Forest floor mass (Mg ha^{-1})	10	41.9	42.9	13.6	15.1	160.0	11.2	72.5	102.3	< **0.001**
Slope (%)	10	33.6	5.1	1.6	25.0	40.0	30.0	37.3	15.2	0.546
Basal area (m^2 ha^{-1})	10	137.8	39.6	12.5	59.7	197.5	109.4	166.1	28.8	0.880

Appendix D. JSRSP downed woody and forest floor detritus summary statistics. Mass estimates are means of three (50 m transect) estimates per plot. Depth and height estimates are means of three plot estimates, which are each means of three measurements per transect.

Variable	*n*	$\bar{x}$	*s*	SE	Min.	Max.	----- 95% CI ----- Lower	Upper	*V* (%)	Shapiro-Wilk P
1-hr W (Mg ha^{-1})	5	2.5	0.4	0.2	2.0	3.0	2.0	3.1	16.2	0.693
1-hr L (Mg ha^{-1})	5	1.4	0.3	0.1	0.9	1.6	1.0	1.7	21.3	**0.036**
1-hr total (Mg ha^{-1})	5	3.9	0.4	0.2	3.4	4.5	3.4	4.4	9.8	0.907
10-hr W (Mg ha^{-1})	5	5.1	1.9	0.9	2.4	7.8	2.7	7.5	38.2	0.614
10-hr L (Mg ha^{-1})	5	0.1	0.1	0.1	0.0	0.2	0.0	0.2	113.5	0.254
10-hr total (Mg ha^{-1})	5	5.2	1.9	0.9	2.4	7.8	2.8	7.6	37.6	0.642
100-hr (Mg ha^{-1})	5	5.3	1.6	0.7	3.9	7.7	3.3	7.2	30.1	0.236
1000-hr DC 1 (Mg ha^{-1})	5	0.2	0.3	0.1	0.0	0.7	-0.2	0.6	142.1	**0.044**
1000-hr DC 2 (Mg ha^{-1})	5	8.3	15.0	6.7	0.0	35.0	-10.3	26.8	181.0	**0.001**
1000-hr DC 3 (Mg ha^{-1})	5	298.7	143.6	64.2	98.3	476.7	120.4	477.0	48.1	0.931
1000-hr DC 4 (Mg ha^{-1})	5	53.1	57.5	25.7	0.0	123.4	-18.3	124.5	108.4	0.199
1000-hr DC 5 (Mg ha^{-1})	5	25.6	50.4	22.6	2.0	115.7	-37.1	88.2	197.3	< **0.001**
1000-hr total (Mg ha^{-1})	5	385.8	117.5	52.5	278.9	534.4	239.9	531.7	30.4	0.219
DWD total (Mg ha^{-1})	5	400.1	118.5	53.0	291.6	550.5	253.0	547.2	29.6	0.234
Surface fuel height (cm)	5	41.3	13.1	5.9	19.2	52.6	25.1	57.6	31.7	0.144
Litter depth (cm)	5	5.9	1.4	0.6	3.7	7.4	4.2	7.7	23.8	0.544
Litter bulk density (Mg ha^{-1} cm^{-1})	6	4.3	0.8	0.3	3.4	5.3	3.5	5.1	17.5	0.626
Litter mass (Mg ha^{-1})	6	13.3	4.7	1.9	7.4	20.4	8.3	18.3	35.7	0.915
Duff depth (cm)	5	1.7	1.0	0.4	0.5	2.8	0.5	2.9	55.5	0.773
Duff bulk density (Mg ha^{-1} cm^{-1})	6	4.1	3.8	1.5	0.0	9.0	0.2	8.1	91.2	0.462
Duff mass (Mg ha^{-1})	6	9.2	9.8	4.0	0.0	23.1	-1.1	19.4	106.4	0.260
Forest floor depth (cm)	5	7.6	1.3	0.6	5.4	8.7	6.0	9.3	17.0	0.056
Forest floor bulk density (Mg ha^{-1} cm^{-1})	6	4.9	1.0	0.4	3.5	6.4	3.8	6.0	20.7	0.963
Forest floor mass (Mg ha^{-1})	6	22.5	9.3	3.8	9.9	36.9	12.7	32.2	41.4	0.991
Slope (%)	5	1.6	1.3	0.6	1.0	4.0	-0.1	3.3	83.9	< **0.001**
Basal area (m^2 ha^{-1})	5	146.0	48.4	21.7	101.0	225.0	85.9	206.1	33.2	0.349

Appendix E. PCRSP downed woody and forest floor detritus summary statistics. Mass estimates are means of three (50 m transect) estimates per plot. Depth and height estimates are means of three plot estimates, which are each means of three measurements per transect.

Variable	*n*	$\bar{x}$	*s*	SE	Min.	Max.	----- 95% CI ----- Lower	Upper	*V* (%)	Shapiro-Wilk P
1-hr W (Mg ha^{-1})	8	1.6	0.4	0.2	1.0	2.4	1.2	1.9	27.8	0.599
1-hr L (Mg ha^{-1})	8	1.5	0.3	0.1	1.0	2.1	1.2	1.8	22.4	0.909
1-hr total (Mg ha^{-1})	8	3.1	0.6	0.2	2.2	4.0	2.6	3.6	19.4	0.488
10-hr W (Mg ha^{-1})	8	4.3	1.7	0.6	2.5	7.0	2.9	5.7	38.8	0.338
10-hr L (Mg ha^{-1})	8	0.1	0.0	0.0	0.0	0.2	0.0	0.1	104.7	0.137
10-hr total (Mg ha^{-1})	8	4.3	1.7	0.6	2.6	7.1	2.9	5.8	39.1	0.273
100-hr (Mg ha^{-1})	8	7.7	2.8	1.0	3.9	12.5	5.3	10.0	36.2	0.840
1000-hr DC 1 (Mg ha^{-1})	8	1.8	2.3	0.8	0.0	5.9	-7.5	3.8	124.5	**0.006**
1000-hr DC 2 (Mg ha^{-1})	8	23.6	19.6	6.9	3.1	50.0	7.2	40.0	83.1	0.107
1000-hr DC 3 (Mg ha^{-1})	8	398.2	292.6	103.4	45.7	936.2	153.7	642.8	73.5	0.673
1000-hr DC 4 (Mg ha^{-1})	8	107.6	89.1	31.5	15.5	251.4	33.2	182.1	82.8	0.143
1000-hr DC 5 (Mg ha^{-1})	8	31.4	37.7	13.3	0.0	93.4	-9.9	62.9	120.0	**0.042**
1000-hr total (Mg ha^{-1})	8	562.7	367.6	130.0	81.7	1287.1	255.3	870.0	65.3	0.416
DWD total (Mg ha^{-1})	8	577.7	366.9	129.7	100.4	1302.2	271.0	884.5	63.5	0.382
Surface fuel height (cm)	8	31.2	12.3	4.3	18.1	56.0	20.9	41.4	39.4	0.219
Litter depth (cm)	8	5.0	1.0	0.4	3.6	6.7	4.2	5.9	20.2	0.844
Litter bulk density (Mg ha^{-1} cm^{-1})	8	3.6	3.3	1.2	0.7	10.9	0.8	6.4	92.8	**0.026**
Litter mass (Mg ha^{-1})	8	9.6	10.2	3.6	1.8	31.2	1.1	18.1	106.4	**0.013**
Duff depth (cm)	8	2.4	0.6	0.2	1.4	3.3	1.9	2.9	25.7	1.000
Duff bulk density (Mg ha^{-1} cm^{-1})	8	7.0	1.8	0.6	5.2	10.7	5.5	8.5	25.5	0.211
Duff mass (Mg ha^{-1})	8	31.4	16.9	6.0	13.8	61.4	17.2	45.5	53.9	0.176
Forest floor depth (cm)	8	7.4	0.9	0.3	6.5	9.0	6.7	8.1	11.6	0.131
Forest floor bulk density (Mg ha^{-1} cm^{-1})	8	5.8	1.5	0.5	3.8	8.1	4.5	7.0	25.3	0.502
Forest floor mass (Mg ha^{-1})	8	41.0	18.0	6.4	22.5	64.0	25.9	56.0	43.9	0.056
Slope (%)	8	4.6	4.0	1.4	1.0	13.0	1.3	8.0	87.2	0.130
Basal area (m^{2} ha^{-1})	8	173.3	33.2	11.7	110.2	206.6	145.6	201.1	19.1	0.317

Appendix F. YRNA downed woody and forest floor detritus summary statistics. Mass estimates are means of three (50 m transect) estimates per plot. Depth and height estimates are means of three plot estimates, which are each means of three measurements per transect.

							----- 95% CI -----			Shapiro-
Variable	*n*	$\bar{x}$	*s*	SE	Min.	Max.	Lower	Upper	*V* (%)	Wilk P
1-hr W (Mg ha^{-1})	8	1.5	0.3	0.1	0.9	2.0	1.2	1.7	21.8	0.396
1-hr L (Mg ha^{-1})	8	1.1	0.2	0.1	0.8	1.4	0.9	1.2	20.3	0.614
1-hr total (Mg ha^{-1})	8	2.5	0.5	0.2	1.6	3.0	2.2	2.9	17.9	0.294
10-hr W (Mg ha^{-1})	8	3.3	1.3	0.5	1.8	6.1	2.1	4.4	41.0	0.192
10-hr L (Mg ha^{-1})	8	0.0	0.0	0.0	0.0	0.1	0.0	0.0	282.8	< **0.001**
10-hr total (Mg ha^{-1})	8	3.2	1.3	0.5	1.8	6.1	2.1	4.4	41.0	0.198
100-hr (Mg ha^{-1})	8	9.2	4.2	1.5	3.0	14.4	5.7	12.6	45.3	0.622
1000-hr DC 1 (Mg ha^{-1})	8	0.2	0.6	0.2	0.0	1.8	-0.3	0.8	282.8	< **0.001**
1000-hr DC 2 (Mg ha^{-1})	8	13.3	19.4	6.9	0.0	56.1	-2.9	29.6	145.8	**0.005**
1000-hr DC 3 (Mg ha^{-1})	8	169.6	165.9	58.7	4.7	380.0	30.9	308.3	97.8	**0.044**
1000-hr DC 4 (Mg ha^{-1})	8	122.8	154.7	54.7	2.2	431.3	-6.6	252.1	126.0	**0.019**
1000-hr DC 5 (Mg ha^{-1})	8	77.1	122.6	43.3	0.5	356.2	-25.4	179.5	159.1	**0.003**
1000-hr total (Mg ha^{-1})	8	383.0	312.0	110.3	9.8	831.6	122.2	643.8	81.5	0.117
DWD total (Mg ha^{-1})	8	397.9	312.7	110.6	28.4	854.9	136.5	659.4	78.6	0.116
Surface fuel height (cm)	8	26.2	4.5	1.6	19.2	33.3	22.4	30.0	17.2	0.977
Litter depth (cm)	8	9.6	2.3	0.8	6.6	13.0	7.8	11.5	23.4	0.822
Litter bulk density (Mg ha^{-1} cm^{-1})	8	5.6	3.1	1.1	3.1	11.8	3.0	8.2	55.2	0.052
Litter mass (Mg ha^{-1})	8	16.7	6.1	2.2	5.4	24.9	11.6	21.8	36.4	0.650
Duff depth (cm)	8	1.3	1.4	0.5	0.0	4.2	0.1	2.5	107.2	0.096
Duff bulk density (Mg ha^{-1} cm^{-1})	8	4.2	3.9	1.4	0.0	8.8	1.0	7.5	91.9	0.056
Duff mass (Mg ha^{-1})	8	20.9	25.7	9.1	0.0	72.0	-0.6	42.3	123.0	0.073
Forest floor depth (cm)	8	10.9	3.4	1.2	6.6	17.2	8.1	13.8	31.1	0.741
Forest floor bulk density (Mg ha^{-1} cm^{-1})	8	6.3	2.9	1.0	3.6	11.8	3.9	8.7	45.1	0.241
Forest floor mass (Mg ha^{-1})	8	37.6	26.2	9.3	10.9	92.3	15.7	59.4	69.7	0.153
Slope (%)	8	23.4	6.3	2.4	17.0	32.0	17.6	29.3	27.0	0.130
Basal area (m^2 ha^{-1})	8	218.7	50.6	17.9	142.4	289.3	176.4	261.0	23.1	0.865

Appendix G. The composition of total downed woody detritus mass partitioned by particle type in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Detritus category	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
	--------------------		%		--------------------
Litter	2.9	3.9	3.1	1.6	3.8
Duff	8.6	12.7	2.2	5.1	4.8
Forest floor (litter + duff)	11.5	16.6	5.3	6.6	8.6
1-hr woody (< 0.6 cm)	0.4	0.9	0.6	0.3	0.3
1-hr leafy (< 0.6 cm)	0.6	0.6	0.3	0.2	0.3
10-hr (0.6 - 2.5 cm)	1.6	2.2	1.2	0.7	0.7
100-hr (2.6 - 7.6 cm)	2.2	3.6	1.3	1.2	2.1
FWD (≤ 7.6 cm)	4.8	7.2	3.4	2.4	3.4
FWD + forest floor	16.3	23.8	8.7	9.1	12.1
1000-hr + DC1 (> 7.6 cm)	3.3	0.9	0.0	0.3	0.0
1000-hr + DC2 (> 7.6 cm)	13.7	9.0	2.0	3.8	3.1
1000-hr + DC3 (> 7.6 cm)	38.1	34.9	70.6	64.4	38.9
1000-hr + DC4 (> 7.6 cm)	25.5	19.5	12.6	17.4	28.2
1000-hr + DC5 (> 7.6 cm)	3.3	12.1	6.1	5.1	17.7
1000-hr + Total (> 7.6 cm)	83.7	76.2	91.3	90.9	87.9

Appendix H. Coefficient of dispersion of woody particle mass estimates within five old-growth coast redwood stands in northwestern California, U.S.A.

Category		HRSP1	HRSP3	JSRSP	PCRSP	YRNA
				(*CD*)		
1-hr	Woody	0.10	0.07	0.06	0.10	0.06
	Leafy	0.16	0.06	0.06	0.06	0.04
10-hr		1.20	0.73	0.69	0.67	0.53
100-hr		2.30	1.69	0.48	1.02	1.92
≤ 7.6 cm woody		2.53	1.63	0.13	0.74	1.74
1000-hr +	DC 1	116.40	2.40	0.45	2.94	1.80
	DC 2	121.73	28.55	27.11	16.28	28.30
	DC 3	89.36	86.80	69.04	215.00	162.28
	DC 4	117.27	41.06	62.26	73.78	194.89
	DC 5	43.88	33.78	99.23	45.26	194.95
> 7.6 cm woody		132.04	77.60	35.77	240.19	254.11
Total woody		127.74	75.82	35.08	233.02	245.68

Appendix I. Composition of 1000-hr + mass (% of total) by particle species in five old-growth coast redwood (*Sequoia sempervirens*) stands.

Species	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
Abies grandis	0.3	0.2	--	--	--
Acer circinatum	--	--	< 0.1	--	--
Arbutus menziesii	--	0.9	--	--	--
Lithocarpus densiflorus	0.2	2.7	--	--	--
Picea sitchensis	--	--	--	0.2	--
Pseudotsuga menziesii	0.1	21.6	--	2.5	--
Sequoia sempervirens	98.4	74.6	94.1	96.8	100.0
Tsuga heterophylla	--	--	5.9	0.5	--
Umbellularia californica	1.0	--	--	--	--

Appendix J. Overstory basal area (m^2 ha^{-1}) and composition (% of total) by species in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Species	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
	-------------- Basal area (m^2 ha^{-1}) --------------				
Abies grandis	0.3	1.4	--	--	--
Arbutus menziesii	--	1.4	--	--	--
Corylus cornuta	0.3	--	--	--	--
Lithocarpus densiflorus	0.3	8.7	1.8	--	--
Picea sitchensis	--	--	--	1.7	--
Pseudotsuga menziesii	0.2	13.3	--	6.3	--
Sequoia sempervirens	135.2	113.0	135.0	163.6	217.0
Tsuga heterophylla	--	--	9.2	1.7	--
Umbellularia californica	0.9	--	--	--	6.9
Total	137.3	137.8	146.0	173.3	223.9

Species	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
	------------- Proportion (% of total) -------------				
Abies grandis	0.2	1.0	--	--	--
Arbutus menziesii	--	1.0	--	--	--
Corylus cornuta	0.2	--	--	--	--
Lithocarpus densiflorus	0.2	6.3	1.3	--	--
Picea sitchensis	--	--	--	1.0	--
Pseudotsuga menziesii	0.1	9.7	--	3.6	--
Sequoia sempervirens	98.5	82.0	92.5	94.4	96.9
Tsuga heterophylla	--	--	6.3	1.0	--
Umbellularia californica	0.6	--	--	--	3.1

Appendix K. Composition of 1000-hr + particle intersections (% of total) by diameter class for each log species present across five old-growth *Sequoia sempervirens* stands in northwestern California, U.S.A.

HRSP1	Diameter Class																						
Species	7.7-9.9	10.0- 19.9	20.0 - 29.9	30.0 - 39.9	40.0 - 49.9	50.0 - 59.9	60.0 - 69.9	70.0 - 79.9	80.0 - 89.9	90.0 - 99.9	100.0 - 109.9	110.0 - 119.9	120.0 - 129.9	130.0 - 139.9	140.0 - 149.9	150.0 - 159.9	160.0 - 169.9	170.0 - 179.9	180.0 - 189.9	190.0 - 199.9	≥ 200.0	*n*	Mean diam. (cm)
Abies grandis	20.0	--	20.0	--	20.0	40.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	5	39.9
Lithocarpus densiflorus	38.9	38.9	16.7	--	5.6	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	18	14.5
Pseudotsuga menziesii	--	--	--	--	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	40.2
Sequoia sempervirens	21.9	35.5	9.1	5.8	4.5	2.9	3.2	2.4	3.2	1.5	1.6	1.5	1.2	1.1	0.3	0.8	0.5	0.1	0.3	0.7	2.1	757	38.1
Umbellularia californica	10.3	44.8	10.3	6.9	13.8	13.8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	29	25.7

HRSP3	Diameter Class																						
Species	7.7-9.9	10.0- 19.9	20.0 - 29.9	30.0 - 39.9	40.0 - 49.9	50.0 - 59.9	60.0 - 69.9	70.0 - 79.9	80.0 - 89.9	90.0 - 99.9	100.0 - 109.9	110.0 - 119.9	120.0 - 129.9	130.0 - 139.9	140.0 - 149.9	150.0 - 159.9	160.0 - 169.9	170.0 - 179.9	180.0 - 189.9	190.0 - 199.9	≥ 200.0	*n*	Mean diam. (cm)
Abies grandis	--	66.7	33.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	3	16.4
Arbutus menziesii	9.1	36.4	45.5	9.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	11	20.4
Lithocarpus densiflorus	37.5	42.9	14.3	3.6	1.8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	56	14.7
Pseudotsuga menziesii	11.8	19.6	11.8	9.8	13.7	11.8	5.9	5.9	--	2.0	7.8	--	--	--	--	--	--	--	--	--	--	51	40.7
Sequoia sempervirens	17.4	15.6	10.8	16.2	9.6	9.6	8.4	4.2	1.8	2.4	--	1.8	0.6	1.2	--	--	--	--	--	--	0.6	167	39.9

JSRSP	Diameter Class																						
Species	7.7-9.9	10.0- 19.9	20.0 - 29.9	30.0 - 39.9	40.0 - 49.9	50.0 - 59.9	60.0 - 69.9	70.0 - 79.9	80.0 - 89.9	90.0 - 99.9	100.0 - 109.9	110.0 - 119.9	120.0 - 129.9	130.0 - 139.9	140.0 - 149.9	150.0 - 159.9	160.0 - 169.9	170.0 - 179.9	180.0 - 189.9	190.0 - 199.9	≥ 200.0	*n*	Mean diam. (cm)
Acer circinatum	100.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1	9.0
Sequoia sempervirens	7.8	25.2	12.2	6.1	4.3	7.0	8.7	5.2	6.1	--	3.5	3.5	2.6	2.6	--	0.9	1.7	0.9	0.9	--	0.9	115	53.6
Tsuga heterophylla	--	15.4	7.7	--	30.8	15.4	15.4	7.7	7.7	--	--	--	--	--	--	--	--	--	--	--	--	13	47.9

PCRSP	Diameter Class																						
Species	7.7-9.9	10.0- 19.9	20.0 - 29.9	30.0 - 39.9	40.0 - 49.9	50.0 - 59.9	60.0 - 69.9	70.0 - 79.9	80.0 - 89.9	90.0 - 99.9	100.0 - 109.9	110.0 - 119.9	120.0 - 129.9	130.0 - 139.9	140.0 - 149.9	150.0 - 159.9	160.0 - 169.9	170.0 - 179.9	180.0 - 189.9	190.0 - 199.9	≥ 200.0	*n*	Mean diam. (cm)
Picea sitchensis	--	--	50.0	50.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2	32.1
Pseudotsuga menziesii	21.4	14.3	7.1	28.6	7.1	--	--	--	7.1	7.1	7.1	--	--	--	--	--	--	--	--	--	--	14	38.4
Sequoia sempervirens	24.5	32.0	8.5	5.9	4.9	4.9	4.6	2.9	2.0	1.6	0.7	0.7	0.3	1.6	1.6	0.3	1.0	0.3	--	--	1.6	306	38.1
Tsuga heterophylla	--	--	50.0	25.0	--	--	25.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4	36.6

YRNA	Diameter Class																						
Species	7.7-9.9	10.0- 19.9	20.0 - 29.9	30.0 - 39.9	40.0 - 49.9	50.0 - 59.9	60.0 - 69.9	70.0 - 79.9	80.0 - 89.9	90.0 - 99.9	100.0 - 109.9	110.0 - 119.9	120.0 - 129.9	130.0 - 139.9	140.0 - 149.9	150.0 - 159.9	160.0 - 169.9	170.0 - 179.9	180.0 - 189.9	190.0 - 199.9	≥ 200.0	*n*	Mean diam. (cm)
Sequoia sempervirens	19.0	26.1	11.3	8.5	7.7	6.3	5.6	4.2	0.7	1.4	2.1	1.4	0.7	--	0.7	0.7	1.4	0.7	0.7	--	< 0.1	142	40.0

Appendix L. Percent of 1000-hr + particle intersections by diameter class in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Diameter class (cm)	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
7.7-9.9	22.0	19.8	7.8	23.9	19.0
10.0-19.9	35.9	22.9	24.0	30.7	26.1
20.0-29.9	9.3	13.2	11.6	9.2	11.3
30.0-39.9	5.7	12.2	5.4	7.4	8.5
40.0-49.9	5.0	8.3	7.0	4.9	7.7
50.0-59.9	3.3	7.6	7.8	4.6	6.3
60.0-69.9	3.0	5.9	9.3	4.6	5.6
70.0-79.9	2.1	3.5	5.4	2.8	4.2
80.0-89.9	3.0	1.0	6.2	2.1	0.7
90.0-99.9	1.4	1.7	--	1.8	1.4
100.0-109.9	1.5	1.4	3.1	0.9	2.1
110.0-119.9	1.4	1.0	3.1	0.6	1.4
120.0-129.9	1.1	0.3	2.3	0.3	0.7
130.0-139.9	1.0	0.7	2.3	1.5	--
140.0-149.9	0.2	--	--	1.5	0.7
150.0-159.9	0.7	--	0.8	0.3	0.7
160.0-169.9	0.5	--	1.6	0.9	1.4
170.0-179.9	0.1	--	0.8	0.3	0.7
180.0-189.9	0.2	--	0.8	--	0.7
190.0-199.9	0.6	--	--	--	--
$\geq$ 200.0	2.0	0.3	0.8	1.5	0.7

Appendix M. Composition of 1000-hr + intersections (% of total) by category of decay for each log species present across five old-growth *Sequoia sempervirens* stands in northwestern California, U.S.A.

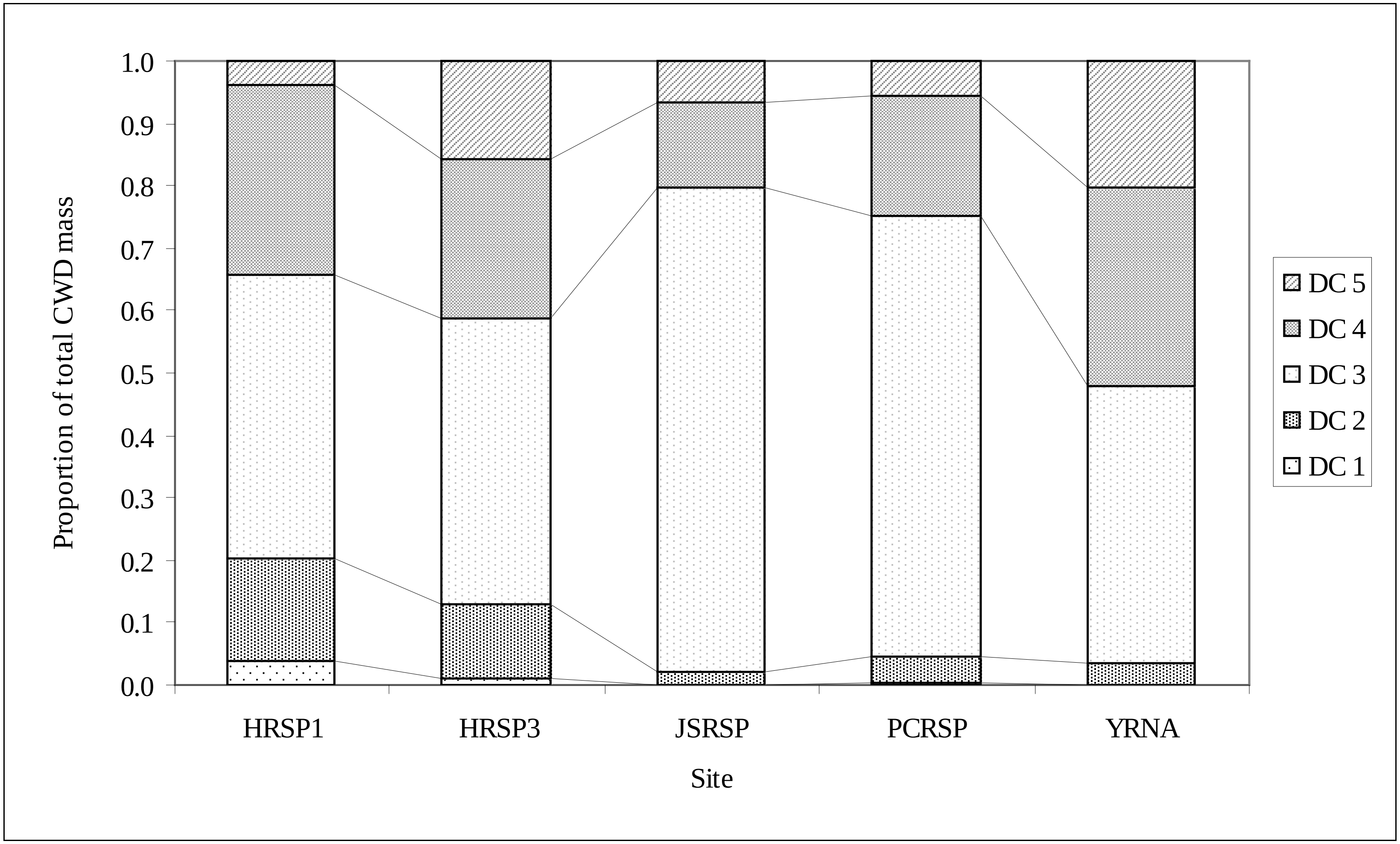
HRSP1	-------- Decay Category --------					
Species	1	2	3	4	5	*n*
Abies grandis	--	16.7	83.3	--	--	5
Lithocarpus densiflorus	10.5	10.5	36.8	36.8	5.4	18
Pseudotsuga menziesii	100.0	--	--	--	--	1
Sequoia sempervirens	10.2	20.5	40.9	23.8	4.6	757
Umbellularia californica	3.5	17.2	37.9	27.6	13.8	29

HRSP3	-------- Decay Category --------					
Species	1	2	3	4	5	*n*
Abies grandis	--	100.0	--	--	--	3
Arbutus menziesii	27.3	36.3	18.2	18.2	--	11
Lithocarpus densiflorus	19.6	25.0	30.4	14.3	10.7	56
Pseudotsuga menziesii	--	29.4	29.4	17.7	23.5	51
Sequoia sempervirens	1.8	13.6	51.5	19.5	13.6	167

JSRSP	-------- Decay Category --------					
Species	1	2	3	4	5	*n*
Acer circinatum	--	--	100.0	--	--	1
Sequoia sempervirens	1.7	7.8	67.8	18.3	4.4	115
Tsuga heterophylla	7.7	7.7	69.2	7.7	7.7	13

PCRSP	-------- Decay Category --------					
Species	1	2	3	4	5	*n*
Picea sitchensis	--	--	50.0	50.0	--	2
Pseudotsuga menziesii	28.6	35.7	7.1	21.5	7.1	14
Sequoia sempervirens	5.6	22.2	45.1	22.9	4.2	306
Tsuga heterophylla	--	--	75.0	25.0	--	4

YRNA	-------- Decay Category --------					
Species	1	2	3	4	5	*n*
Sequoia sempervirens	0.7	14.1	40.8	30.3	14.1	142



Appendix N. Composition of 1000-hr + mass by decay category in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Appendix O. The ten largest diameter 1000-hr + decay category 1 particles sampled in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A. Dashed lines indicate that no 1000-hr + decay category 1 particles other than those listed were found.

	----- HRSP1 -----		----- HRSP3 -----		----- JSRSP -----		----- PCRSP -----		----- YRNA -----	
Rank	Species	Diameter (cm)	Species	Diameter (cm)	Species	Diameter (cm)	Species	Diameter (cm)	Species	Diameter (cm)
1	SESE	216.0	LIDE	38.2	TSHE	11.5	PSME	36.7	SESE	16.4
2	SESE	103.8	SESE	32.2	SESE	11.4	PSME	31.8	--	--
3	SESE	102.1	LIDE	24.5	SESE	8.6	SESE	16.9	--	--
4	SESE	79.6	LIDE	23.9	--	--	SESE	16.1	--	--
5	SESE	76.3	ARME	22.3	--	--	SESE	12.6	--	--
6	SESE	73.7	ARME	22.0	--	--	SESE	12.0	--	--
7	SESE	64.4	LIDE	20.3	--	--	SESE	11.0	--	--
8	SESE	59.3	ARME	19.5	--	--	SESE	10.7	--	--
9	SESE	48.4	LIDE	19.3	--	--	PSME	10.1	--	--
10	SESE	45.6	LIDE	16.9	--	--	SESE	10.0	--	--

ARME = *Arbutus menziesii*
LIDE = *Lithocarpus densiflorus*
PSME = *Pseudotsuga menziesii*
SESE = *Sequoia sempervirens*
TSHE = *Tsuga heterophylla*

Appendix P. The coefficient of variation (*V*) associated with mass estimates of downed woody particles in five old-growth coast redwood (*Sequoia sempervirens*) stands in northwestern California, U.S.A.

Category		HRSP1	HRSP3	JSRSP	PCRSP	YRNA
		(*V*, %)				
1-hr	Woody	27.2	18.2	16.2	27.8	21.8
	Leafy	25.8	23.2	21.3	22.4	20.3
10-hr		44.8	37.0	37.7	39.1	41.0
100-hr		50.6	43.6	30.1	36.2	45.3
≤ 7.6 cm woody		36.9	30.0	9.4	22.1	34.2
1000-hr +	DC 1	302.1	104.1	142.1	124.5	282.8
	DC 2	150.3	112.3	181.0	83.1	145.8
	DC 3	77.3	99.4	48.1	73.5	97.8
	DC 4	108.2	91.4	108.4	82.8	126.0
	DC 5	185.1	105.2	197.3	120.0	159.1
> 7.6 cm woody		63.3	63.5	30.4	65.3	81.5
Total woody		60.6	60.0	29.6	63.5	78.6

Appendix Q. Mean number of 1000-hr + particle intersections along sample transects in five old-growth coast redwood stands. Significantly different estimates among sites determined from one-way ANOVA ($\alpha = 0.05$) and Tukey-Kramer post hoc tests.

	HRSP1	HRSP3	JSRSP	PCRSP	YRNA*	P-value
# of particle intersections	810	288	129	326	142	--
# of transects	81	30	15	24	24	--
Mean # of particles transect^{-1}	10.0	9.6	8.6	13.6	5.9	0.16
Transect length (m)	50	50	50	50	25	--

*YRNA intersections were doubled for ANOVA to account for the 25 m transects in order to compare with the 50 m transects at all other sites.

Appendix R. Percent error ($\frac{SE \times 100}{\bar{X}}$; Brown 1974) of downed woody and forest floor detritus mass estimates in five old-growth coast redwood (*Sequoi*a *sempervirens*) stands in northwestern California, U.S.A. Bold and italicized values identify estimates associated with more than 20 percent error.

DWD Category	HRSP1	HRSP3	JSRSP	PCRSP	YRNA
1-hr woody (Mg ha^{-1})	5.1	5.9	7.1	10.1	7.5
1-hr leafy (Mg ha^{-1})	5.1	7.1	9.6	8.1	7.6
1-hr total (Mg ha^{-1})	3.7	4.4	4.4	6.9	6.3
10-hr (Mg ha^{-1})	8.5	11.8	16.9	13.8	14.5
100-hr (Mg ha^{-1})	9.8	13.8	13.5	12.8	16.0
1000-hr + total (Mg ha^{-1})	12.2	***20.1***	13.6	***23.1***	***28.8***
1000-hr + DC 1 (Mg ha^{-1})	***58.2***	***32.7***	***66.7***	***44.0***	***100.0***
1000-hr + DC 2 (Mg ha^{-1})	***28.9***	***35.5***	***81.0***	***29.4***	***51.5***
1000-hr + DC 3 (Mg ha^{-1})	14.9	***31.4***	***21.5***	***26.0***	***34.6***
1000-hr + DC 4 (Mg ha^{-1})	***20.8***	***28.9***	***48.5***	***29.3***	***44.6***
1000-hr + DC 5 (Mg ha^{-1})	***35.6***	***33.3***	***88.3***	***42.4***	***56.2***
Woody total (Mg ha^{-1})	11.7	19.0	13.2	***22.5***	***27.8***
Surface fuel height (cm)	12.7	16.1	14.2	13.9	6.1
Litter depth (cm)	4.3	5.2	10.6	7.1	8.3
Litter mass (Mg ha^{-1})	11.5	15.4	14.5	***37.6***	12.9
Litter bulk density (Mg ha^{-1} cm^{-1})	10.2	17.8	7.2	***32.7***	19.5
Duff depth (cm)	16.2	12.6	***25.0***	9.2	***37.7***
Duff mass (Mg ha^{-1})	***21.7***	***41.0***	***43.4***	19.1	***43.5***
Duff bulk density (Mg ha^{-1} cm^{-1})	9.9	12.2	***37.3***	9.0	***32.5***
Forest floor depth (cm)	6.7	7.3	7.6	4.0	11.0
Forest floor mass (Mg ha^{-1})	17.8	***32.4***	16.9	15.5	***24.6***
Forest floor bulk density (Mg ha^{-1} cm^{-1})	9.7	12.7	8.4	9.0	16.0