Upland Log Volumes and Conifer Establishment Patterns in Two Northern, Upland Old-Growth Redwood Forests, A Brief Synopsis[1]

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Abstract
We characterized the volume, weight and top surface area of naturally fallen logs in an old-growth redwood forest, and quantified conifer recruit densities on these logs and on the surrounding forest floor. We report significantly greater conifer recruit densities on log substrates as compared to the forest floor. Log substrate availability was calculated on a per hectare basis using the line-intersect method. This method is used to estimate the amount of coarse woody debris present, by measuring log diameters intersected along randomly oriented transects. Conifer recruitment on intersected logs was characterized by recording recruit species, height class and substrate for each established individual. Conifer recruit densities on the forest floor were obtained for two old-growth redwood stands by establishing narrow strip plots. We found redwood logs of intermediate decay to be the most abundant woody substrate available for conifer recruitment. Where conifers had established on the forest floor, we found them most frequently on exposed mineral soil. These results confirm the use of logs by conifers in early establishment and growth, and suggest these substrates may affect stand composition and structure over the course of centuries. Differences in life-history traits between redwood and a potential competitor, western hemlock, along with the reported recruit densities, suggest redwood will remain the dominant conifer species in these stands, in the absence of significant disturbance.

Key words: coarse woody debris, disturbance, logs, nursery, recruitment

Introduction

Redwood *(Sequoia sempervirens)* is a long-lived (up to 2,000+ years) conifer that can attain great height (100+ meters tall) and massive girth (>3 meters dbh). In the last century, interest in the dwindling collection of remaining old-growth redwood stands has increased. Now, at less than 9.5 percent of their original extent (Fox 1989), these old-growth stands hold immeasurable aesthetic, cultural and spiritual values, in addition to their unique ecological qualities (Noss 2000).

The last three decades have produced a number of discoveries about redwood ecology. For example, researchers have found old-growth redwood forests contain

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some of the largest volumes of standing and downed wood biomass in the world (Bingham 1984, Bingham and Sawyer 1988, Fujimora 1977) and may serve as significant carbon sinks, thereby influencing landscape-scale carbon cycles. Old-growth redwood forests contain little known assemblages of species including epiphytic lichens in the canopy (Sillett 1999), rich invertebrate collections on the forest floor (Olson 1992), and a highly diverse collection of fungal species (Largent 1998).

The Northern portion of redwood's range most closely resembles the coastal forests of Washington and Oregon with a notable exception; redwood takes the place of Douglas-fir *(Pseudotsuga menziesii)* as the dominant overstory tree while Douglas-fir assumes a sub-dominant role in newly cleared areas or canopy gaps. Both regions are underlain by sedimentary formations, where mass wasting and slide-and-flow processes are common (Aalto and Harper 1989). Fire and windthrow also are modes of disturbance in upland settings. Signs of low intensity surface fires can be found in old-growth redwood stands (Stuart 1987), and select old-growth trees have fire scars that extend 30 to 70 meters up the boles. Severe windstorms hitting the coast of northern California and southern Oregon uproot old-growth trees and break off the trunks of others (Sawyer and others 2000). Massive logs (>two meters in diameter) can cover as much as 19 percent of the redwood forest floor. Like the coastal forests of Oregon and Washington, the predominant disturbance processes (low intensity fire and wind throw) tend to accumulate logs. Redwood logs, because of their sheer size and resistance to decay (Espinosa-Garcia and others 1996), can last for centuries on the forest floor, making them important components of ecosystem structure and function (Franklin and others 1981).

Upland forests of northern Humboldt and Del Norte counties provide the setting for this study. These stands appear to contain very few redwood seedlings and saplings. Young trees can be found along a trail's edge, or on a mound of upturned road, but among undisturbed ground, young redwoods appear to exist at extremely low densities. By contrast, western hemlock seedlings and saplings are fairly abundant, growing on logs, the forest floor, and even on other trees. Redwood seedlings and saplings also can be found on logs, but less frequently than western hemlock (Bingham 1984).

How it is then that redwood remains the dominant conifer in these forests? What disturbances, if any, affect stand composition over the course of centuries? Some ecologists have suggested that western hemlock is overtaking redwood as the dominant conifer, because pre-European disturbance regimes have been altered (Cooper 1965, Daubenmire and Daubenmire 1975). What disturbances might managers introduce to maintain the desired stand structure and species composition if it is changing due to a lack of redwood regeneration? Such questions are beyond the scope of this study. However, this study seeks to describe conifer establishment patterns in two northern old-growth upland forests to lay the groundwork for addressing these questions in the future.

This study was designed as a continuation of earlier research conducted in 1982 to 1984 (Bingham 1984). This earlier work accomplished two objectives: (1) estimate, by species and decay class, the quantity of naturally fallen decaying logs on the forest floor and (2) characterize conifer regeneration on logs in an upland old-growth redwood forest.

Naturally fallen logs play a central role in the abiotic and biotic functions of

Pacific Northwest forests (Franklin and others 1981, Norse 1990). Logs help maintain the productive capacity of the soil by helping maintain higher moisture levels (Bernsten 1960, Maser and others 1984), preventing surface erosion, moderating soil surface temperatures and providing a source of nutrient inputs (Maser and others 1984, Triska and Cromack 1980). Large coarse woody debris also store significant amounts of carbon and nitrogen (Grier 1978, Larsen and others 1978, Roskoski 1977), which gradually become available to other forest organisms.

Logs are an important substrate for tree establishment in a number of forests (Stewart and Burrows 1994) including Appalachian spruce-fir forests (White and others 1985), tropical forests (Nakashizuka 1989), and New Zealand temperate beech (Nothofagus) forests (Stewart and Burrows 1994). The phenomenon is well documented in northern temperate rainforests (Bingham and Sawyer 1988, Gray and Spies 1997, Thornburgh 1969). Logs serve as water reservoirs in forests that experience a summer dry period (Gray and Spies 1995, Harmon and Cromack 1987). One study found logs of intermediate decay to have almost three times the moisture content than the forest floor in August, and less seasonal variation in moisture (Marra and Edmonds 1994).

Higher nutrient levels on logs may also facilitate conifer establishment on these substrates compared to the forest floor. Nutrients are generally abundant on the forest floor in the northern and central redwood forests (Popenoe 1987, Zinke and others 1996), however, nitrogen may be limiting (Sawyer and others 2000). Logs may provide a level of nitrogen not available on the forest floor. For example, in the western hemlock/spruce forests of coastal Oregon, Grier (1978) reported a rapid increase in log nitrogen and other nutrients the first 20 years on the ground. A separate study of respiration rates on logs and the forest floor in temperate rainforests, indicate higher respiration rates on newly decaying logs (Marra and Edmonds 1994) compared to the forest floor. These researchers suggest the higher rates can be attributed to the release of more labile forms of carbon and nitrogen in the early stages of log decay.

Methods

We selected two upland, old-growth redwood stands in northwestern California to study conifer establishment patterns on logs and the forest floor. The northern Yurok site was chosen because it resembles Prairie Creek Redwoods State Park, where Bingham's study (Bingham 1984) was conducted. At the Yurok site, we calculated conifer recruit densities on logs and the forest floor. At the southern Prairie Creek site, we calculated conifer recruit densities on the forest floor, so that we could compare these to conifer recruit densities on logs calculated by Bingham (1984) at this same site. Combining Bingham's study with this study gives two estimates of coarse woody debris volumes for upland old-growth redwood forests, and two descriptions of conifer establishment patterns on logs and the forest floor.

To estimate the area's volume of coarse woody debris, we used the same line intersect technique (Van Wagner 1968) as Bingham (1984). A temporary system of 13 transects were established oriented in southeasterly and southwesterly directions down the slope. Line length varied with topography (range 180 meters to 420 meters, mean = 304.29 meters). Along each line we established intercept points every 60 meters. At each of these intercept points, we chose a random direction, and established a short (30 meter) transect. Along this transect, we measured diameter and length for every log (diameter >25 centimeters and length >4 meters). This method has been shown to best estimate wood volumes with the least effort (Brown and Roussopoulos 1974). Estimates obtained for the Yurok site are directly comparable to those generated by Bingham (1984).

The line intersect method for estimating coarse woody debris volumes also provided an opportunity to assess conifer establishment on decaying logs. The sampled logs were inspected on the top and sides for established (>5 centimeters tall) conifers. Species and height classes were recorded and later collapsed into three life stages: seedlings (>5 cm to 50 cm), saplings (>50 cm to 6m) and trees (>6m). Redwood sprouts originating from redwood logs were not included. The underlying logs were identified to species using anatomical features of the wood and placed into three decay classes:

1. Slightly decayed logs–bark is entirely or mostly present. Large branches may be intact. Plant growth on the log, if any, is light and can include young, understory shrub seedlings.

2. Intermediately decayed logs–broadest category. Materials are mostly sound, may contain some rot, but can support their own weight. Branch material is often gone but bark may still be present. Plant growth on the log can be quite extensive, including mature shrubs and young trees.

3. Highly decayed logs–material are mostly rotten. Logs are oval shaped and cannot support their own weight. Since this category of log resembles the forest floor, plant growth on the log is variable.

A log species and decay class together constitute a substrate; thus three predominant log species (redwood, Douglas-fir, hemlock) and three decay classes gave a total of nine log substrates.

Established conifer density on the forest floor was sampled for both sites using narrow strip plots (2 meters by 60 meters). At the Yurok site, these strip plots were oriented parallel to the lines used to establish the intercepts. We established the strip plots from topographic high points at both sites, and worked downhill for varying distances. Line lengths varied because of variable distances between site boundaries though the sampling units used to compare recruit densities (“strip plots”) were always the same.

We calculated log volume per hectare for each of the nine log substrates using Van Wagner’s equation (1) (Brown and Roussopoulos 1974, Van Wagner 1968):

$$\text{Equation 1: } v = \frac{\Pi^2 \sum d^2}{l} ac$$

Where,

v = volume (m3) of logs per m2 of forest floor.

d = diameter of each log intersected (m).

l = total length of all transects (m).

a = correction for non-horizontal orientation bias.

c = the average slope correction factor.

We calculated top surface area (TSA) estimates of log substrates per hectare of forest floor using the following equation (Lamberson 1984):

$$\text{Equation 3: TSA} = \frac{2.13\sum d}{l} ac$$

where,

TSA = the upper ½ surface area of logs, excluding ends, per unit area of forest floor (m^2/m^2).

d = the diameter of each log intersected (m).

l = the total length of all transects (m).

c = the slope correction factor.

a = correction for non-horizontal orientation bias.

Estimates of volume, weight and top surface area are all converted to a per hectare basis by multiplying the results by 10,000 m^2/ha.

Results

Log volume and weight estimates between stands were highly variable. The log total volume estimate for the Yurok site (1,457 m^3/ha) is one and a half times larger than the Prairie Creek site estimate (957 m^3/ha) *(tables 1, 2)*. Redwood logs make up the largest percentage of the overall log volume at both sites and Douglas-fir constitutes a notable percentage at the Prairie Creek site. Redwood logs of intermediate decay make up the majority of log volume at the Yurok and Prairie Creek sites, 64.8 percent and 55.2 percent respectively.

Table 1—*Volumes (m^3/ha) and weights (mt/ha)[a] of decaying logs on the forest floor at the Yurok site. Decay classes: 1- slightly decayed, 2- intermediately decayed, 3- highly decayed.*

	Redwood		W. hemlock		Douglas-fir		Totals	
Decay Class	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**
1	55.15	22.06	0.00	0.00	7.66	3.68	62.81	25.74
2	943.66	358.59	2.76	1.05	41.59	18.30	988.01	377.94
3	394.16	118.25	4.90	1.47	7.43	2.23	406.49	121.95
Total	1,393	499	8.00	3.00	57.00	24.00	1,457.00	525.63

[a] mt = metric tons

Table 2—*Volumes (m^3/ha) and weights (mt/ha) of decaying logs on the forest floor at Prairie Creek (Bingham 1984). Decay classes: 1- slightly decayed, 2- intermediately decayed, 3- highly decayed.*

	Redwood		W. hemlock		Douglas-fir		Totals	
Decay Class	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**	**Volume (m^3/ha)**	**Weight (mt/ha)**
1	56	23	22	9	16	8	94	40
2	528	202	10	4	68	30	606	236
3	236	71	4	1	17	5	257	77
Total	820	296	36	14	101	43	957	353

Redwood logs represent most of the log area available for conifer colonization at both sites: 94 percent at the Yurok site and 78 percent at the Prairie Creek site *(tables 3, 4)*. Redwood logs of intermediate decay are the most readily available of all substrate types representing 62.1 percent of the available log area at Yurok site and 45.6 percent at the Prairie Creek site.

At both sites, conifer establishment on logs is patchy. Recruits were found on 64 of the 160 logs (40 percent) at the Yurok site, and Bingham (1984) found recruits on 130 of 276 logs (47 percent) at the Prairie Creek site. A total of 415 recruits were found on logs at the Yurok site, and 1,048 recruits were found on logs at the Prairie Creek site (Bingham 1984).

At both sites, of the number of recruits by log size and decay class was highly variable. For example, at the Yurok site a 1.5 meter diameter redwood log had 46 recruits on its upper surface, and a 1.7 meter diameter redwood log of similar decay and length had no recruits. Bingham (1984) had similar results. Overall recruitment on logs of all species was higher at Prairie Creek (197 recruits/ha,) than at the Yurok site (119 recruits/ha) despite more available log substrate at the Yurok site.

As in Bingham's study, western hemlock was the most abundant conifer species on logs, with an estimated 103 recruits/ha at the Yurok site. There are six redwood recruits per hectare at the Yurok site (third most common species) and 56 redwood recruits per hectare at the Prairie Creek site. Redwood logs of intermediate decay hold the highest percentage of conifers of all log substrates (72.5 percent Yurok site; 44.2 percent Prairie Creek site).

Table 3—*Top surface areas of each decay class available for conifer establishment at the Yurok site. Values represent the upper one-half surface area, excluding log ends, per hectare of forest floor (m^2/ha). Decay classes: 1- slightly decayed, 2- intermediately decayed, 3- highly decayed.*

Decay Class	Redwood	W. hemlock	Douglas-fir	Total	Percent
1	47.66	0.00	18.54	66.20	3
2	1206.16	7.94	67.52	1281.62	66
3	568.00	10.59	17.21	595.80	31
Total	1821.82	18.53	103.27	1943.62	
Percent	94	1	5		100

Table 4—*Top surface areas of each decay class available for conifer establishment at the Prairie Creek site (Bingham 1984). Values represent the upper one-half surface area, excluding log ends, per hectare of forest floor (m^2/ha). Decay classes: 1- slightly decayed, 2- intermediately decayed, 3- highly decayed***.**

Decay Class	Redwood	W. hemlock	Douglas-fir	Total	Percent
1	86	50	44	180	12
2	681	31	135	847	57
3	403	18	45	466	31
Total	1170	99	224	1493	
Percent	78	7	15		100

This study confirms the observations of researchers and park managers that redwood forest floor recruit densities are low to non-existent (12 redwood recruits/ha at the Yurok site and 16 redwood recruits/ha at the Prairie Creek site). Nearly all of these recruits were greater than six meters tall, making it difficult to determine their origin (seed or sprout).

Despite low recruit densities on logs and the forest floor at the Yurok site, differences between these two major substrate categories are still apparent. The proportion of forest floor sampling units (in other words, strip plots) containing no recruits is nearly twice as high (84.5 percent; n = 58) as the same proportion for the log sampling units (46.6 percent; n = 71). Similarly, 72 percent of ground sampling units at Prairie Creek had no recruits, and 53 percent log sampling units had no recruits (Bingham 1984). When recruits are present on either of these two major substrate categories, differences in mean conifer densities (# recruits/m^2) between logs and the forest floor at the Yurok site are statistically significant ($p = 0.001$) *(table 5)*. An analogous comparison for the Prairie Creek site cannot be made because the raw data from Bingham's original study are not available. However, the overall number of recruits on logs per hectare at Prairie Creek site (197) is clearly higher than the number of recruits per hectare of forest floor (38). Differences between recruit densities on the forest floor between sites were not significant ($p = 0.506$).

Table 5—*Average number of conifer recruits when recruits present, per square meter of substrate (± S.D.). Recruit densities on logs vs. the forest floor are significantly different at the Yurok site (p = 0.001). Forest floor recruit densities between sites are not significantly different (p = 0.506).*

Substrate Category	Yurok site	Prairie Creek site
Logs	0.082 (0.10)	Not available
Forest floor	0.012 (0.011)	0.015 (0.010)

Conclusions

Upland old-growth redwood forests in the northern portion of the species range contain some of highest quantities of coarse woody debris in the world (Bingham and Sawyer 1988, Franklin and Waring 1980, Fujimora 1977). This is in large part due to the massive size of live trees, redwood's slow rate of decomposition (Espinosa-Garcia and others 1996) and a combination of historic forest processes that favored the accumulation of log material.

The role of fire in the redwood region has been debated for decades. Early studies (for example, Veirs 1980, Stuart 1987) relied on stump records or indirect measurements (sprouting frequency) and tended to over-estimate fire return intervals. More recent studies (Brown and Baxter 2003; Brown and others 1999; Brown and Swetnam 1994; Finney and Martin 1989, 1992) have taken direct measurements nearer ground level, thereby recording more frequent fires (two 22-year intervals) characterized by low flame length typical of many old-growth fires. Together, these studies suggest that high severity fires have historically been relatively infrequent and that low severity fires occurred every two to three decades. Though the volume of log material consumed by old-growth wildfires has not been recorded, these studies in combination with the log volumes reported in this study suggest that rates of log accumulation (windthrow) exceed the rates of log export (via fire) in northern old-growth redwood forests.

Considerable variation in the quantity of coarse wood debris exists between apparently similar old-growth sites. Slope, aspect and distance to the ocean effect overstory species composition (Mahony 2000), which ultimately influences log volume. Where geographic locations are similar, mid and low slope positions generally support a higher proportion of large redwood trees than ridge and upper slope positions, where white woods become more common.

Conifer recruit densities are highest on redwood logs of intermediate decay. This substrate type is the most abundant in the stands studied. Other log substrates were not present in sufficient quantity to resolve substrate preferences between log species. Conifer recruit densities on the forest floor are highest on exposed mineral soil, as also indicated anecdotally in previous studies (for example, Metcalf 1924), but in general, the forest floor was found to be an inhospitable place for recruitment. Conifer recruit densities on logs are significantly higher than those found on the forest floor though on both general substrate categories, the distribution of recruits was highly variable. Studies have suggested that this variability may be related to microsite variables that effect establishment (for example, Gray and Spies 1997).

Western hemlock establishes frequently on log substrates (Christy and Mack 1983, Thornburgh 1969, Zobel and Antos 1991) and appears to survive in a co-dominant and suppressed form on redwood logs of intermediate decay in northern old-growth redwood forests. Differences in gross life history traits (for example, size, longevity) between redwood and western hemlock and the recruit densities presented here, suggest redwood will remain dominant in these stands, even in the absence of significant disturbance (for example, fire). This conclusion pertains only to northern upland old-growth redwood forest.

References

Aalto, K.R.; Harper, G.D. 1989. **Geologic evolution of the northernmost coast ranges and western Klamath mountains, California**. Washington, DC: American Geophysical Union.

Bernsten, C.M. 1960. **Planting Sitka spruce and Douglas-fir on decayed wood in coastal Oregon**. Res. Note PNW-197. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Bingham, B.B. 1984. **Decaying logs as a substrate for conifer regeneration in an upland old-growth redwood forest**. Arcata, CA: Humboldt State University. M.S. thesis.

Bingham, B.B.; Sawyer, J.O. 1988. **Volume and mass of decaying logs in an upland old-growth redwood forest**. Canadian Journal of Forest Research 18: 1649-1651.

Brown, J.K.; Roussopoulos, P.J. 1974. **Eliminating biases in the planar intersect method for estimating volumes of small fuels**. Forest Science 20: 350-356.

Brown, P.M.; Baxter, W.T. 2003. **Fire history in coast redwood forests of the Mendocino Coast**. Northwest Science 77: 147-158.

Brown, P.M.; Swetnam, T.W. 1994. **A cross-dated fire history from coast redwood near Redwood National Park, Californi**a. Canadian Journal of Forest Research 24: 21-31.

Bunnell, F.L.; Chan-McLeod, A.C. 1997. **Terrestrial vertebrates**. In: Schoonmaker, P.K.; von Hagen, B.; Wolf, E.C., eds. The rainforest of home: profile of a North American bioregion. Washington, DC: Island Press; 103–130.

Christy, J.E.; Mack, R.N. 1983. **Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic**. Journal of Ecology 71: 75–93.

Cooper, D.W. 1965. **The coast redwood and its ecology**. Eureka, CA: Humboldt County Agricultural Extension Service.

Daubenmire, R.F.; Daubenmire, J. 1975. **The status of coastal redwood, *Sequoia sempervirens***. Unpublished report prepared for the USDI, National Park Service. Arcata, CA: Redwood National Park.

Espinosa-Garcia, F.J.; Rollinger, J.L.; Langeheim, J.H. 1996. **Coastal redwood leaf endophytes: their occurrence, interactions, and response to host volatile terpenoids**. In: Redlin, S.C.; Carris, L.M., eds. Endophytic fungi in grasses and woody plants: systematics, ecology and evolution. St. Paul, MN: American Phytopathology Society; 101–130.

Finney, M.A.; Martin, R.E. 1989. **Fire history in a *Sequoia sempervirens* forest at Salt Point State Park, California**. Canadian Journal of Forest Research 19: 1451–1457.

Finney, M.A.; Martin, R.E. 1992. **Short fire intervals recorded by redwoods at Annadel State Park, California**. Madrono 39: 251-262.

Fox, Lawrence III. 1989. **A classification, map and volume estimate for the coast redwood forest in California**. Final report. Interagency agreement number 8CA52849. Sacramento, CA: The Forest and Rangeland Resources Assessment Program, California Department of Forestry and Fire Protection.

Franklin, J.F.; Waring, R.H. 1980. **Distinctive features of the northwestern coniferous forest: Development, structure and function**. In: Waring, R.H., ed. Forests: fresh perspectives from ecosystems analysis. Annual Biology Colloquium, 1979. Corvallis, OR: Oregon State University: 59–85.

Fujimori, T. 1977. **Stem biomass and structure of a mature *Sequoia sempervirens* stand on the Pacific Coast of northern California**. Journal of the Japanese Forestry Society 59: 431-441.

Gray, A.N.; Spies, T.A. 1995. **Water content measurement in forest soils and decayed wood using time domain reflectometry**. Canadian Journal of Forest Research 25: 376-385.

Gray, A.N.; Spies, T.A. 1997. **Microsite controls on tree seedling establishment in conifer forest canopy gaps**. Ecology 78: 2458–2473.

Grier, C.C. 1978. **A *Tsuga heterophylla-Picea sitchensis* ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs**. Canadian Journal of Forest Research 8: 198–206.

Harmon, M.E.; Cromack, K., Jr. 1987. **Course woody debris in mixed-conifer forests, Sequoia National Park, California**. Canadian Journal of Forest Research 17: 1265–1272.

Largent, D.L. 1998. **Species of mushrooms, boletes, chanterelles, coral fungi, and tooth fungi found in the Redwood National and States Parks between 1993 and 1997**. Unpublished report. Redwood National Park, Arcata, CA.

Larsen, M.J.; Jurgensen, M.F.; Harvey, A.E. 1978. **N_2 fixation associated with wood decayed by some common fungi in western Montana**. Canadian Journal of Forest Research 8: 341-345.

Mahony, T.M.; Stuart, J.D. 2000. **Old-growth forest associations in the northern range of coastal redwood**. Madrono 47: 53-60.

Marra, J.L.; Edmonds, R.L. 1994. **Coarse woody debris and forest floor respiration in an old-growth coniferous forest on the Olympic Peninsula, Washington, USA**. Canadian Journal of Forest Research 24: 1811-1817.

Maser, C.; Trappe, J.M.; Cline, S.P.; Cromack, K., Jr.; Blaschke, H.; Sedell, J.R.; Swanson, F.J. 1984. **The seen and unseen world of the fallen tree.** Gen. Tech. Rep. PNW-GTR-164. Portland, OR: Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture.

Metcalf. W. 1924. **Artificial reproduction of redwood (*Sequoia sempervirens*)**. Journal of Forestry 22: 873-893.

Nakashizuka, T. 1989. **Role of uprooting in composition and dynamics of an old-growth forest in Japan**. Ecology 70: 1273–1278.

Norse, E.A. 1990. **Ancient forests of the Pacific Northwe**st. Washington, DC: Island Press.

Noss, R.F. 2000. **The redwood forest: history, ecology and conservation of the coast redwoods**. Covelo, CA: Island Press.

Olson, D.F.; Roy, D.F.; Walters, G.A. 1990. ***Sequoia sempervirens* (D. Don) Endl**. In: Burns, R.M.; Honkala, B.H., eds. **Silvics of North America**. **Volume 1. Conifers**. Agric. Handbook. 654. Washington, DC: U.S. Department of Agriculture; 541-551.

Olson, D.M. 1992. **The northern spotted owl conservation strategy: implications for Pacific Northwest invertebrates and associated ecosystem processes**. Final Report prepared for the Northern Spotted Owl EIS Team. USDA Forest Service, Order number 40-04HI-2-1650.

Popenoe, J.H. 1987. **Soil series descriptions and laboratory data from Redwood National Par**k. Technical Report 20. Orick, CA: Redwood National Park.

Roskoski, J.P. 1977. **Nitrogen fixation in northern hardwood forests**. New Haven, CT: Yale University. Ph.D. dissertation.

Sawyer, J.O.; Sillett, S.C.; Popenoe, J.H.; LaBanca, A.; Scholars, T.; Largent, D.L.; Euphrat, F.; Noss, R.F.; Van Pelt, R. 2000. **Characteristics of redwood forests**. In: Noss, R.F. ed. The redwood forest: history, ecology and conservation. Covelo, CA: Island Press; 39-79.

Sillett, S.C. 1999. **Tree crown structure and vascular epiphyte distribution in *Sequoia sempervirens* rain forest canopies**. Selbyana 20: 76-97.

Snyder, J.A. 1992. **The ecology of *Sequoia sempervirens*: an addendum to On the edge: Nature's last stand for coast redwoods**. San Jose, CA: San Jose State University. M.S. thesis.

Stewart, G.H.; Burrows, L.E. 1994. **Coarse woody debris in old-growth temperate beech (Nothofagus) forests of New Zealand.** Canadian Journal of Forest Research 24: 1989-1996.

Stuart, J.D. 1987**. Fire history of an old-growth forest of *Sequoia sempervirens* (Taxodiaceae) forest in Humboldt Redwoods State Park, CA**. Madrono 34: 128–141.

Thornburgh, D.A. 1969. **Dynamics of the true fir-hemlock forests of western Washington**. Seattle: University of Washington. Ph.D. dissertation.

Triska, F.J.; Kromack, K., Jr. 1980. **The role of wood debris in forests and streams**. In: Waring, R.H., ed. Forests: fresh perspectives from ecosystem analysis. Corvallis, OR: Oregon State University Press; 171-190.

Van Wagner, C.E. 1968. **The line intersect method in forest fuel sampling**. Forest Science 14: 20-26.

Viers, S.D. 1981. **The influence of fire in coastal redwood forests**. In: Proceedings of the fire history workshop; 1980 October 20-24; Tucson, AZ. Gen. Tech. Rep. RM-GTR-81. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 93-95.

White, P.S.; MacKenzie, M.D.; Busing, R.T. 1985. **Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests**. Canadian Journal of Forest Research 15: 233-240.

Zinke, P.J.; Stangenberger, A.G.; Bertenshaw, J.L. 1996. **Pattern and process in forests of *Sequoia sempervirens* (D.Don) Endl**. In: LeBlanc, J. ed. Proceedings of the conference on coast redwood forest ecology and management; June 18-20, 1996; Arcata, CA. University of California, Cooperative Extension, Forestry.

Zobel, D.B.; Antos, J.A. 1999. **Growth and development of natural seedlings of Abies and Tsuga in old-growth forests**. Journal of Ecology 79: 985-998.