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Understory plant establishment on old-growth stumps and the forest floor in western Washington

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Abstract

Coarse woody debris (CWD) provides an important regeneration niche for many tree species, but its role in understory plant establishment has not been well studied. To examine the role of CWD in understory plant establishment, we compared woody vegetation and ferns occurring on 50 paired stump and ground plots (substrates) in a coniferous and a deciduous forest (sites) in Olympia, WA. Plant species richness, evenness, and diversity were similar across substrates and sites. However, Bray–Curtis ordinations revealed clear separation between stump and ground vegetation at each site. *Vaccinium parvifolium* and *Gaultheria shallon* dominated stump vegetation, while *Rubus ursinus* and *Polystichum munitum* were major components of ground vegetation. *V. parvifolium* and *G. shallon* co-occurred on both substrates at the coniferous site, but not at the deciduous site where *Rubus spectabilis* dominated ground vegetation, probably because of higher light intensity. In areas where *R. spectabilis* is dominant, elevated CWD microsites may increase local species richness by providing refugia for species unable to persist under the *R. spectabilis* canopy. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Coarse woody debris; Refugia; Regeneration niche; *Rubus spectabilis*; Species richness

1. Introduction

Coarse woody debris (CWD) is an important component of many temperate and tropical forests and has been the subject of extensive recent research, particularly in the northwest forests of North America (Harmon et al., 1986). CWD, which includes snags, fallen logs, pieces of wood, large branches, and stumps, provides habitat for numerous organisms and plays a role in many ecological processes, including nutrient cycling, energy flow, and disturbance (Spies et al., 1988).

The role of "nurse logs" as establishment sites for tree seedlings has been a major theme in CWD research. CWD creates a mosaic of substrates on the forest floor, which results in a variety of microsites. Microsites provide seedlings of different species with distinct regeneration niches and thus facilitates species coexistence through resource partitioning (Grubb, 1977). McKee et al. (1982) found that 94–98% of all tree seedlings in a *Picea sitchensis* (Bong.) Carriere-*Tsuga heterophylla* (Raf.) Sarg. forest in Washington were growing on fallen logs that occupied only 6–11% of the forest floor. McGee and Birmingham (1997) showed differences between species composition and densities of tree seedlings growing on fallen logs and the forest floor in two northeastern hardwood forests. Others have shown similar patterns of association

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between tree seedling recruitment and CWD in the United States (Christy and Mack, 1984), Sweden (Hofgaard, 1993), New Zealand (Lusk and Odgen, 1992) and Chile (Lusk, 1995). Many hypotheses have been offered to explain the differential survival of tree seedlings on CWD including competition for light, soil pathogens, waterlogging, nutrient availability, browsing, and seed size (for discussion, see Harmon and Franklin, 1989). Harmon and Franklin (1989) tested a number of these hypotheses experimentally in two Pacific Northwest coastal forests and suggested that competition for light from shrubs and herbs was the principle reason why tree seedling recruitment was primarily limited to CWD.

Although there has been considerable research on the role of CWD in seedling establishment, most studies have focused only on tree species (e.g. Harmon and Franklin, 1989; Gray and Spies, 1997). Nonetheless, there is evidence to suggest that CWD may also be important for the maintenance of understory plant species richness at local scales. Dennis and Bateson (1974) found 11 of the 24 species present in a South Carolina swamp were confined exclusively to stumps and other elevated CWD. Sharitz (1996) reported a strong association between woody seedlings and stumps in two South Carolina swamps and suggested that CWD was important in maintaining the overall species richness of the system. Understanding the relationship between CWD and understory plant species is important because these plants can have a significant influence on forest nutrient dynamics, microclimates, and successional pathways (Macguire and Forman, 1983; Tappeiner et al., 1991).

The objective of this study was to investigate the role of elevated CWD microsites (old-growth conifer stumps) in understory plant and fern establishment in two common Pacific Northwest forest types. We document the differential utilization of stump versus ground substrates by woody plant species and examine differences in plant communities associated with these two substrates.

2. Materials and methods

2.1. Description of study sites

The study was conducted in the East Campus Reserve of The Evergreen State College, 8.25 km west of Olympia, WA, USA (47°04′20″N, 122°58′43″W). The 75 ha reserve consists of deciduous, coniferous, and mixed forest types. We established two study sites, one in a deciduous dominated forest approximately 10 ha in size and the other in an adjacent conifer dominated forest approximately 15 ha in size. *Alnus rubra* Bong. (red alder) is the dominant overstory species in the deciduous forest (Table 1) and *Rubus spectabilis* Pursh (salmonberry) and *Polystichum munitum* (Kaulf.) C. Presl (sword fern) are the most common understory species (Trivett, 1998). *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), *T. heterophylla* (western hemlock) and *Thuja plicata* D. Don (western red cedar) are the major overstory species at the conifer site contributing 41, 19, and 18% of the total stem density, respectively (Table 1). *A. rubra* is frequently encountered in canopy gaps and *Gaultheria shallon* Pursh (salal) and *P. munitum* are the most prevalent understory species (Trivett, 1998). Historic records and our stump data suggest the reserve was a nonharvested

Table 1
Forest characteristics for deciduous and coniferous sites in the East Campus Reserve of The Evergreen State College, Olympia, WA (47 04′20″N, 122 58′43″W) in 2000[a]

Forest characteristic	Site	
	Deciduous	Coniferous
Tree density (stems per ha)[b]		
Alnus rubra	371	84
Acer macrophyllum	45	18
Tsuga heterophylla	22	90
Thuja plicata	11	84
Pseudotsuga mensiezii	0	198
Prunus emarginata	0	6
Total tree density[b]	449 (0.57)[c]	481 (0.61)[c]
Tree diameter at breast height (m)[d]	0.37 (0.01)	0.41 (0.02)
Stump density (per ha)[e]	44	38
Stump area (m^2)[f]	0.89 (0.08)	0.55 (0.07)
Stump height (m)[f]	2.96 (0.11)	2.09 (0.10)
Rubus spectabilis height (m)[g]	2.15 (0.08)	NA[h]

[a] Standard errors are in parentheses.

[b] Data from 20 points using the point quarter method.

[c] Standard errors were calculated only for total tree density based on Krebs (1999).

[d] Data from 80 trees, as identified by the point quarter method, per site.

[e] Data from Baker et al. (1975), unpublished.

[f] Data from 50 stumps per site.

[g] Data from 50 randomly located points.

[h] Not applicable.

conifer dominated forest prior to clearcutting in the early 1930s (Hall et al., 1976). The reserve was left to naturally regenerate and has not been disturbed except for selective harvesting in the coniferous forest that occurred in the 1960s.

The reserve is characterized by a cool maritime climate, with a mean annual temperature of 10.5°C, and mean annual precipitation of 129 cm (Trivett, 1998). Most precipitation (approximately 90%) accumulates during the fall, winter and spring months (Trivett, 1998). The predominant soils in the reserve are the Alderwood gravelly sandy loam and Yelm fine sandy loam series, which are derived from glacial and post-glacial materials (USDA, 1990). Slope throughout the reserve is <5% (Trivett, 1998).

2.2. Sampling

In February 2000, we established a 250 m transect at each site (hereafter deciduous site and coniferous site), located near the center of each forest to minimize edge effects. We marked all stumps visible from the two transects and then randomly selected 25 at each site for sampling. Our samples were limited to stumps (1) created during timber harvests in the 1930s as determined from decay class, size, and height and (2) having a solid and relatively flat upper surface (<30° slope). The majority of stumps at both sites had either relatively flat upper surfaces or very steep upper surfaces, the latter being indicative of advanced decay. Stumps with steep upper surfaces were excluded because seedlings rarely established on the acutely sloping surfaces and we wanted to minimize variance associated with substrate conditions (McGee and Birmingham, 1997). All 50 stumps were classified as decay class 3 in the log decomposition system of Maser et al. (1979). Since bark was generally either absent or found in trace amounts, identification of the species of the stumps was difficult. Stumps that could be positively identified were either *T. heterophylla* or *P. menziesii*. The diameter at breast height and height of each stump was recorded. At each stump, we also established a paired ground plot. Ground plots were located 4 m away from the stump (to assure that no plants associated with the debris at the base of the stump were sampled) along one of the four randomly selected cardinal directions. The area of each ground plot was equal to the area of its paired stump. At each stump and ground plot, we counted the number of stems of woody plant species and ferns (i.e. ramets for clonally reproductive species). Plant stems rooted in either the side of the stumps or in the debris at the base of the stumps were not counted.

Stand characteristics of the two sites were determined using the point-quarter method (Krebs, 1999), with 20 randomly located points at each site. The height of *R. spectabilis* cover at the deciduous site was estimated from 50 randomly located points in the stand. The tallest *R. spectabilis* stem within a 2-m radius was taken to represent the height of the cover at each point. If no stems were present within the 2-m radius, a value of 0 m was given at that point.

2.3. Statistical analysis

We used two factor (substrate and site) analysis of covariance (ANCOVA) with stump surface area and stump height as covariates, to determine if natural log (species richness + 1) was different between substrates and between sites. Species richness was log-transformed to improve normality, homoscedasticity, and additivity (Zar, 1984). Similarly, we used two factor analysis of variance (ANOVA) to determine if Simpson's index of diversity and Camargo's measure of evenness (Krebs, 1999) were equal between substrates and sites. Simpson's and Camargo's indices were normally distributed as determined by Lilliefor's test (Wilkinson, 1992). We compared stem densities of each species using a Kruskal–Wallis two factor (substrate and site) nonparametric ANOVA. A Kruskal–Wallis ANOVA was used because stem densities were strongly non-normal even after applying various transformations.

Bray–Curtis ordinations were used (PC-ORD, McCune, 1999) to discern general trends in species composition of the two substrates at the deciduous and coniferous sites. Stem density data were transformed using the Beals smoothing technique (Beals, 1984) before conducting the ordination. Three plots (one at the deciduous site and two at the coniferous site) with no species present were excluded to avoid zero truncation (Beals, 1984). Pearson's correlation coefficients were used to determine the relationship between the densities of the six most common species and the first axis ordination scores (McCune, 1999). All statistics were considered significant at $P = 0.05$.

3. Results

We encountered a total of 14 species at the two sites. Three species were found only on stumps, four were found only on the ground, and seven were found on both substrates (Fig. 1). There were no significant differences in species richness between stump and ground plots at either site ($F_{1,94} = 0.00004$, $P = 0.995$) or between substrates (stump versus ground) within each site ($F_{1,94} = 0.0163$, $P = 0.889$) Also, there was no significant interaction between substrate and site ($F_{1,94} = 0.3006$, $P = 0.585$). Plot area ($F_{1,94} = 2.8038$, $P = 0.097$) and stump height ($F_{1,94} = 0.0005$, $P = 0.9827$) had no significant effect on species richness, probably because of the small range of areas and heights sampled (Table 1). Simpson's index of diversity values were not significantly different between substrates ($F_{1,73} = 1.087$, $P = 0.301$) or sites ($F_{1,73} = 0.171$, $P = 0.680$) and there was no interaction between substrate and site ($F_{1,73} = 0.004$, $P = 0.947$). Likewise, there was no significant difference in Camargo's measure of evenness between substrates ($F_{1,73} = 140$, $P = 0.709$) and sites ($F_{1,73} = 0.077$, $P = 0.783$) and there was no interaction between substrate and site ($F_{1,73} = 0.122$, $P = 0.728$) (Table 2).

There were significant differences in stem densities of five of the six most abundant species across the combinations of substrates and sites (Fig. 2). *G. shallon* and *Vaccinium parvifolium* Smith each had higher stem densities on stumps than on the ground at both sites (Kruskal–Wallace [KW] $\chi^2_{0.05,1} = 29.20$, $P < 0.001$ and KW $\chi^2_{0.05,1} = 53.20$, $P < 0.001$, respectively). In addition, *G. shallon* was more abundant at the deciduous site than the coniferous site (KW $\chi^2_{0.05,1} = 4.88$, $P < 0.05$). Conversely, *R. spectablilis*, *Rubus ursinus* Cham. & Schldl. and *P. munitum* each had higher stem densities on the ground than on stumps at both sites (KW $\chi^2_{0.05,1} = 10.72$, $P < 0.005$, KW $\chi^2_{0.05,1} = 28.54$, $P < 0.001$, KW $\chi^2_{0.05,1} = 8.69$, $P < 0.005$, respectively). In addition, *R. spectabilis* was more abundant at the deciduous site than the conifer site (KW $\chi^2_{0.05,1} = 8.91$, $P < 0.005$) and there was a significant interaction of substrate and site (KW $\chi^2_{0.05,1} = 8.91$, $P < 0.005$). There were no significant differences in the stem densities of *Polypodium glycyrrhiza* D. Eaton in all combinations of substrates and sites (KW $\chi^2_{0.05,1} = 3.46$, $P < 0.100$).

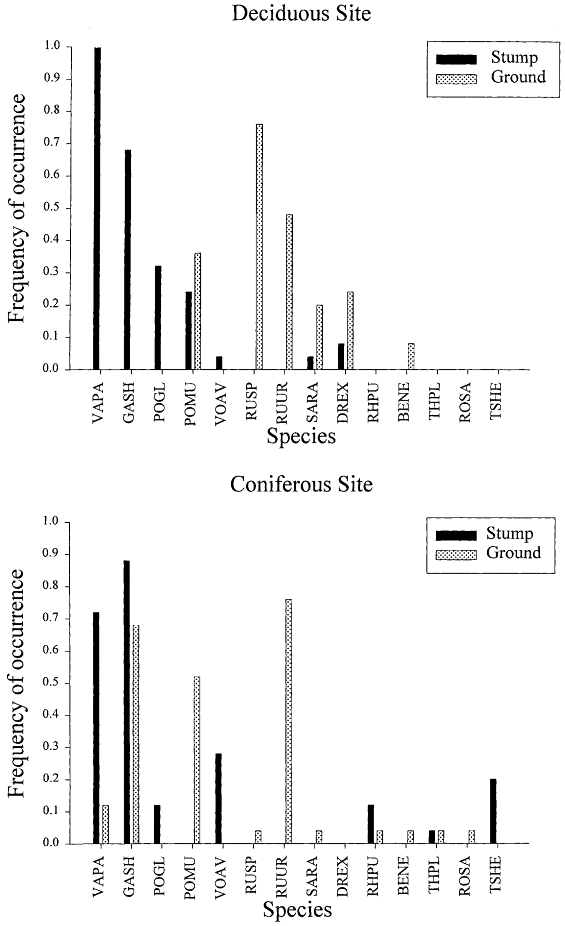

Fig. 1. Species presence/absence data in paired stump and ground plots at the deciduous and coniferous sites in The Evergreen State College East Campus Reserve, Olympia, WA (47°04′20″N, 122°58′43″W) in 2000. The deciduous site was dominated by *Alnus rubra* and to a lessor extent *Acer macophyllum* in the overstory while the coniferous site was dominated by *Pseudotsuga mensiezii* in the overstory. See Table 1 for details of site characteristics. Species abbreviations: VAPA (*Vaccinium parvifolium*), GASH (*Gaultheria shallon*), POGL (*Polypodium glycrrhiza*), POMU (*Polystichum munitum*), VAOV (*Vaccinium ovatum*), RUSP (*Rubus spectabilis*), RUUR (*Rubus ursinus*), SARA (*Sambucus racemosa*), DREX (*Dryopteris expansa*), RHPU (*Rhamnus purshiana*), BENE (*Berberis nervosa*), THPL (*Thuja plicata*), ROSA (*Rosa* sp.), TSHE (*Tsuga heterophylla*).

The Bray–Curtis ordinations illustrated differences between the stump and ground communities at both sites (Fig. 3). Stump plots at both sites had low first axis scores while ground plots at both sites had high first axis scores. Plots with low first axis scores were

Table 2
Species richness, Camargo's measure of evenness, and Simpson's index of diversity of stump and ground plots in the East Campus Reserve of The Evergreen State College, Olympia, WA (47 04′20″N, 122 58′43″W) in 2000[a]

Community measure	Site			
	Deciduous		Coniferous	
	Stump	Ground	Stump	Ground
Species richness	2.40 (0.25)	2.68 (0.33)	2.36 (0.17)	2.28 (0.20)
Species evenness	0.70 (0.03)	0.70 (0.04)	0.70 (0.04)	0.67 (0.03)
Species diversity	0.44 (0.05)	0.49 (0.05)	0.46 (0.05)	0.51 (0.04)

[a] The deciduous site was dominated by *Alnus rubra* and to a lessor extent *Acer macophyllum* in the overstory while the coniferous site was dominated by *Pseudotsuga mensiezii* in the overstory. There were 25 plots per substrate (stump or ground) at each site (deciduous or coniferous), totaling 100 plots. Standard errors are in parentheses.

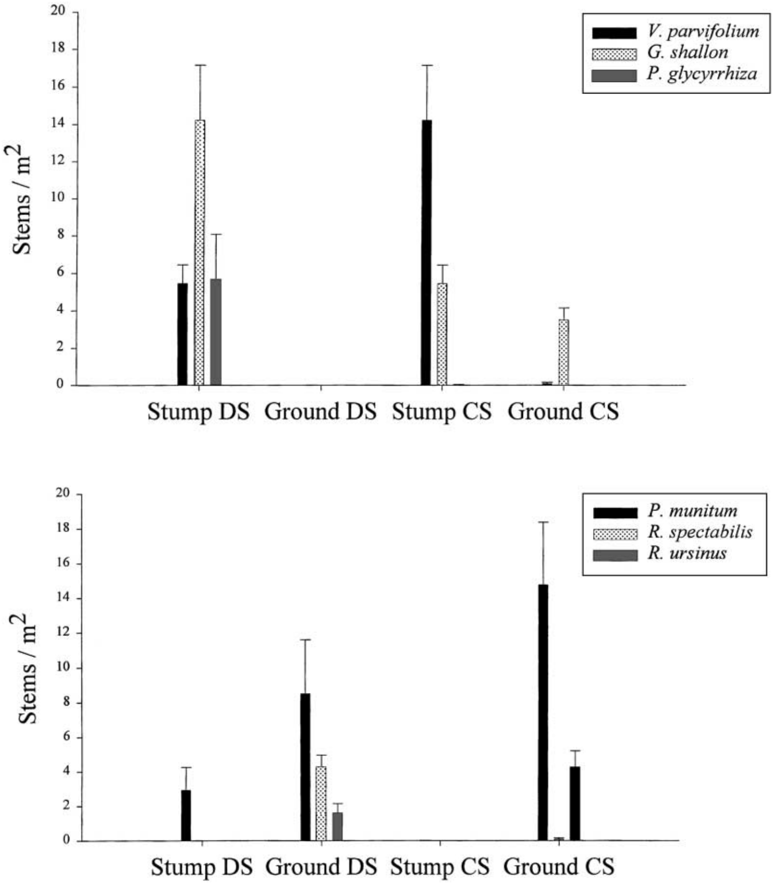

Fig. 2. Mean stem densities and standard errors for six most abundant species in paired stump and ground plots in the deciduous (DS) and coniferous sites (CS) in The Evergreen State College East Campus Reserve, Olympia, WA (47°04′20″N, 122°58′4″W) in 2000. See Table 1 for details of site characteristics.

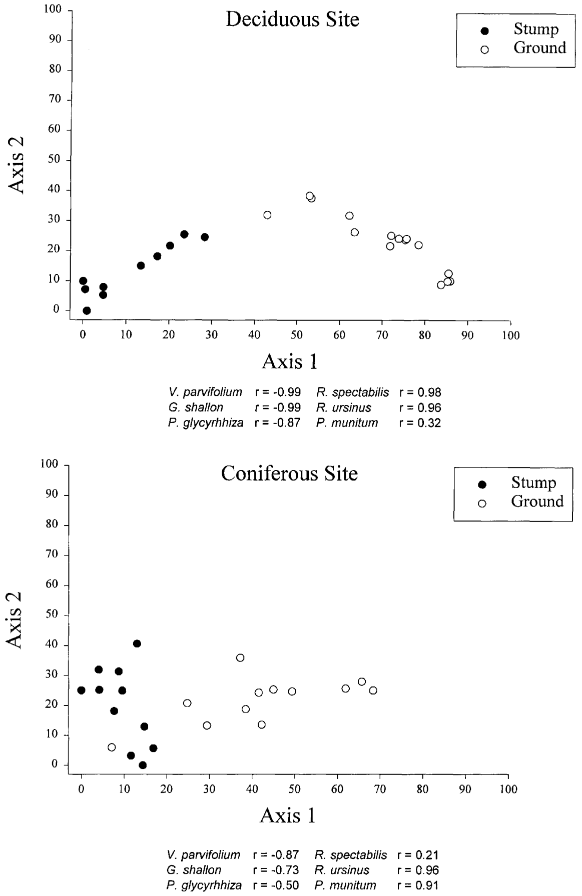

Fig. 3. Bray–Curtis ordinations of plant community composition in paired stump and ground plots in the deciduous and coniferous sites (49 and 48 plots, respectively) sites in The Evergreen State College East Campus Reserve, Olympia, WA (47°04′20″N, 122°58′43″W) in 2000. See Table 1 for details of site characteristics. The distances between plots (represented as circles) reflect their respective degrees of dissimilarity in species composition. Pearson correlation coefficients (*r*) are calculated for six most abundant species. *G. shallon*, *V. parvifolium*, and *P. glycyrrhiza* densities are negatively correlated with the first-axis coordinates, while *P. munitum*, *R. ursinus*, and *R. spectabilis* densities are positively correlated with the first-axis coordinates at both sites.

dominated by *V. parvifolium*, *G. shallon*, and *P. glycyrrhiza*, while plots with high first axis scores had high densities of *P. munitum*, *R. ursinus*, and *R. spectabilis* (Fig. 3). Although separation between the two substrates was clear at both sites, stump and ground vegetation appeared to be more distinct in the deciduous site than the coniferous site.

4. Discussion

Stump and ground plots at both sites had similar species richness, evenness, and diversity. The composition and stem densities of species growing on stumps and the ground, however, differed considerably at both sites. These differences were most pronounced at the deciduous site, where three of the four most common species on stumps were not found on the ground. The presence of stumps at the deciduous site increased understory plant species richness compared to areas in which stumps were absent. The presence of stumps also increased the species richness of the coniferous site, but only one of the three most common stump species was unique to stumps.

The species composition of stump vegetation at the deciduous site was more similar to stump and ground vegetation at the coniferous site than ground vegetation at the deciduous site. Differences between the stump and ground vegetation at the deciduous site probably resulted from the dominance of *R. spectabilis* in the understory. *R. spectabilis* is a clonal shrub that grows particularly well in *A. rubra* forests, where greater amounts of light pass through the forest overstory than in coniferous forests, particularly in the spring before leaf-out (Franklin and Pechanec, 1967). *R. spectabilis* can form a dense and continuous cover (Carlton, 1988). Moreover, the vigorous vegetative growth of aerial stems and rhizomal extension of *R. spectabilis* can result in its persistence as the dominant understory species for long periods of time (Tappeiner et al., 1991). Dense *R. spectabilis* cover can preclude the establishment of other plant species to the extent that it may severely retard forest succession (Tappeiner et al., 1991; Minore and Weatherly, 1994).

Stumps were considerably taller than the height of the *R. spectabilis* cover at the deciduous site and the tops of all 25 stumps at the deciduous site were above any understory plant cover. Elevated stump tops may provide a refugia for species unable to persist under the dense *R. spectabilis* cover and thus allow species to colonize the deciduous site that would otherwise not persist on the forest floor. *G. shallon*, which occurred frequently and at relatively high stem densities on stumps at both sites, has higher growth rates with increasing light intensities. For example, Messier (1992) showed *G. shallon* biomass increased six-fold when light conditions increased from heavily shaded (5%) to full sunlight (100%). *G. shallon* is tolerant of low light conditions once established, but may not be able to establish in the low light environment below *R. spectabilis* canopy (Tappeiner and Zasada, 1993).

Part of the reason for this differential survival of *G. shallon* and other species on stumps may be related to seed size (Tappeiner and Zasada, 1993). *G. shallon*, *V. parvifolium*, and *Vaccinium ovatum* Pursh have small seed sizes relative to other understory shrubs (Scott, 1981). In the dense litter layer of the deciduous site, small seeds may lack the energy reserves necessary to either emerge to reach sunlight or to penetrate down to the soil (Franklin and Pechanec, 1967). Christy and Mack (1984) suggested that the shedding of litter build up on decaying logs facilitates the growth of small seeded species. In a study comparing CWD and forest floor microsites in a Chilean rainforest, Lusk (1995) found that large seeded species preferentially established on the forest floor, while smaller seeded species were found mainly on logs and stumps.

In contrast to the deciduous site, it appeared that small seed size did not preclude the establishment of *G. shallon*, *V. parvifolium*, or *V. ovatum* on the ground at the conifer site. *T. heterophylla* and *P. glycyrrhiza* were the only species exclusive to stumps at the coniferous site, although we found *P. glycyrrhiza* growing on the boles of *A. rubra* and *Acer macrophyllum* Pursh at both sites. Stumps and other elevated CWD may become increasingly important refugia for *P. glycyrrhiza* as deciduous trees are replaced by coniferous trees during forest succession. More importantly, CWD characteristics may determine its role as refugia for *P. glycyrrhiza* and other species since decay rates are related to the size and species of CWD (Harmon et al., 1986). Our finding for *T. heterophllya* agrees with previous studies documenting the strong preferential establishment of *Tsuga* seedlings on CWD (McKee et al., 1982; Christy and Mack, 1984).

G. shallon, *V. parvifolium*, and *V. ovatum* had significantly higher stem densities on stumps than the ground at the coniferous site. Although we have no clear explanation for the differences in stem densities, it may be that elevated CWD microsites have higher moisture contents during the growing season than the ground soils, receive greater quantities or quality of light, have less root competition from trees on the forest floor, or are released from wildlife browsing (Huffman et al., 1994).

R. spectabilis at the coniferous site appeared to be strongly associated with canopy gaps. The pattern in these gaps was similar to the pattern at the deciduous site, i.e. *R. spectabilis* formed dense patches of cover and *G. shallon* and the two *Vaccinium* species were absent from the ground vegetation. These observations along with our findings at the deciduous site give additional support to the hypothesis that understory competition for light is responsible for differences in plant density on CWD and the forest floor (Harmon and Franklin, 1989). Our results differ slightly from the findings of Harmon and Franklin (1989) because we found a woody shrub rather than mosses or herbs to be the primary light competitor. Despite these differences, the general mechanism of seedling exclusion from the ground appears to be the same.

This study suggests that at local levels CWD such as stumps, particularly tall old-growth conifer stumps, play an important role in maintenance of plant community richness. Our results support the work of Sharitz (1996), which found that CWD had a similar effect on plant community richness. Future studies examining a greater range of stump areas, heights, and decay classes would provide more detailed information on the regeneration niche requirements of understory plant species associated with CWD. Manipulative experiments in which seedlings were planted onto a variety of different substrates and elevations would also be helpful in shedding further light on the specific role of CWD in plant establishment. Our results suggest that *R. spectabilis* significantly affects understory plant establishment and dynamics. Field experiments examining the effect of overstory composition and *R. spectabilis* on understory species, particularly why *R. spectabilis* was absent from CWD, will provide a deeper understanding of understory plant communities in Pacific Northwest forests.

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