

HABITAT STRUCTURE AND PREY AVAILABILITY AS PREDICTORS OF THE ABUNDANCE AND COMMUNITY ORGANIZATION OF SPIDERS IN WESTERN OREGON FOREST CANOPIES

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ABSTRACT. The significance of habitat structure and prey availability in spider biology has been well investigated in a number of communities, but only briefly in forest canopies. This study gathered indirect evidence for the importance of these two factors as determinants of spider abundance and diversity in arboreal communities of western Oregon. Arthropods were collected by harvesting and bagging tips (1 m long) of lower crown branches from red alder (*Alnus rubra*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), noble fir (*Abies procera*) and Douglas-fir (*Pseudotsuga menziesii*). Several characteristics of arthropod habitats were measured: tree diameter at breast height, maximum horizontal and vertical branch spread, number of branching angles and leaves, and total biomass of twigs and foliage. The highest numbers of spiders per branch were collected from structurally more complex tree species including Douglas-fir and noble fir. These tree species also had the highest spider species richness. The greatest similarity in spider community structure was found among tree species with shared branch characteristics such as needles. The biomass of foliage and prey availability were the best predictors of spider abundance on individual tree species. Biomass of twigs alone accounted for almost 70% and 60% of the variation in total spider abundance and species richness, respectively, across a wide range of arboreal habitats. Prey availability accounted for less of the variation. Selected habitat variables also predicted the abundance of several prey groups including Aphidoidea, Psocoptera, Diptera and Collembola. Our results suggest that habitat structure and prey availability in combination may play significant roles in structuring the spider community of western Oregon forest canopies.

The significance of habitat structure in spider biology has been a topic of numerous ecological studies. This interest is undoubtedly due to the great abundance and diversity of spiders (Coddington & Levi 1991), the variety of ecological roles they play (Foelix 1982; Wise 1993) and the intimate dependence of these arachnids on specific habitat features ensuring an optimal thermal environment, proper construction of their webs and retreats, and conduction of vibratory signals (Foelix 1982; Riechert & Gillespie 1986; Uetz 1991). The importance of habitat structure relative to the abundance and community structure of spiders has been extensively studied in a variety of natural communities including deserts (Riechert 1976; Lubin et al. 1993), grasslands and

shrub communities (Duffey 1978; Schaefer 1978; Hatley & MacMahon 1980), and forest floor (Uetz 1975; Cady 1984; McIver et al. 1992).

Trees are architecturally diverse habitats supporting a remarkable array of arthropods (Strong et al. 1984). Spiders are an important component of these arboreal arthropod communities in temperate (Moldenke et al. 1987; Schowalter 1995; Halaj et al. 1996, 1997) and tropical forests (Stork 1991; Russell-Smith & Stork 1994). Their predatory role in some canopy systems has been well documented (Loughton et al. 1963; Fichter 1984). Despite the apparent dependence of spiders on habitat structure and their implied importance in forest canopies, relatively few studies have investigated spider-habitat interactions in these systems. Stratton et al. (1979) investigated spider assemblages associated with branches of red pine (*Pinus resinosa*), white spruce

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(*Picea glauca*), and white cedar (*Thuja occidentalis*) in northeastern Minnesota. Tree species differed significantly in spider abundance and community structure, probably due mostly to differences among the tree species in the branch physical structure. Jennings & Dimond (1988) and Jennings et al. (1990) suggested that curved needles of red spruce (*Picea rubens*) provide a better habitat for spiders than flat needles of balsam fir (*Abies balsamea*) in east-central Maine. In a series of studies conducted in southern Sweden (Gunnarsson 1988; 1990; Sundberg & Gunnarsson 1994), it has been suggested that a higher needle density of Norway spruce (*Picea abies*) improves spider habitat quality, possibly by providing increased protection against foliage-foraging birds (Askenmo et al. 1977).

The objective of this study was to make initial observations of how habitat structure and prey availability influence arboreal spiders in western Oregon. We intended to determine if there were significant associations between selected habitat variables of several host-tree species and the abundance and diversity of associated arthropod fauna. By investigating several host-tree species with fundamentally different branch structure simultaneously, we could identify commonalities of spider habitats across a wide range of arboreal communities. Based on indirect observational evidence and experimental data from some arboreal systems (e.g., Stratton et al. 1979; Gunnarsson 1990), we hypothesized that spider abundance and community structure could be predicted by a combination of the availability and characteristics of their habitats, and prey abundance in tree canopies.

METHODS

Study sites and tree species.—This study was conducted at the H.J. Andrews Experimental Forest (44°13'30"N, 122°09'46"W), a Long-Term Ecological Research Site, and UNESCO Man and the Biosphere Reserve, in the western Cascade Range of Oregon, near Blue River, in Lane and Linn Counties, USA. Six study sites were selected in March 1993. The main criterion for site selection was the presence of at least 20 dominant or co-dominant trees (diameter at breast height < 20cm) of the selected species at a particular site. Tree species chosen included: red alder (*Alnus rubra*), western redcedar, (*Thuja plicata*), west-

ern hemlock, (*Tsuga heterophylla*), noble fir (*Abies procera*) and Douglas-fir (*Pseudotsuga menziesii*) (Table 1). These are common species found in western Oregon (Franklin & Dyrness 1988), and they possess a broad range of structural characteristics.

Lower elevation sites: Three study sites identified as A, B and C were selected at elevations ranging from 597–805 m in the *Tsuga heterophylla* zone (Franklin & Dyrness 1988). This is a temperate, mesophytic formation with a wet and mild maritime climate. The mean annual precipitation and temperature range from 1500–3000 mm, and 7.4–10.4 °C, respectively (Franklin & Dyrness 1988). Tree species sampled on each of the sites in this zone included red alder, western redcedar, western hemlock, and Douglas-fir. The ground vegetation was dominated by Pacific rhododendron (*Rhododendron macrophyllum*), *Berberis nervosa* and bracken fern (*Pteridium aquilinum*).

Higher elevation sites: Since noble fir occurs at lower elevations only sparsely, three additional study sites (D, E and F) were added to sample this tree species at elevations ranging from 1195–1292 m in the *Abies amabilis* zone (Franklin & Dyrness 1988). This zone is considered a cool or subalpine formation with a short growing season and significant snowfall. The mean annual precipitation and temperature range from 2100–3000 mm, and 5.5–6.0 °C, respectively (Franklin & Dyrness 1988). The study site vegetation included dense patches of beargrass (*Xerophyllum tenax*), salal (*Gaultheria shallon*) and various berries (*Vaccinium* spp.). As a reference, co-occurring Douglas-fir was also sampled at these higher elevation sites. At all sites, trees were selected along a transect (10 m × 50 m) placed in the forest stand. This procedure was repeated by selecting multiple transects until 20 trees of each species occurring at the particular site were designated. Thus, the size of the study site was determined by the number and distribution of sampled trees. With the exception of occasional pockets of red alder and western redcedar, this procedure normally resulted in sampling fairly interspersed trees of all species.

Field and laboratory procedures.—On each tree, four accessible non-interdigitated tips of branches (sampling units) of constant length (1 m) were removed arbitrarily from

Table 1.—Summary of study site and tree characteristics potentially important to arthropod habitat quality. Statistics are results of two-way ANOVAs to compare habitat variables separately at lower and higher study sites. Means (\pm SE) followed by different letters are significantly different (LSD; $P < 0.01$). * Indicates a significant site by host-tree species interaction effect.

Host species	Elev. range (m)	Sampling period	Trees									
			Diameter at breast height (cm)	Horiz. branch spread (cm)	Vertic. branch spread (cm)	Foliage biomass (g)	No. leaves (n)	Wood biomass (g)	No. branching angles (n)			
Lower sites												
Red alder	597–805	June 13–26	57	4.27 (0.28)b	39.17 (1.48)d	25.10 (0.84)d	19.91 (0.77)d	126.57 (4.50)b	24.83 (0.88)d	28.46 (1.50)b		
Western redcedar		June 10–28	60	13.90 (0.77)a	69.11 (1.35)b	39.81 (1.08)a	110.65 (3.82)a	278.62 (6.04)a	48.42 (1.56)c	16.15 (0.29)c		
Western hemlock		June 12–29	60	14.41 (0.73)a	63.28 (1.26)c	28.42 (0.65)c	78.17 (3.30)c	—	54.12 (1.88)b	—		
Douglas-fir		June 2–July 2	60	14.31 (0.66)a	76.51 (1.56)a	32.04 (1.02)b	95.83 (3.49)b	—	65.68 (2.20)a	120.91 (5.65)a		
				$F = 75.37^*$ $df = 3,225$ $P < 0.001$	$F = 146.86$ $df = 3,224$ $P < 0.001$	$F = 48.16^*$ $df = 3,224$ $P < 0.001$	$F = 488.87^*$ $df = 3,225$ $P < 0.001$	$F = 435.45^*$ $df = 1,111$ $P < 0.001$	$F = 175.41^*$ $df = 3,225$ $P < 0.001$	$F = 729.39^*$ $df = 2,168$ $P < 0.001$		
Higher sites												
Noble fir	1195–1292	July 3–11	60	13.67 (0.43)	69.21 (1.28)	15.61 (0.51)b	195.79 (5.63)a	—	118.28 (3.15)a	235.07 (8.07)a		
Douglas-fir		July 4–12	60	14.40 (0.50)	67.72 (1.09)	29.77 (0.69)a	132.95 (4.02)b	—	89.15 (2.46)b	129.32 (4.78)b		
				$F = 0.13$ $df = 1,114$ $P = 0.719$	$F = 0.58$ $df = 1,114$ $P = 0.447$	$F = 361.80^*$ $df = 1,114$ $P < 0.001$	$F = 89.32$ $df = 1,114$ $P < 0.001$	—	$F = 56.44$ $df = 1,114$ $P < 0.001$	$F = 159.83^*$ $df = 1,114$ $P < 0.001$		

the lower third of the tree canopy with a hand pruner. Each branch was quickly placed in a heavy-duty plastic bag and transported to the laboratory. In order to prevent cannibalism in sample bags, and to facilitate the removal of arthropods from the branches, a 3 sec spray of a pyrethrin-based insecticide (Hi-Power[®] Ant, Roach & Spider Spray Formula II; Ortho, San Ramon, California, USA) was applied inside each bag before sealing it. In the laboratory, each sample branch was shaken vigorously within the bag to remove arthropods. Dislodged arthropods were collected by washing the bag with tap water. All specimens were preserved in 75% ethyl alcohol.

Spiders were sorted and identified to the lowest possible taxa, and further categorized into eight functional groups based on foraging strategy similarities. Hunting spiders included: (1) agile hunters of the families Salticidae and Oxyopidae, (2) ambushers of the family Thomisidae, (3) runners of the family Philodromidae and (4) nocturnal hunters comprising Clubionidae, Anyphaenidae and Gnaphosidae. Web builders were divided into categories of spiders with similar web characteristics and included: (1) orb weavers of the families Araneidae, Tetragnathidae, and Uloboridae, (2) cobweb spiders, family Theridiidae, (3) sheet-web weavers of the family Linyphiidae and (4) hackled-band weavers, family Dictynidae. The rest of the arthropod community was sorted and identified to order. The abundance of all arthropods other than spiders was used as an estimate of the spider food base. Voucher specimens of arthropods collected in this study have been deposited in the insect collection of the Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon, USA.

To obtain a manageable group of branches, three out of four branches harvested from each tree were randomly selected to measure several characteristics of spider habitat. To assess arthropod-habitat relationships, only the arthropods collected from this subset of branches were used in correlation analyses; but arthropod abundance and diversity, however, were compared using specimens from all four branches. Maximum horizontal and vertical branch spread (cm) were defined as maximum perpendicular distances to the branch axis, measured horizontally and vertically, re-

spectively. We hypothesized that increased spread of branches would increase the probability of intercepting spiders during their dispersal by ballooning, and thus may be a reliable indicator of their abundance in the canopy. Conversely, flatter branches with shorter vertical spread might increase the exposure of spiders to visually foraging predators (e.g., birds) and thus be negatively correlated with spider densities. Total number (n) of branching angles (axils) was defined as the number of acute angles, measured between two branchlets. The number of branching angles reflects the architectural complexity of the branch, and thus may be related to the quality of the spider habitat. The number of leaves (n) was counted on alder branches, whereas composite leaves were counted on branches of western redcedar. Total biomass of foliage and stems (g) was estimated separately by weighing after oven-drying. These variables are correlated with the total amount of available surface area on the branch, and may also reflect its structural complexity. Diameter (cm) at breast height (1.3 m above ground) was measured on each tree. Tree diameter is directly related to tree size, and may provide an indirect measure of the total amount of spider habitat available on a particular tree.

Statistical analyses.—The number and diversity of arthropods, and values of habitat variables measured on individual branches were averaged for each tree (experimental unit). This estimate was used in all statistical analyses. Differences in arthropod abundance on individual tree species were assessed with multi-factor ANOVA, with tree species and sites as factors. All treatment means were compared and separated with the Fisher's protected least significant difference (LSD) test (Steel & Torrie 1980). Lower and higher elevations were compared with a t -test. In order to satisfy the assumption of homogeneous variance in ANOVA, variables were \ln -transformed, as appropriate, prior to all analyses. In all cases, the original means and their standard errors are reported here. Spider diversity was estimated with the Shannon diversity index (H') (Pielou 1975). Overlap in the spider community structure and species composition were estimated with the formula in Schoener (1968) and with the Sørensen similarity index (C_s) (Southwood 1992), respectively. Multiple

regression analyses were used to select the best subset of habitat variables predicting arthropod abundance and spider diversity: (1) individually for each host-tree species (using samples pooled across all sites at which it occurred) and (2) across host-tree species (using samples pooled from all tree species and sites). Since we expected predictor variables to be linearly related, stepwise procedures were used to control for multicollinearity among the variables. Adjusted R^2 values were used to select best regression models; maximum R^2 and minimum mean square error terms were used as variable selection criteria. All statistical analyses were performed with SAS computer programs (SAS Institute Inc. 1994).

RESULTS

Arthropod habitat characteristics.—

There were significant differences in branch characteristics among host-tree species (Table 1). With the exception of red alder, all tree species across lower elevation sites were similar in size as measured by their trunk diameter. In addition, Douglas-fir trees of similar size were sampled at lower and higher elevations ($t = 0.05$; $df = 4$; $P = 0.962$). At lower elevations, branches of Douglas-fir had the widest horizontal spread, the highest number of branching angles, and contained the greatest amount of wood biomass. Branches of redcedar had the greatest vertical spread, reflecting the "hanging" arrangement of its foliage, and provided the greatest amount of foliage biomass per 1 m branch tip (Table 1). There were no differences in the horizontal spread of Douglas-fir and noble fir branches across higher elevation sites. Branches of noble fir were significantly flatter, but contained significantly more branch biomass and number of branching angles than those of Douglas-fir. Douglas-fir at higher elevations had narrower branches, but contained significantly more branch biomass (all $P < 0.05$) than individuals of the same species at lower sites (Table 1).

Spider abundance.—There were significant differences in the total numbers of spiders per branch tip among host-tree species across lower elevation sites ($F = 108.23$; $df = 3, 225$; $P < 0.001$; Fig. 1A). Although spider densities varied with sites ($F = 4.44$; $df = 2, 225$; $P = 0.013$), host-tree effects were

site independent (species*site interaction; $F = 1.03$; $df = 6, 225$; $P = 0.406$). The highest spider densities at lower elevations were collected from Douglas-fir (mean \pm SE; 5.36 ± 0.54), whereas red alder supported the lowest densities per branch tip (0.85 ± 0.14). Spider densities on hemlock (2.63 ± 0.22) and redcedar (2.06 ± 0.13) were not significantly different, and were intermediate compared with red alder and Douglas-fir. Significantly more spiders were collected from Douglas-fir branches (9.92 ± 0.47) compared with noble fir (8.20 ± 0.33) at higher elevations ($F = 6.46$; $df = 1, 114$; $P = 0.012$), and similar differences between these two species were present at all higher sites (Fig. 1A). In addition, significantly more spiders were found at higher than lower-site Douglas-fir ($t = 6.69$; $df = 4$; $P = 0.003$).

Among hunting spiders, densities of agile and nocturnal hunters followed a similar trend as overall spiders across tree species, with the lowest numbers on red alder and the highest numbers on Douglas-fir ($F = 34.08$; $df = 3, 225$; $P < 0.001$, and $F = 11.02$; $df = 3, 225$; $P < 0.001$, respectively; Fig. 2A, B). Densities of both spider groups on Douglas-fir and noble fir, however, were not statistically different. All trends for these two spider groups were similar across sites (all species*site terms; $P > 0.05$). Densities of running spiders tended to be significantly higher on redcedar, and on Douglas-fir at lower elevations ($F = 14.91$; $df = 3, 225$; $P < 0.001$), and with the exception of site D, greater on Douglas-fir than noble fir at higher elevations ($F = 26.16$; $df = 1, 114$; $P < 0.001$; Fig. 2C). Both trends for running spiders, however, were slightly inconsistent as indicated by significant species*site interactions ($P = 0.04$, and $P = 0.015$, respectively). Douglas-fir at both elevation ranges supported a similar abundance of agile hunters ($t = 1.84$, $df = 4$; $P = 0.140$); however, there were more running spiders and nocturnal hunters collected from higher than lower-site Douglas-fir ($P = 0.006$, and $P = 0.005$, respectively).

Densities of sheet-web weavers varied significantly among the tree species, being highest on Douglas-fir, followed by hemlock, redcedar and red alder ($F = 84.57$, $df = 3, 225$; $P < 0.001$; Fig. 3A). This tree species effect, however, was site-dependent ($F = 5.93$; $df = 6, 225$; $P < 0.001$). For example, there were

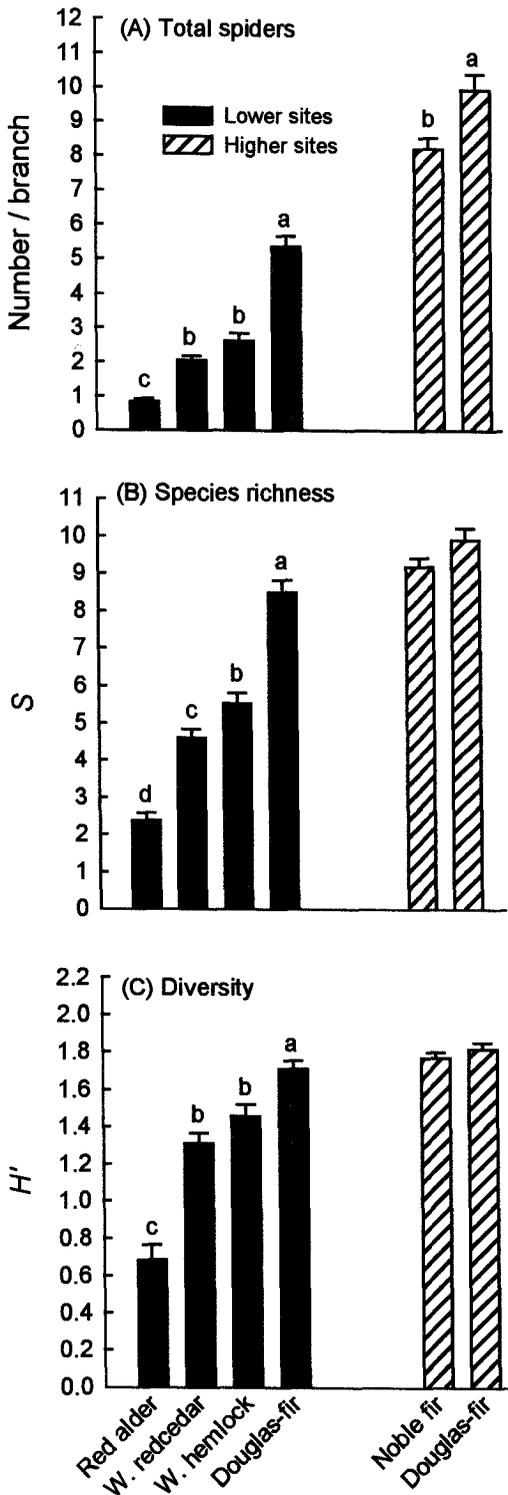


Figure 1.—Mean values (\pm SE) of total spider density (A), species richness (B) and species diversity (C) on individual host-tree species. Species

no differences between hemlock and Douglas-fir at site C, or alder and redcedar at site A. Both Douglas-fir and noble fir supported equal densities of these spiders at higher elevations (Fig. 3A). There were more sheet-web weavers collected from Douglas-fir at higher than at lower sites; the trend, however, was not statistically significant ($t = 1.54$; $df = 4$; $P = 0.197$). Significantly more orb-weavers were collected from redcedar and Douglas-fir than red alder and hemlock at all lower sites ($F = 5.93$, $df = 3, 225$; $P < 0.001$), and from Douglas-fir than noble fir at all higher sites ($F = 20.48$, $df = 1, 114$; $P < 0.001$; Fig. 3B). In addition, there was a significant positive effect of elevation for orb-weavers on Douglas-fir ($t = 3.40$, $df = 4$; $P = 0.027$). Overall, densities of cobweb spiders tended to be significantly greater on Douglas-fir than any other tree species at lower elevations ($F = 18.46$, $df = 3, 225$; $P < 0.001$; Fig. 3C). This trend, however, was site-dependent; for example, there were no differences among tree species at site A. Douglas-fir and noble fir supported approximately equal densities of cobweb spiders at all high elevation sites, and similarly there were no significant differences in cobweb spider abundance between lower and higher-elevation Douglas-fir (all $P > 0.05$).

Non-Araneae arthropod abundance.—

The abundance of potential spider prey varied significantly with host-tree species ($F = 21.67$, $df = 3, 219$; $P < 0.001$; Fig. 4A). Douglas-fir consistently supported the highest densities of potential prey individuals per branch tip (21.33 ± 3.23), followed by western hemlock (15.98 ± 2.80) and red alder (15.48 ± 1.79), whose prey densities did not differ significantly. Redcedar provided the lowest prey abundance among the tree species (9.14 ± 1.15). Similarly, Douglas-fir supported larger arthropod numbers than noble fir (36.41 ± 2.35 , and 18.29 ± 1.39 , respectively) at higher elevations ($F = 63.96$, $df = 1, 114$; $P < 0.001$), and a significant species*site term ($F = 5.20$, $df = 2, 114$; $P = 0.007$) reflected only a varying magnitude of

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richness and diversity were calculated from all specimens collected on one tree (four branches per tree). Bars with different letters are statistically different (LSD; $P < 0.05$).

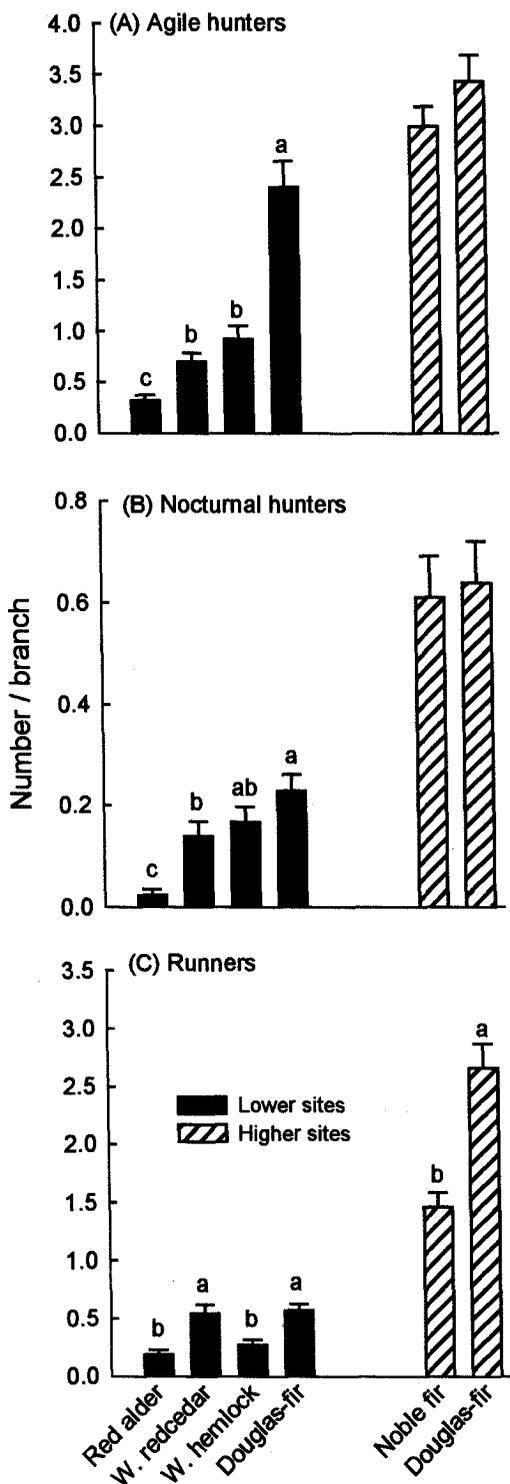


Figure 2.—Mean densities (\pm SE) of agile hunters (A), nocturnal hunters (B) and runners (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

difference between these two species (Fig. 4A). Aphids, the most abundant potential prey species collected in the study (29.10% of all non-Araneae arthropods), were significantly more abundant on red alder and Douglas-fir than on redcedar and hemlock which supported similarly low densities ($F = 100.77$, $df = 3,219$; $P < 0.001$; Fig. 4B). Aphid densities were greater on Douglas-fir than noble fir at higher elevations ($F = 55.93$, $df = 1,114$; $P < 0.001$), however, the magnitude of the difference varied with sites ($F = 3.88$, $df = 2,114$; $P = 0.023$). Branches of Douglas-fir supported significantly more total non-Araneae arthropods and Aphidoidea at higher than lower elevations ($t = 4.98$; $df = 4$; $P = 0.008$, and $t = 3.86$; $df = 4$; $P = 0.018$, respectively). Psocoptera were the second most abundant potential prey organisms (14.0%). Their abundance was consistently greater on Douglas-fir, hemlock, and redcedar than red alder ($F = 146.90$, $df = 3,219$; $P < 0.001$), nevertheless, the magnitude of difference varied with sites (species*site: $P = 0.008$). Douglas-fir and noble fir had consistently similar densities of psocids at higher elevations (Fig. 4C). Although on average there were more psocids collected from lower than higher-site Douglas-fir, this trend was not statistically significant ($t = 1.58$; $df = 4$; $P = 0.189$).

Spider community structure.—There were significant differences in the number of spider species and their diversity among the tree species at lower elevations ($F = 97.50$, $df = 3,225$; $P < 0.001$, and $F = 54.72$, $df = 3,223$; $P < 0.001$, respectively; Fig. 1B,C). On average, the highest number of species was collected from Douglas-fir (8.50 ± 0.32), followed by western hemlock (5.52 ± 0.29), redcedar (4.60 ± 0.24), and red alder (2.37 ± 0.21). With the exception of site B (interaction term for richness: $F = 3.22$, $df = 6,225$; $P = 0.005$, and diversity $F = 2.30$, $df = 6,223$; $P = 0.04$), this trend was consistent across all lower elevation sites. A similar number of species and diversity were found on Douglas-fir (species; 9.90 ± 0.32) and noble fir (species; 9.18 ± 0.24) at all higher sites (Fig. 1B,C). There were no significant differences in spider species richness or diversity between lower and higher-elevation Douglas-fir ($P = 0.186$, and $P = 0.182$, respectively).

Numerically, hunting spiders dominated the spider community on all host-tree species

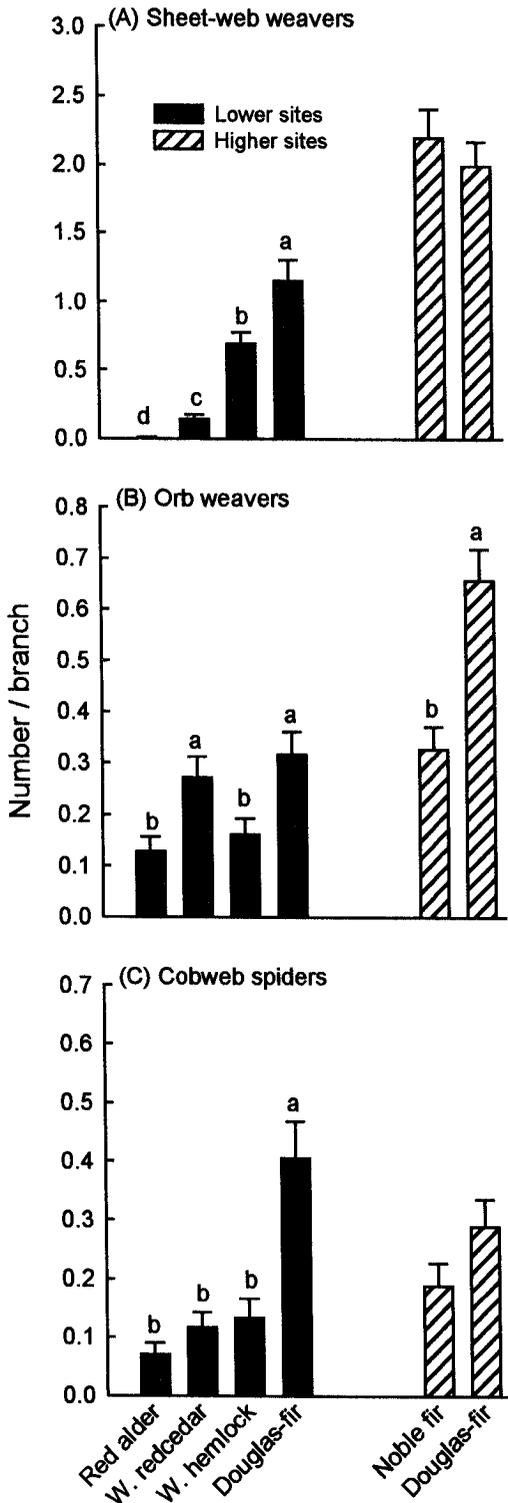


Figure 3.—Mean densities (± SE) of sheet-web weavers (A), orb-weavers (B), and cobweb spiders (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

(Fig. 5). Agile hunters and runners were the dominant hunting groups, and a salticid, *Metaphidippus aeneolus* Curtis 1892, accounted for as much as 55% of hunting spiders and 35% of all spiders in the arboreal community (Fig. 5, Table 2). The guild of web-building spiders on red alder and redcedar was dominated by orb-weavers, whereas sheet-web weavers were predominant among web-building spiders on conifers with needles (Fig. 5). The highest similarities in the community structure were found between Douglas-fir and western hemlock at lower sites, with an overlap ranging from 83–94%, and Douglas-fir and noble fir at higher elevations (81–91%). Conifers with needles also shared as much as 74–80% of spider species (Table 3). Similarities in spider community structure and species composition between lower and higher-site Douglas-fir were ranging from 67–91%, and 71–81%, respectively.

Arthropod-habitat associations.—*Patterns on individual host-tree species:* Spider abundance was significantly associated with habitat variables of individual host-tree species (Table 4). From 10–45% of variation in spider abundance was associated with the amount of foliage and prey abundance on branch tips. In red alder, number of leaves and leaf biomass alone explained 13% and 16% of the variation, respectively; the contribution of prey abundance alone was 13%. On western hemlock, foliage biomass accounted for 36%, whereas prey abundance alone accounted for 19% of variation in spider abundance, respectively. Although abundance of prey alone was selected as the best predictor of spider abundance on noble fir, foliage biomass alone could explain 12% of the variation. As much as 22% of variation in spider abundance on Douglas-fir at lower elevations was assigned to foliage biomass, whereas the number of branching angles contributed 15%; vertical branch spread and tree diameter alone contributed only 5 and 0.4%, respectively.

Patterns across all host-tree species: As much as 75% of variation in the total abundance of spiders on sampled trees was related to the amount of foliage, wooden twigs, and prey availability (Table 5). The amount of wooden twigs alone accounted for 68% of the variation in spider abundance across a wide range of arboreal habitats on five tree species with great differences in their branch architec-

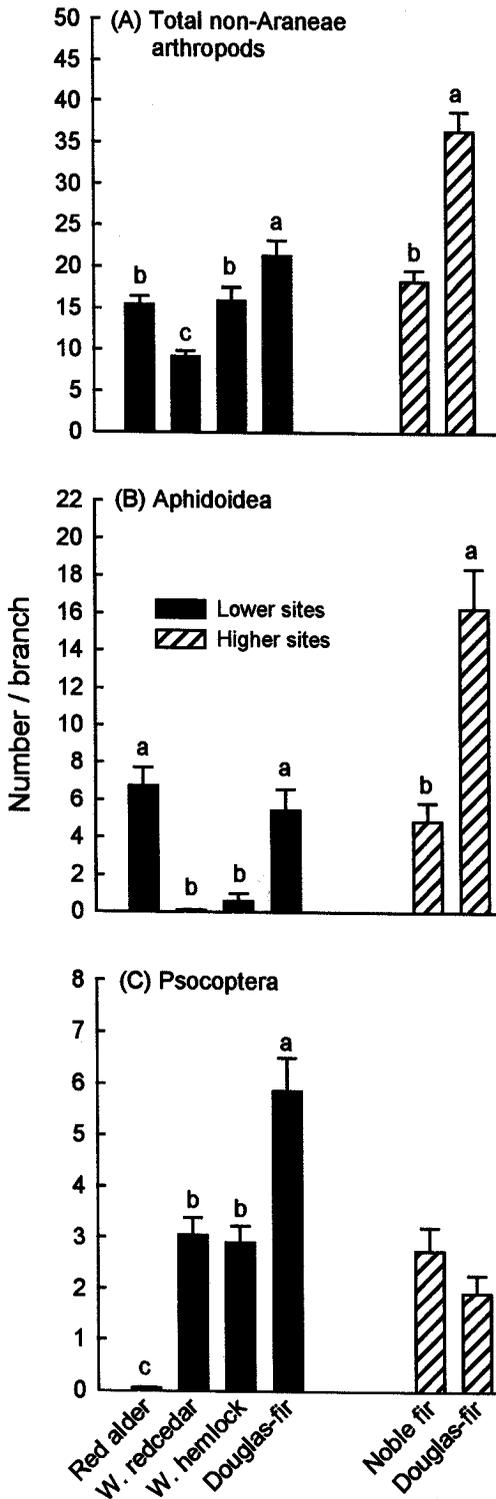


Figure 4.—Mean densities (\pm SE) of total potential spider prey organisms (A), aphids (B) and psocids (C) on individual host-tree species. Bars with different letters are statistically different (LSD; $P < 0.05$).

ture. The amount of foliage biomass explained almost 60% of the variation in spider abundance, and the availability of prey accounted for approximately ¼ of the variation. Adding these two variables into the prediction model, however, resulted in only a slight increase in its fit (7%) after accounting for the predictive power of wooden twigs (Table 5, Fig. 6). Biomass of wooden twigs alone was also a fair predictor of the abundance of agile hunters, sheet-web weavers and runners, explaining 49%, 44% and 34% of the variation in the abundance of these spider groups, respectively. The habitat variables measured in this study, however, did not appear to be strong predictors of the abundance of nocturnal hunters, or orb and cobweb weavers (Table 5). Models combining the biomass of branch wood and foliage, branch horizontal spread and the abundance of prey explained as much as 66% and 48% of the variation in spider species richness and diversity, respectively (Table 5).

Selected habitat variables did not appear to be strong predictors of the total abundance of potential spider prey. The best model combining biomass of wood and foliage explained only 16% of the variation in the abundance of total arthropods other than spiders. Similarly, with the exception of Psocoptera, numbers of the most abundant prey groups in tree canopies—aphids, adult Diptera and Collembola—could not be predicted with a great accuracy using the selected habitat variables (Table 5).

DISCUSSION

The number of spiders, their species richness, and diversity in tree canopies increased with what a human observer might subjectively label as “structural complexity” of the host-tree species. For example, needle-covered branches of western hemlock unarguably appear to be more complex than leaves of red alder, and, similarly, Douglas-fir with its longer needles and “bushier” branches could be classified as more complex than redcedar. Similar patterns have been observed elsewhere. For example, a higher spider abundance on foliage of red spruce than on balsam fir in east-central Maine suggests that the curved needles of red spruce provide a more complex and better habitat for spiders than flat needles of balsam fir (Jennings & Dimond 1988; Jennings et al. 1990). Stratton et al.

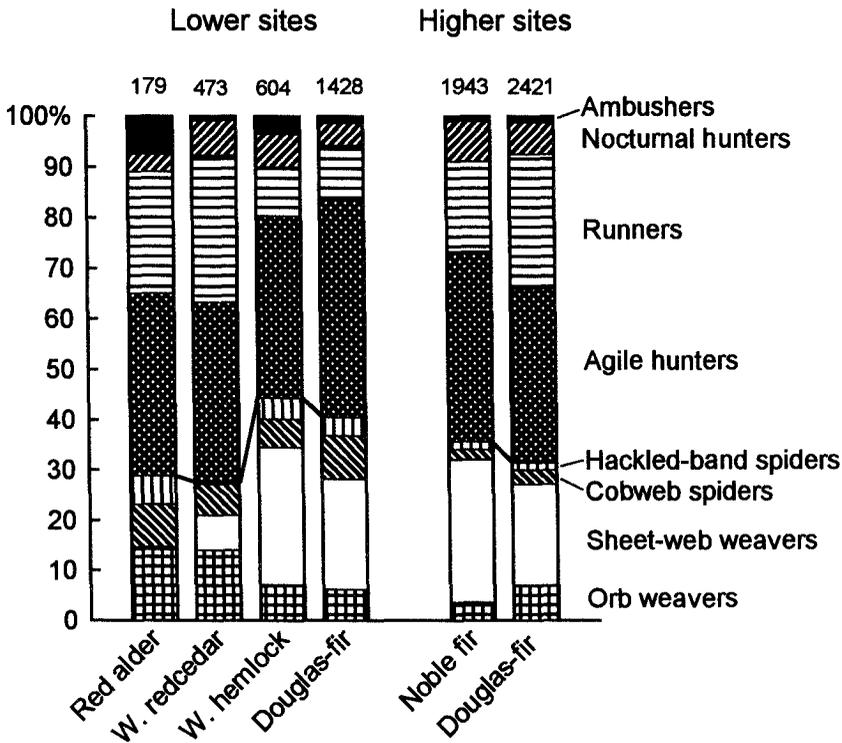


Figure 5.—Relative abundance of dominant spider groups on host-tree species at lower and higher-elevation sites. Numbers above columns indicate absolute densities of spiders collected from individual host trees. Solid lines between columns separate the web-building (below line), and hunting (above line) spider groups.

(1979) found higher spider densities and slightly more species on the more complex white spruce than white cedar in northern Minnesota.

Interestingly, the same host-tree species, Douglas-fir, supported a larger spider population at higher than lower elevations. Nocturnal hunters and running spiders in particular, were 2.8–4.6× more abundant on higher than lower-site Douglas-fir. A similarly high spider abundance was also observed on noble fir. This species, however, was not sampled at lower elevations, and so a direct comparison with other species is obscured by the “elevation” effect observed for Douglas-fir. A significant positive effect of altitude on arboreal spider abundance was also noticed by Russell-Smith & Stork (1994) in a tropical rain forest of Indonesia. Although no variables of spider habitat were measured in this study, it was suggested that differences in spider abundance could have been related to varying canopy architecture.

The term “plant architecture” was originally proposed by Lawton & Schröder (1977) to describe a wide array of plant structural attributes. Two main components of plant architecture are the size and the variety of above-ground parts. The size *per se* hypothesis predicts that larger plants (or habitat patches) are more likely to be discovered and colonized by arthropods, and consequently they support larger populations and a greater diversity of species (Lawton 1983). In addition, larger habitats generally have lower extinction and emigration rates (MacArthur & Wilson 1967; Kareiva 1985). The resource diversity hypothesis predicts that plants with a greater variety of structural variables or resource types (e.g., sites used for resting, sexual display, or feeding) support a greater abundance and diversity of arthropods (Lawton 1983).

On individual tree species, the greatest amount of variation in spider densities was explained by foliage biomass. Noble fir was an

exception, with prey availability being the critical variable. Similarly, from 60% to almost 70% of spider abundance across several host-tree species was related to branch biomass; either in the form of wooden twig or foliage. A similar coupling between spider abundance and habitat availability has been reported from a variety of communities (Duffey 1974; Hatley & MacMahon 1980; Rypstra 1986; Gunnarsson 1988). For example, correlative and experimental studies have shown that Norway spruce branches containing more foliage biomass support significantly more spiders than those with a reduced needle density in forest communities of southern Sweden (Gunnarsson 1988, 1990). Rypstra (1986) has documented strong correlations between the abundance of web-building spiders found on undergrowth vegetation and the biomass of this vegetation. Interestingly, this pattern was consistent across three distinct communities, ranging from tropical Gabon through subtropical Peru to temperate sites in the northeastern United States. This strongly suggests that spider abundance in tree canopies closely follows the availability (amount) of habitat substrate provided by host-tree species. Then, for example, although western hemlock appears structurally more complex than red alder, the disparity in the number of spiders that live on their branches may simply mirror differences in the branch biomass that both tree species can produce. Similarly, a greater spider abundance on higher-elevation Douglas-fir may be attributed to a greater biomass availability on this species at higher than lower sites.

From 40–57% of variation in spider species richness and diversity was related to branch biomass. This may be yet another example of a species-area relationship as both spider abundance and diversity increased with the amount of branch biomass. Similarly, Duffey (1974) and Uetz (1975) uncovered strong correlations between species richness and the depth (amount) of forest litter in communities of wandering spiders. Total habitat availability alone, however, does not sufficiently explain observed patterns of spider abundance and diversity. After accounting for the effect of branch biomass, still more habitat variables such as prey availability, number of individual leaves, branching angles, or branch spread entered the prediction models. These may reflect fine-grained qualities of the habitat (microcli-

mate, web-constructing sites or refugia), allowing a greater niche diversification and coexistence of more spider species. For example, Greenstone (1984) documented a strong positive relationship between the diversity of web-building spiders and vegetation structural diversity across several habitat types ranging from tropical meadow in Costa Rica to scrub sites in California.

To illustrate the above arguments, there were more spiders collected from Douglas-fir than noble fir at higher elevations; yet, noble fir branches of comparable length contained more biomass than Douglas-fir. Similarly, redcedar branches contained significantly more foliage biomass than western hemlock or Douglas-fir, but supported fewer spider species than either host-tree species. Prey availability, or subtle differences in the branching pattern, resulting in a more favorable microclimate, may be responsible for this discrepancy. Indeed, Douglas-fir branches at all higher elevation sites contained twice the number of total non-Araneae arthropods, and more than three times the densities of aphids than noble-fir branches; redcedar was the most prey-poor of all species (Fig. 4). A greater predation pressure by birds on more exposed flat branches of noble fir (lower vertical branch spread) can also be a factor reducing spider abundance on this tree species.

Despite differences in spider abundance between Douglas-fir and noble fir, spider communities on both tree species were very similar. Likewise, Douglas-fir branches at all lower elevations had significantly more spiders than western hemlock, and yet both species supported almost identical spider assemblages. Conversely, non-Araneae arthropod community (order level) on western hemlock and Douglas-fir were only 55–57% similar, and the community of Douglas-fir and noble fir at higher elevations overlap 66–77% (Halaj 1996). It appears that some underlying habitat characteristics common to all of these tree species, rather than similarities in their prey communities, are responsible for similarities in spider assemblage structure. All of these species are conifers with needles, which may be the critical habitat variable for some spider groups. For example, both absolute and relative densities of sheet-web weavers were greater on conifers with needles compared to red alder or redcedar. Some species, such as

Table 2.—Arboreal spider community structure in western Oregon. Spider densities are pooled numbers of individuals collected from host-tree species across all study sites.

	Red alder	West- ern red- cedar	West- ern hem- lock	Douglas-fir		
				Lower sites	Higher sites	Noble fir
Agile hunters						
Oxyopidae						
<i>Oxyopes scalaris</i> Hentz 1845	2	15	37	71	3	1
Salticidae						
<i>Eris marginata</i> (Walckenaer 1837)		1	1			
<i>Habrocestum</i> sp. Simon 1876	1	1	1	1		
<i>Metaphidippus aeneolus</i> Curtis 1892	58	139	170	542	836	707
<i>Metaphidippus albeolus</i> Chamberin & Ivie 1941			2			
<i>Metaphidippus</i> sp. F. O. P. Cambridge 1901	3	2			1	1
<i>Phidippus johnsoni</i> (G. & E. Peckham 1883)		1				
Ambushers						
Thomisidae						
<i>Coriarachne versicolor</i> (Keyserling 1880)	1					
<i>Misumena vatia</i> (Clerck 1757)	8		16	11	15	5
<i>Misumenops celer</i> (Hentz 1847)	4	2	4	1	1	1
<i>Xysticus gosiutus</i> Gertsch 1933		1		5	9	8
Nocturnal hunters						
Anyphaenidae						
<i>Anyphaena pacifica</i> (Banks 1896)	2	12	10	25	36	15
Clubionidae						
<i>Clubiona moesta</i> Banks 1896			1			9
<i>Clubiona trivialis</i> C. L. Koch 1843	4	19	27	38	115	125
Gnaphosidae						
<i>Sergiolus montanus</i> (Emerton 1890)						2
Runners						
Philodromidae						
<i>Apollophanes margareta</i> Lowrie & Gertsch 1955		2	9	17	40	56
<i>Philodromus oneida</i> Levi 1951				5		1
<i>Philodromus rufus pacificus</i> Banks 1898	21	103	37	95	223	106
<i>Philodromus speciosus</i> Gertsch 1934		1		4	3	1
<i>Philodromus spectabilis</i> Keyserling 1880	21	19	10	31	375	171
<i>Philodromus</i> sp. Walckenaer 1825		4				1
<i>Tibellus oblongus</i> (Walckenaer 1802)			1	1		
Cobweb spiders						
Theridiidae						
<i>Argyrodes fictilium</i> (Hentz 1850)			1			
<i>Dipoena nigra</i> (Emerton 1882)		2	2	31	2	1
<i>Euryopsis formosa</i> Banks 1908	1					
<i>Theridion aurantium</i> Emerton 1915			1			
<i>Theridion differens</i> Emerton 1882		4		24	19	3
<i>Theridion lawrencei</i> Gertsch & Archer 1942		11	19	56	42	24
<i>Theridion melanurum</i> Hahn 1831						1
<i>Theridion neomexicanum</i> Banks 1901	4	1		1	7	2
<i>Theridion sexpunctatum</i> Emerton 1882	3	4	2			1
<i>Theridion simile</i> C. L. Koch 1836	1		1	4		2
<i>Theridion varians</i> Hahn 1831			1			2
<i>Theridion</i> sp. Walckenaer 1805	6	5	6	6	1	2

Table 2.—Continued.

	Red alder	West- ern red- cedar	West- ern hem- lock	Douglas-fir		
				Lower sites	Higher sites	Noble fir
Hackled-band weavers						
Dictynidae						
<i>Dictyna olympiana</i> Chamberlin 1919	10	2	25	53	33	29
Orb weavers						
Araneidae						
<i>Araneus gemma</i> (McCook 1888)				5	10	1
<i>Araniella displicata</i> (Hentz 1847)	19	22	16	50	140	57
<i>Cyclosa conica</i> (Pallas 1772)		8	5	7	2	2
Undetermined genus, sp. 1	4	6	5	3		6
Tetragnathidae						
<i>Metellina curtisi</i> (McCook 1893)		8		1		
<i>Tetragnatha laboriosa</i> Hentz 1850				1	7	
<i>Tetragnatha versicolor</i> (Walckenaer 1841)	2	4	1	17	12	4
Uloboridae						
<i>Hyptiotes gertschi</i> Chamberlin & Ivie 1935		15	15	6		
Sheet-web weavers						
Lynphiidae						
<i>Ceraticelus atriceps</i> (O. P.-Cambridge 1874)			58	84	39	345
<i>Pityohyphantes costatus</i> (Hentz 1850)				3	32	16
<i>Pityohyphantes rubrofasciatus</i> (Keyserling 1886)		10	57	106	87	44
<i>Neriene litigiosa</i> (Keyserling 1886)		18	14	25		
Undetermined genus, sp. 1	1	3	30	94	319	100
Undetermined genus, sp. 2					1	
Undetermined genus, sp. 3			2		8	29
Undetermined	3	28	17	4	3	62

Table 3.—Overlap in spider community structure and similarity of spider species composition for pairwise within-site host-tree species comparisons as determined with the Schoener's index of overlap and Sørensen similarity index, respectively. * Results of 9 pairwise between-site comparisons.

Host species	Index	Lower sites			Higher sites
		Red alder	Western redcedar	Western hemlock	Douglas-fir Noble fir
Red alder	Community	1	0.71–0.74	0.57–0.77	0.58–0.67
	Species	1	0.50–0.60	0.50–0.51	0.41–0.56
Western redcedar	Community	—	1	0.62–0.71	0.58–0.75
	Species	—	1	0.60–0.68	0.60–0.78
Western hemlock	Community	—	—	1	0.83–0.94
	Species	—	—	1	0.74–0.80
Douglas-fir lower sites	Community	—	—	—	1
	Species	—	—	—	1
Douglas-fir higher sites	Community	—	—	—	0.67–0.91*
	Species	—	—	—	0.71–0.81*
					0.81–0.91 0.71–0.79

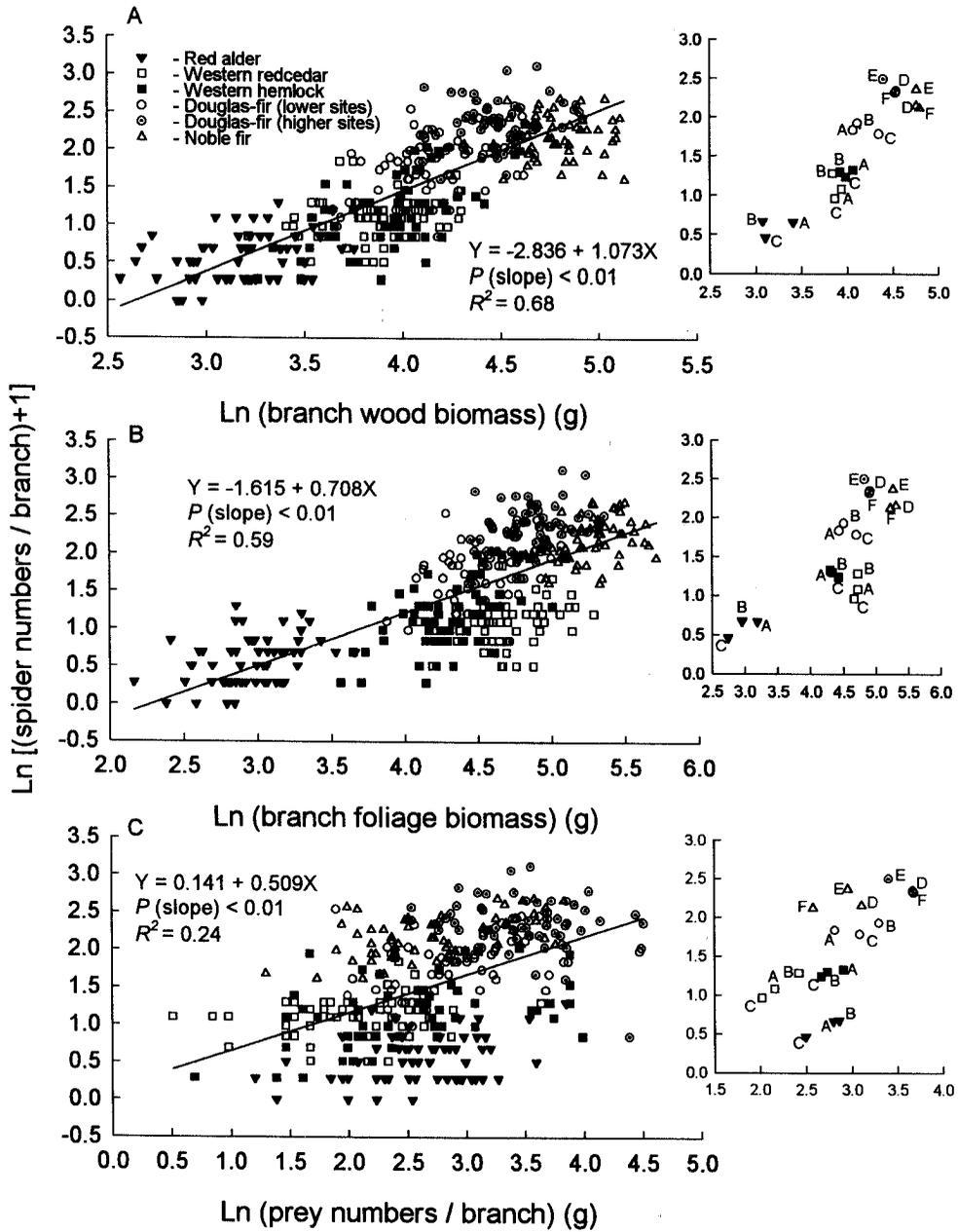


Figure 6.—The best prediction model for the total abundance of spiders in samples pooled across five host-tree species and six collecting sites. The model combines the branch wood biomass (A), branch foliage biomass (B) and the abundance of potential spider prey (C). Data points represent average variable values from three branches harvested on each tree ($n = 20$ trees, but $n = 17$ for red alder at site C). The inserts in the right portion of the graph display site averages.

Ceraticelus atriceps (O.P.-Cambridge 1874), were found exclusively on these hosts (Table 2). We commonly observed small linyphiids spinning their delicate webs around the base

of needles on Douglas-fir and western hemlock, and perhaps this habitat feature is essential to their foraging success. Similarly, Stratton et al. (1979) found a greater proportion of

Table 4.—Best models to predict spider densities on individual host-tree species in western Oregon. Y, spider density; DB, diameter at breast height; AG, number branching angles; HS, horizontal branch spread; VS, vertical branch spread; LF, number of leaves; FL, foliage biomass; WD, wood biomass; PY, prey density. * Amount of variation in the response variable explained by this variable alone as indicated by R^2 . ** $P < 0.05$. *** $P < 0.01$.

Host species	Best model	F (df)***	R^2_{adj}
Red alder	$\ln(Y) = +LF + FL + PY$ (0.13) (0.16) (0.13)*	8.03 (3,53)	0.31
Western redcedar	$\ln(Y) = +\ln(FL) + \ln(LF)$ (0.07) (0.10)	7.52 (2,55)	0.21
Western hemlock	$\ln(Y) = +\ln(FL) + \ln(PY)$ (0.36) (0.19)	22.98 (2,56)	0.45
Noble fir	$\ln(Y) = +\ln(PY)$	25.28 (1,58)	0.30
Douglas fir lower sites	$Y = -\ln(DB) + \ln(VS) + \ln(FL) + \ln(AG)$ (<0.01) (0.05) (0.22) (0.15)	9.79 (4,57)	0.45
Douglas fir higher sites	$\ln(Y) = +FL$	6.80 (1,57)**	0.11

linyphiids on red pine and white spruce compared to structurally simpler white cedar. Nevertheless, effects of community structure of potential spider prey on spider abundance and diversity deserve future investigations.

It has been generally accepted that structurally more complex habitats provide a wider selection of web-attachment sites and thus are more suitable for web-building spiders (Robinson 1981; Rypstra 1983; and reviews in Uetz 1991). Significant positive correlations between some groups of web builders and structural features of habitat in this study partly support this hypothesis (Table 5). With the exception of sheet-web weavers, however, correlations between densities of web-building spiders and habitat variables were weak. In addition, orb-weaving spiders did not appear to discriminate between red alder and western hemlock. Similarly, with the exception of lower-site Douglas-fir, cobweb spiders did not show a clear response in abundance to the complexity of individual host-tree species (Fig. 3). Some web-builders may be more flexible in utilizing the available habitat structure than others, and so a tight relationship between the abundance of these spiders and structural complexity of their habitat may not be universal principle. For example, orb weavers can spin webs across wider spaces in the canopy and their requirements for habitat complexity may be simpler, perhaps satisfied with a few attachment points. By the same

token, it may be argued that our habitat variables did not precisely reflect fine-tuned habitat requirements of some web-builders, which may explain lower prediction power of our models. The abundance of hunting spiders also correlated with structural variables of their habitat. Increased amount and complexity of branch habitat may provide a greater assortment of retreat building sites and hiding places for hunting spiders (Hatley & MacMahon 1980; Gunnarsson 1990). We commonly observed various hunters (Clubionidae, Salticidae and Philodromidae) in their diurnal and nocturnal retreats spun among needles on several host-tree species.

Higher densities of spiders were associated with increased densities of available prey organisms. This pattern was seen on individual host-trees species as well across several taxa. Correlative studies and field experiments have demonstrated spider numerical responses to prey densities (see review in Wise 1993) and our results further support these findings. Nevertheless, the prey variable generally explained less variation in spider abundance and diversity than the habitat alone. Individual spider groups may have specific prey requirements, and so it is conceivable that our broad prey category may not have been sensitive enough to detect stronger spider-prey associations. It is also plausible that food simply was superabundant in this system, thus precluding the detection of strong correlations.

Table 5.—Best models to predict densities of selected arthropod groups, spider species richness, and diversity across all host-tree species and sites in western Oregon. Variable codes as in Table 4. * Amount of variation in the response variable explained by this variable alone as indicated by R^2 . ** $P < 0.01$.

Group	Best model	F (df)**	R^2_{adj}
	Density		
Araneae	$\ln(Y) = +\ln(FL) + \ln(WD) + \ln(PY)$ (0.60)* (0.68) (0.24)	345.31 (3,341)	0.75
Agile hunters	$\ln(Y) = -\ln(HS) + \ln(WD) + \ln(PY)$ (0.13) (0.49) (0.15)	129.73 (3,341)	0.53
Runners	$\ln(Y) = +\ln(WD) + \ln(PY)$ (0.34) (0.19)	116.73 (2,342)	0.41
Nocturnal hunters	$\ln(Y) = -\ln(VS) + \ln(FL) + \ln(PY)$ (0.03) (0.21) (0.08)	41.82 (3,341)	0.27
Sheet-web weavers	$\ln(Y) = -\ln(VS) + \ln(WD) + \ln(PY)$ (0.07) (0.44) (0.17)	114.63 (3,341)	0.50
Orb weavers	$\ln(Y) = +\ln(VS) + \ln(WD) + \ln(PY)$ (<0.01) (0.09) (0.05)	14.80 (3,341)	0.12
Cobweb spiders	$\ln(Y) = +\ln(HS) + \ln(PY)$ (0.06) (0.04)	14.57 (3,342)	0.08
Total prey	$\ln(Y) = -\ln(FL) + \ln(WD)$ (0.05) (0.11)	31.38 (2,342)	0.16
Aphidoidea	$\ln(Y) = -\ln(HS) - \ln(FL) + \ln(WD)$ (0.01) (<0.01) (0.02)	18.90 (3,341)	0.14
Psocoptera	$\ln(Y) = +\ln(DB) + \ln(HS) + \ln(FL) - \ln(WD)$ (0.27) (0.24) (0.21) (0.11)	46.99 (4,340)	0.36
Adult Diptera	$\ln(Y) = +\ln(VS) + \ln(WD)$ (0.01) (0.17)	43.42 (2,342)	0.20
Collembola	$\ln(Y) = +\ln(DB) + \ln(FL) - \ln(WD)$ (0.11) (0.07) (<0.01)	34.27 (3,341)	0.23
	Species richness		
Araneae	$\ln(Y) = +\ln(HS) + \ln(FL) + \ln(WD) + \ln(PY)$ (0.36) (0.52) (0.57) (0.20)	164.23 (4,340)	0.66
	Diversity		
Araneae	$\ln(Y) = +\ln(HS) + \ln(FL) + \ln(PY)$ (0.35) (0.40) (0.10)	105.00 (3,339)	0.48

For example, a 2.4-fold increase in prey availability following experimental removals of ants from Douglas-fir canopies did not translate into increased densities of web-building spiders at a nearby study site (Halaj et al. 1997). The relative importance of habitat structure and prey availability may also vary temporally as it was suggested for spider communities in forest litter (Uetz 1975) and agricultural crops (Rypstra & Carter 1995).

Structural complexity of habitat predicted the abundance of potential spider prey across several host-tree species. The availability of sites for oviposition, resting, basking, or overwintering is closely linked to plant architecture

(Strong et al. 1984); and thus both spiders and non-Araneae arthropods may respond to similar habitat features. Predicting the abundance of some groups (e.g., phytophagous species) based on their habitat architecture, however, may be difficult (Southwood et al. 1982). These groups are likely constrained by the nutritional quality of the host plant. Thus, a simple addition of habitat substrate, or an increase in its complexity, being heterogeneous in nutritional quality (e.g., habitat transition from alder to western hemlock), may not be followed by a strong corresponding increase in their abundance (Table 5).

In conclusion, this study documented sig-

nificant associations between the structure of branch microhabitat, prey availability, and the abundance and diversity of spiders in forest canopies. Nevertheless, these data should be interpreted with caution. Throughout the study, we assumed that plant biomass directly reflects the availability (surface area) of habitat to plant-dwelling arthropods. However, equal amounts of biomass may have different surface areas depending on the arrangement or fragmentation of the foliage. It is quite likely that an increase in plant biomass could indicate increasing surface area as well as the complexity of the host plant. Similarly, two host-tree species with equal surface area may differ in the weight of their branches if the densities of their plant tissue are different. Although most of the trends in arthropod abundance and spider community structure were strikingly similar at individual study sites, significant site*host-species interactions were present (Table 1, and throughout Results). This weakens the generality of our conclusions. Differences in the stand structure, modifying the site microclimate and composition of the herbaceous layer, may account for some of the discrepancies in the general trend. We suggest that colonization rates of habitats by dispersing arboreal spiders may reflect the patch size (habitat size *per se* hypothesis), and thus a greater abundance and more spider species would tend to accumulate on host-tree species whose branches provide more biomass. Subsequently, unique qualities of the host (e.g., local prey availability, branching complexity or microclimate; resource diversity hypothesis) perceived through various sensory channels would influence spider's decision to stay or leave a particular branch (e.g., see reviews in Riechert & Gillespie 1986). This would further modify differences in spider abundance and community structure across arboreal habitats. Due to the observational nature of this work, no cause-and-effect conclusions can be drawn. Experimental work is needed to ascertain the significance of specific features of spider habitat and prey availability, as well as temporal changes in their relative importance, as related to the abundance and community structure of these predators in forest canopies.

ACKNOWLEDGMENTS

We thank Alan B. Cady, Arthur J. Boucot, John D. Lattin, Samuel D. Marshall, David A.

Perry, Ann L. Rypstra and Sean D. Walker for reading and commenting on earlier versions of the manuscript. We also thank Lisa M. Ganio and Thomas E. Sabin for their statistical assistance. This research was supported by funds from the Forest Research Laboratory provided to Darrell W. Ross and NSF Grant DEB-9011663 to John D. Lattin.

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Manuscript received 18 April 1997, revised 25 September 1997.