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Canopy Arthropod Communities in Relation to Forest Age and Alternative Harvest Practices in Western Oregon

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Abstract

Arthropod community structure and herbivory were compared in replicate Douglas-fir and western hemlock canopies in intact old-growth (>400 yr old), and Douglas-fir only in partially-harvested old-growth, natural mature (150 yr old) stands, and regenerating plantations (10-20 yr old) in a 15,000 ha area including the H.J. Andrews Experimental Forest in western Oregon. Species diversity and abundances of several taxa, especially predators and detritivores, were significantly lower in plantations, compared to older forests. Mature, old-growth, and partially-harvested stands showed few significant differences, but principal components analysis (PCA) suggested some differences in community structure and indicated that old-growth was least variable (tighter clustering) in arthropod diversity and abundance, whereas partially-harvested stands were most variable. Defoliation was higher in the mature stands, probably because these stands were composed of relatively dense and pure Douglas-fir. Although old-growth appeared to be the source of greatest arthropod biodiversity in these forests, arthropod communities in Douglas-fir canopies may largely recover old-growth structure by 150 years, and partially-harvested stands retain substantially greater arthropod diversity than do regenerating plantations.

Key Words: Diversity, herbivory, disturbance, succession, <u>Pseudotsuga</u>, <u>Tsuga</u>

Introduction

Arthropods represent a major species pool, including important pests and biological control agents, in forest canopies. Canopy arthropod responses to changing environmental conditions can have dramatic effects on forest productivity and nutrient cycling processes (e.g., Schowalter et al., 1986, 1991), but responses to changing forest conditions or management practices are poorly known, largely because of taxonomic complexity, difficulty of canopy access, and unreplicated treatments. Current concerns over protection of biological diversity and forest health under alternative management scenarios require that quantitative data from replicated plots be available for assessment of canopy arthropod responses to changing environmental conditions.

Previous studies have compared canopy communities in stands of different ages or disturbance histories (e.g., Schowalter, 1989, 1994; Schowalter and Crossley, 1987; Simandl, 1993). Two major questions were raised by these studies. First, how soon do canopy communities recover during succession? Second, does less severe disturbance, such as partial harvest (Franklin, 1989; McComb et al., 1993), produce less change in canopy communities than does more severe disturbance, such as clearcutting?

These questions concern forest managers worldwide, especially those who seek alternative management strategies that protect biodiversity and forest health. Information on effects of forest management is particularly important in the Pacific

Northwest region of North America where the fate of remnant natural forests, that have been rapidly fragmented and converted to young monocultures, is the subject of intense debate. Declining abundances of many indigenous species and outbreaks of others (Schowalter, 1986; Witcosky et al., 1986; Lattin, 1993), have led to consideration of alternative harvest systems that should retain more diversity (Franklin, 1989; McComb et al., 1993). This study was designed to compare canopy arthropod diversity, community structure, and herbivory among intact mature and old-growth conifer stands and partially harvested and clearcut stands in western Oregon.

Materials and Methods

Site Description

This study was conducted during 1992 in a 15,000 ha area that included the 6400 ha H.J. Andrews Experimental Forest located 80 km east of Eugene, Oregon in the central western Cascade Mountains at latitude 44°N, longitude 122°W. The Andrews Forest is a Long Term Ecological Research (LTER) site and Man and the Biosphere (MAB) Biosphere Reserve administered jointly by the USDA Forest Service (Willamette National Forest and Pacific Northwest Res. Stn.) and Oregon State University. The surrounding area is administered by the Willamette National Forest.

Elevation ranges from 400 to 1500 m. A maritime climate prevails, with wet, relatively mild winters and dry, warm summers. Precipitation averages 2300 mm per year and is strongly seasonal with 75% occurring from November through March. However, 1992 was the sixth year of a drought during which precipitation averaged 1970 mm, or 85% of normal.

Vegetation at the Andrews Forest is dominated (40% of land area) by old-growth forest (>400 yrs old), composed primarily of emergent Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) and a subcanopy of western hemlock (Tsuga heterophylla (Raf.) Sarg.) and western redcedar (Thuja plicata Donn), with dominant trees >400 years old and often exceeding 70 m in height and 125 cm dbh. Douglas-fir and western hemlock represent 70% of stand biomass in old-growth stands (Grier and Logan, 1977). Natural stands about 150 years old and composed almost entirely of Douglas-fir occupy about 20% of the Andrews and are abundant in the surrounding forest (Franklin and Dryness, 1973; Grier and Logan, 1977; Waring and Franklin, 1979). Two alternative silvicultural systems are represented as well. Douglas-fir plantations (10-40 years old) have been created through clearcut harvest and replanting throughout the forest area. Maples (Acer spp.), alders (Alnus spp.) and snowbrush (Ceanothus velutinus Dougl. ex. Hook) are often common in these plantations. Partially harvested stands with 8-20 green trees retained/ha (about 35% of original Douglas-fir density, S. Acker unpubl. LTER data) have been created primarily for shelterwood or seed tree purposes in the past and for ecosystem management more recently. These stands eventually develop an understory of young conifers, either planted or natural regeneration, as well as abundant shrubs and hardwoods.

Experimental Methods

Six stands each of intact old-growth (>400 years old), mature (150 years old), regenerating plantation (10-20 years old) and partially harvested (green trees retained) old-growth (3-20 years post-harvest) treatments were selected for study on the basis of their geographic distribution over the entire area. Partially-harvested old-growth stands were selected to be more than 3 years old to ensure wind-firmness of remnant old-growth Douglas-fir. Harvested stands were >10 ha; natural mature and old-growth stands were >25 ha.

Old-growth sites represented the range of elevation and upslope and riparian locations characterizing this area. At each of the old-growth sites, one Douglas-fir (56-76 m in height, 93-165 cm in dbh) and one western hemlock (49-64 m in height, 69-83 cm in dbh) were rigged with pulleys and ropes for canopy access. All trees were selected on the basis of canopy dominance and climber safety.

Mature and partial harvest sites also represented the range of elevation and ecological conditions. Most mature sites included scattered remnant old-growth trees, and some had multi-tree gaps and/or a developing hemlock understory (up to 10 m height). At each of the mature and partial harvest sites, one Douglas-fir (42-52 m in height for mature, 67-70 m for partial harvest; 62-84 cm in dbh for mature, 92-150 for partial harvest) was rigged as above. Western hemlock was not sufficiently represented for sampling in these stands.

Douglas-fir saplings in plantations were accessible from the ground (2-3 m in height). Western hemlock was not available for comparison in the young stands.

Sampling techniques were identical to those described by Schowalter (1989). Each stand was sampled in May (prior to budbreak), June (at budbreak), August (mid-season) and October (late growing season) to represent seasonal changes in arthropod communities. Rigged trees were sampled at upper (within 5 m of top), middle and lower crown levels to represent within-tree variation. In the young plantations, three randomly-selected saplings were sampled.

Sampling involved quickly enclosing one 0.5-0.7 m foliage-bearing branch from each crown level or sapling in a 60-l plastic bag, clipping the branch and sealing the bag. Although some highly mobile or nocturnal invertebrates might be underrepresented by this sampling technique, the resident fauna of functional concern is largely sedentary, and other sampling techniques tend to be biased toward more mobile arthropods that often are less directly associated with particular plants (e.g., Wolda, 1979; Majer and Recher, 1988).

Samples were chilled at 4° C until they could be processed in the laboratory. Individual branchlets were removed sequentially and examined for invertebrates. Each branchlet was examined quickly for mobile arthropods, then examined microscopically for smaller or less mobile arthropods. Finally, plant debris in the bag was examined microscopically for any remaining invertebrates. Representative immatures were reared for adult identification. This method allowed organisms to be maintained live but inactive until processing, reducing the likelihood that dead arthropods would be overlooked. Arthropods were tabulated by taxon.

Foliage was examined for evidence of needle or bud consumption or damage, and proportion of branchlets with foliage consumed was recorded. Plant material was dried at 50° C to constant weight.

Data Analysis

Arthropod population intensities (number per kg dry weight of plant material) and percentage foliage missing as a result of herbivory were pooled by tree species and site. Each of the five species x treatment combinations had a sample size of 24 (6 sites x 4 sample dates). These data for each arthropod taxon and defoliation were transformed as necessary to achieve normality and constancy of variance and analyzed by 1-way analysis of variance (ANOVA) with five levels of tree species x stand treatment as the main effect (SAS Institute Inc., 1982). Some taxa with small numbers of individuals were combined into larger phylogenetic or functional groups to facilitate analyses. Linear regression and correlation techniques (SAS Institute Inc., 1982) were used to evaluate relationships between taxa. Principal components analysis (SAS Institute Inc., 1982), using abundances of all taxa, was used to assess similarities in community structure between treatments. Multiple analysis of variance

(MANOVA) of principal components 1-5 was used to validate principal components analysis. Shannon-Wiener diversity (Price, 1984) was calculated from species abundance for each tree species x site combination and analyzed by 1-way ANOVA as above.

Results

Average arthropod population intensities, percent foliage missing, and diversity by treatments are shown in Table 1. All herbivore and detritivore and most predator taxa were relatively slow moving or sessile and could not escape collection. Predaceous Diptera, Hymenoptera and Coleoptera are relatively mobile and could be underrepresented, especially in older trees.

Significant patterns of association with tree species or treatment were found for several arthropod taxa (Table 1). The most dramatic difference was found for adelgids which were about 200X more abundant in the plantations than in older trees (F=14; df=4,25; P=0.0001). The Cooley spruce gall adelgid, Adelges cooleyi (Gillette), was particularly abundant, reproducing parthenogenetically on Douglas-fir in the absence of spruce. The related hemlock woolly adelgid (Adelges tsugae Annand) occurred on western hemlock. Overall, sap-sucking herbivores were significantly more abundant in plantations than in other treatments (F=10; df=4,25; P=0.0001). Sawflies (Neodiprion sp.) were more abundant in mature Douglas-fir and old-growth hemlock than in other treatments (F=3.4; df=4,25; P=0.023). Neuroptera were significantly more abundant in mature canopies than in other treatments (F=5.3; df=4,25; P=0.0030). Bdellid mites were more abundant in old-growth trees than in younger trees (F=3.2; df=4,25; P=0.030). An oribatid mite (Camisia carrolli Andre) was most abundant in old-growth hemlock (F=4.2; df=4,25; P=0.0094). Overall, detritivores were more abundant in hemlock and partially-harvested stands than in plantations (F=3.1; df=4,25; P=0.035). A seed bug, Kleidocerys sp., was present as adults on older trees, but immatures were found only on western hemlock cones (F=3.1; df=4,25; P=0.032).

Several taxa approached significant relationships to tree species or treatment (Table 1). Western spruce budworm (Choristoneura occidentalis Freeman) was less abundant in partially-harvested stands (and absent in hemlock) than in other treatments (F=1.4; df=3,23; P=0.087). Among predators, parasitic Hymenoptera were less abundant in plantations and old-growth Douglas-fir (F=2.6; df=4,25; P=0.061). Podurids were more abundant in partially harvested stands (F=2.3; df=4,25; P=0.083). Finally, adults of insects with aquatic immatures (Aquatic insects), primarily midges, were more abundant in mature Douglas-fir and old-growth hemlock than in other treatments (F=2.6; df=4,25; P=0.058). When hemlock was eliminated from analyses, philodromid spiders were less abundant in plantations (P=0.082).

Plantations harbored a small subset of taxa represented in older trees. Diversity, measured by the Shannon-Wiener index indicated significantly (F=24; df=4,20; P=0.0001) lowest diversity in plantations, intermediate diversity in western hemlock, and highest diversity in old-growth, mature, and partially-harvested Douglas-fir (Table 1).

A large number of significant ($P < 0.05$) correlations indicated species interactions or similar responses to tree species or treatments. Correlations with $R > 0.50$ ($P < 0.005$) are shown in Table 2. Correlations between other Lepidoptera and predaceous beetles; other Lepidoptera and salticid spiders; erythraeid mites and miscellaneous Homoptera; predatory Hemiptera and other seed insects; giant conifer aphids (*Cinara pseudotaxifoliae* Palmer) and *Lestodiplosus* sp., a predaceous fly; giant conifer aphids and salticid spiders; and bdellid mites and Psocoptera probably indicate trophic interactions. I observed ants (*Camponotus* spp.) tending adelgids and aphids in plantations, but this correlation was not significant, probably because of the small number of ants in samples. Other correlations shown in Table 2 may indicate similar responses to environmental conditions.

Principal components analysis (PCA) integrated abundance data to indicate community associations and at least partially discriminated among tree species and treatments. However, five principal components addressed only 53% of the variation in the data. Principal component 1 (accounting for 15% of variation) was sufficient to separate the six plantations from the remaining treatments (Figure 1). Taxa with highest eigenvectors were *Jugatala* sp. 1 (0.32), *Scapheremaeus* (0.30), podurids (0.29), bdellid mites and *Jugatala* sp. 2 (0.26). Addition of principal component 2 (13% of variation) partially distinguished the five tree species x treatment combinations (Figure 1). Taxa with highest PC2 eigenvectors were sawflies (-0.28), giant conifer aphids, salticid and anyphaenid spiders (all 0.28) and miscellaneous Lepidoptera (0.27). Taxa with highest PC3 eigenvectors (10% of variation) were pine needle scales (0.35), predaceous Hemiptera and entomobryids (0.30), Neuroptera (0.29) and philodromid spiders and Camisia (-0.26). Principal components 1 and 4 (9% of variation) distinguished the Douglas-fir treatments best. Taxa with the highest PC4 eigenvectors were aranid spiders and erythraeid mites (0.34), miscellaneous Homoptera (0.30) and thrips 1 (-0.30). Old-growth and mature clusters overlap little, and partially-harvested sites generally are clustered in a narrow band between PC4 values of 0 and -1 (Figure 1).

Old-growth Douglas-fir generally had the tightest clustering, followed by mature and plantation Douglas-fir; partially-harvested Douglas-fir and old-growth hemlock showed greatest scatter in data, even when outliers were removed (Figure 1). Outliers were not obviously different from other replicates in tree condition, degree of isolation or exposure, site history, or composition of surrounding forest. Principal components 1 and 5 (6% of variation) illustrate the treatment variation as concentric rings containing old-growth Douglas-fir in the center, surrounded by mature and partially-harvested Douglas-fir; plantation Douglas-fir remained distinct (Figure 1). Taxa with the highest PC5 eigenvectors were seed insects (-0.34), thrips 1 and entomobryids (0.29), Jugatala sp. 2 (-0.26) and black pineleaf scales (-0.25).

However, only principal component 1 showed significant differences among treatments (P = 0.0077), based on MANOVA and verified with ANOVA. Means comparison, using Fisher's protected LSD multiple comparison test and a 0.005 level for significance (to maintain an experiment-wise level of 0.05 with 10 comparisons), indicated that PC1 values for regenerating plantations differed significantly from those for partially-harvested stands (P = 0.0005) and hemlock (P = 0.0002).

Most defoliators in these forests are relatively immobile and foliage consumption is concentrated along short sections of branchlets. Measureable foliage loss could be attributed largely to western spruce budworm and sawflies. Defoliation was significantly (F=6.7; df=4,25; P=0.0008) highest in mature Douglas-fir (3.7%, range 0-11%), with old-growth intermediate (1.9%, range 0-6%)(Table 1). Needle necrosis and loss to adelgids occurred but could not be measured precisely.

Population sizes for the various taxa can be calculated by multiplying intensities in Table 1 by foliage biomasses for the various treatments. Foliage averaged 65% of total dry mass in samples; mosses and lichens represented a small but conspicuous component. Douglas-fir foliage biomass is estimated at 1400 kg/ha in 10-20 year old plantations (Schowalter 1989); 3500 kg/ha in partially harvested old-growth, 26000 kg/ha in 150 year old mature stands, and 15000 kg/ha in old-growth; western hemlock foliage biomass is estimated at 6500 kg/ha in old-growth, and <20 kg/ha in younger or partially harvested stands (S. Acker, unpubl. LTER data; 2-3 stands per treatment). Results (Figure 2) indicate that densities and evenness of representation of the functional groups are highest in old-growth Douglas-fir and lowest in regenerating plantations. This greater overall diversity of arthropods on old-growth Douglas-fir is augmented by the only partially overlapping diversity of arthropods on western hemlock.

Discussion

This study expanded a database initiated in 1986 for old-growth and plantation canopies at the Andrews Forest (Schowalter, 1989). This developing long-term data base will be necessary to assess annual variation in canopy arthropod community structure and to analyze responses to changing environmental conditions, such as reduced precipitation.

Canopy arthropod abundances and diversity for old-growth and plantation treatments in 1992, the sixth year of drought, generally were similar to data from 1986 (Schowalter, 1989), an average year following one year of drought. Cooley spruce gall adelgid abundance was about 25% of that measured in 1986. The major defoliator in 1986, a budmoth (<u>Zeiraphera</u> <u>hesperiana</u> Mutuura and Freeman), was absent from 1992 samples; western spruce budworm, a minor component in 1986, was the major defoliator in 1992. Between 1987 and 1992, epidemic budworm populations in eastern Oregon expanded into the vicinity through

Santiam Pass, 30 km NE. Overall, defoliation was somewhat higher in 1992 than the negligible amounts in 1986. However, bud mortality to _Z_. _hesperiana_ in 1986 reduced potential foliage production by about 14%. Old-growth and plantation diversities (Shannon-Wiener) were similar between 1986 and 1992.

Functional organization of the old-growth and plantation canopy communities and effects on foliage losses remained relatively constant between 1986 and 1992. Sap-sucking phytophages and associated predators dominated the plantations both years, whereas defoliators, sap-suckers, predators and detritivores co-dominated the old-growth. The difference in functional organization, especially involving sap-sucking species, between disturbed and undisturbed canopies also occurs in eastern deciduous forests (Schowalter and Crossley, 1987) and tropical rainforests (Schowalter, 1994). These disturbance-related trends in functional organization and the individual species populations fluctuations observed in this study between 1986 and 1992 indicate that canopy arthropod communities are sensitive to, and potential indicators of, environmental change.

This study included mature and partially-harvested stands in order to address the questions a) when do canopy communities acquire old-growth structure, and b) how do old-growth communities respond to the less severe disturbance imposed by partial harvest, compared to clearcut harvest? Few individual taxa showed significant differences in abundance between mature, old-growth, and partially-harvested stands, but younger or managed canopies generally supported more variable subsets of a canopy community that was least variable in old-growth canopies (Table 1, Figure 1). Neuroptera were significantly more abundant in mature Douglas-fir than in other treatments. Sawfly abundance differed significantly between mature and partial-harvest treatments, with old-growth intermediate. Percent defoliation was significantly higher in mature stands than in other treatments (except old-growth Douglas-fir, Table 1).

Multivariate techniques were explored as a means of indicating the degree to which canopy arthropod assemblages differed among the treatments. PCA distinguished the community structure in plantations from that in other treatments and partially distinguished community structure between the natural mature, partial-harvest, and old-growth Douglas-fir.

Particularly interesting is the comparison of variability among treatments. Old-growth had more consistent community structure, as evidenced by tighter clustering in all principal component combinations (Figure 1), than did other treatments. Natural succession may be reflected in canopy arthropod communities as reduced variation in community structure, due to increasing habitat diversity and resource availability and to more moderate microclimate. However, MANOVA indicated that only PC1 differed significantly among treatments and only significantly distinguished regenerating plantations from partially-harvested stands and from old-growth western hemlock.

These data have major implications for future directions in forest management. First, old-growth appears to be the source of greatest arthropod biodiversity in this landscape. Arthropods associated with Douglas-fir reached greatest diversity in old-growth, and the incompletely overlapping taxonomic representation on western hemlock increased overall arthropod diversity in old-growth, in contrast to lower diversity in mature stands with nearly pure Douglas-fir canopies and significantly lower diversity in plantations. Partially-harvested stands maintained habitat for most old-growth associated species, but this treatment showed greater variability in arthropod species representation and abundances compared to old-growth. Even for arthropod taxa apparently favored by partial harvest, isolated remnant trees (about 35% of original Douglas-fir density, S. Acker unpubl. LTER data) support smaller populations than do more abundant hosts in intact forests. Arthropods associated exclusively with hemlock, e.g., <u>Kleidocerys</u>, were present only as dispersing adults in stands without hemlock. Hence, if preserving biodiversity associated with old-growth is a management goal, adequate representation of old-growth, or old-growth resources, on the landscape will be necessary to provide refuges for arthropods requiring these resources.

Elevated host density permits arthropod population growth, leading to outbreaks of particularly responsive species. Defoliator abundances were greatest in relatively pure Douglas-fir plantations and mature stands, where host foliage was nearly continuous over stand area, and lowest in partially-harvested stands, where host trees were widely scattered. Defoliation intensity was higher in mature stands (and old-growth) than in other treatments. These data are consistent with studies demonstrating that concentrated resources promote populations of adapted herbivores, whereas scattered hosts are less conducive to population outbreaks (e.g., Kareiva, 1983; Nebeker et al., 1985; Schowalter and Turchin, 1993, Schowalter et al. 1986). More diverse vegetation disrupts host-discovery by dispersing arthropods and limits reproduction and survival (Courtney, 1986; Visser, 1986; Schowalter and Turchin, 1993). This effect of host density probably reflects the combination of accessibility and intraspecific competitive stress of closely spaced hosts and favorable microclimate (Mitchell et al., 1983; Amman et al., 1988; Schowalter and Turchin, 1993). Schowalter and Turchin (1993) concluded that landscapes with a high proportion of stands composed largely of a single tree species and narrow age range will be susceptible to pest outbreaks, whereas landscapes composed of more diverse stands and stand types will tend to restrict incipient outbreaks.

Finally, this study did not clearly distinguish arthropod communities in canopies of natural mature and old-growth Douglas-fir, probably because of developing old-growth characteristics (remnant old-growth, developing hemlock understory, and treefall gaps) in many of these natural mature stands. Only the young plantations were easily distinguished by PCA (Figure 1) and MANOVA, largely on the basis of community simplification, especially as indicated by absence of many predator and detritivore taxa common in older trees. The recent conversion of large portions of old-growth and mature forest to young plantations (>75% of the Willamette National Forest in the past 50 years) likely has reduced regional populations of many of these predator and detritivore species that apparently do not survive or readily disperse into young stands, even from adjacent population sources in older forests (cf., Kruess and Tscharntke 1994). Reduced predator diversity increases the probability that herbivores with rapid response to environmental change will escape population regulation by surviving predators.

The combination of concentrated resources and impoverished predator fauna likely explains the elevated abundances of herbivores in plantations. Too few of the partially-harvested stands had adequate conifer regeneration for comparison with plantations (the two partially-harvested stands with 10-20 yr old regeneration also showed a preponderance of Adelges cooleyi). The remnant trees in partially-harvested stands maintained overall diversity and predator and detritivore populations to a greater extent than did plantations and had lower abundances of herbivores.

Conclusion

The results of this study are similar to earlier results for old-growth and plantation canopies. Differences in species presence and abundance for the resident faunas of these treatments may reflect annual variation or effects of long-term drought to an unknown extent.

Old-growth canopies supported the greatest diversity of canopy arthropods, perhaps because these canopies provide the greatest and most consistent diversity of foliar, branch, and epiphytic habitats and moderate microclimatic conditions. Younger and/or disturbed stands with lower diversity of habitats, and/or more extreme microclimatic conditions, supported subsets of the arthropod fauna found in old-growth canopies. Plant diversity in old-growth stands likely limits populations of herbivore species to a greater extent than do younger, more homogeneous forests. Partially-harvested stands showed arthropod diversity and community structure more closely resembling old-growth than did plantations, indicating that partial-harvest systems may retain greater arthropod biodiversity than do clearcut plantation systems. Plantation canopy faunas were distinct from those in older stands. However, the natural mature and old-growth canopies were not completely distinguishable, indicating that old-growth canopy arthropod community structure may be approached in 150 year old natural stands. Future studies should address the degree to which commercial forests, harvested at 50-80 years, support canopy arthropod communities representative of these older forests.

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Table 1. Mean arthropod intensities (No./kg dry wt. plant material), percentage defoliation, nd Shannon-Wiener diversity in forest canopies in the western Cascades of Oregon.[1] Numbers in arentheses are one standard error of the mean.

	Douglas-fir				Hemlock
AXON	Plantation No./kg	Partial Harvest No./kg	Mature No./kg	Old-growth No./kg	Old-growth No./kg
erbivores					
Defoliators	16 (15)	5.4 (3.9)	9.8 (7.8)	7.2 (6.7)	8.9 (5.8)
W. spruce budworm	12 (14)a	0.37 (0.9)b	3.5 (4.2)b	3.1 (3.6)b	1.7 (4.2)b
Other Lepidoptera	3.9 (6.1)	4.0 (3.0)	0.9 (1.4)	1.6 (2.0)	1.5 (2.5)
Sawflies	0 b	1.0 (1.5)b	5.5 (4.6)a	2.5 (2.9)ab	5.7 (5.3)a
Sap-suckers	6200 (3900)a	500 (620)b	240 (170)b	170 (120)b	1100 (1900)b
Kellogg scale	8.1 (1.3)	78 (14)	23 (14)	20 (20)	72 (86)
Pine needle scale	0	140 (330)	47 (80)	11 (7.8)	900 (1900)
Black pineleaf scale	29 (49)	200 (260)	130 (120)	89 (110)	17 (30)
Adelgids	6100 (4000)a	45 (20)b	18 (6.9)b	40 (31)b	72 (54)b
Giant conifer aphids	36 (59)	29 (70)	13 (20)	3.5 (7.0)	0
Other Homoptera	6.6 (7.4)	6.8 (8.2)	8.3 (7.9)	7.4 (11)	30 (61)

Table 1 cont.

Thrips sp. 1	0	0.7 (1.1)	0	0.5 (1.2)	5.2 (1.2)
Thrips sp. 2	2.2 (5.5)	3.3 (5.5)	2.0 (3.3)	4.1 (5.7)	1.6 (4.0)
Predators	74 (69)	57 (23)	57 (40)	68 (47)	68 (29)
Carpenter ants	5.3 (8.6)	0.30 (0.7)	0	0.35 (0.86)	0
Coleoptera	8.4 (14)	2.2 (1.9)	0	2.6 (4.1)	3.8 (4.4)
Neuroptera	0 b	0.3 (0.9)b	5.4 (2.9)a	2.0 (1.7)b	2.3 (3.7)b
<u>Lestodiplosus</u>	17 (26)	5.7 (4.9)	5.5 (7.3)	8.9 (7.5)	6.7 (5.6)
Other Diptera	0	0.3 (0.6)	0	0	0.7 (1.8)
Hemiptera	0	1.3 (1.6)	4.2 (4.5)	1.2 (1.9)	3.2 (4.7)
Hymenoptera	0 c	3.5 (3.3)abc	4.8 (5.3)a	0.6 (1.4)bc	4.1 (3.7)ab
Bdellid mites	0 c	6.4 (6.1)ab	1.3 (2.2)bc	5.1 (4.7)abc	7.7 (6.1)a
Erythaeid mites	0	0	0	0	2.6 (6.5)
Anyphaenid spiders	15 (14)	7.4 (2.3)	5.6 (4.9)	13 (13)	3.8 (9.3)
Aranid spiders	12 (22)	6.8 (2.7)	14 (14)	12 (16)	14 (13)
Lycosid spiders	4.3 (1.0)	1.3 (2.1)	1.4 (2.3)	0.3 (0.8)	1.2 (2.9)
Philodromid spiders	1.5 (3.8)	9.0 (6.2)	8.4 (5.5)	7.8 (4.8)	8.4 (8.6)
Salticid spiders	11 (15)	12 (13)	6.1 (12)	12 (12)	7.0 (5.0)
Other spiders	0	0.8 (1.2)	0.6 (1.4)	1.4 (3.4)	2.2 (2.6)

able 1 cont.

etritivores	1.3 (3.3)b	100 (120)a	49 (40)ab	60 (26)ab	110 (62)a
Psocoptera	0	5.4 (4.2)	2.1 (4.6)	4.6 (6.4)	5.7 (5.5)
Podurids	0 b	34 (44)a	9.8 (16)ab	9.8 (12)ab	2.6 (4.0)b
Entomobryids	1.3 (3.3)	0.5 (1.2)	0	0	6.3 (11)
Camisia	0 b	7.5 (5.0)b	4.5 (9.6)b	11 (8.8)b	28 (24)a
Jugatala sp. 1	0	15 (22)	1.5 (2.0)	3.9 (3.7)	8.3 (6.7)
Jugatala sp. 2	0	27 (35)	25 (26)	26 (24)	50 (53)
Scapheremaeus	0	10 (13)	4.7 (5.4)	3.0 (4.0)	8.5 (10)
Other oribatid mites	0	1.6 (1.9)	1.4 (3.4)	1.9 (3.4)	4.6 (4.3)
iscellaneous	3.4 (8.3)	9.0 (6.5)	11 (9.9)	9.9 (15)	19 (25)
Kleidocerys	0 b	2.0 (1.8)b	0.3 (0.7)b	0.7 (1.6)b	6.4 (7.8)a
Other seed predators	0	3.5 (4.5)	0.4 (1.0)	2.3 (4.8)	9.4 (2.1)
Wood boring beetles	0	1.4 (1.7)	0.8 (1.9)	0.6 (1.4)	0.6 (1.4)
Aquatic insects	0 b	1.0 (2.5)b	4.2 (4.6)a	0.4 (1.0)b	2.6 (2.1)ab
Other Coleoptera	0	0.9 (2.1)	0.6 (0.9)	0	0.6 (1.3)
Other Diptera	3.4 (8.3)	0.3 (0.7)	4.9 (8.6)	5.9 (15)	0

Table 1 cont.

Defoliation (%)	0.6 (0.8)bc	0.8 (1.0)bc	3.7 (4.0)a	1.9 (2.4)ab	0 bc
Shannon-Wiener Diversity	0.7 (0.3)c	2.4 (0.2)a	2.6 (0.4)a	2.8 (0.2)a	1.8 (0.6)b

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[1] For variables with significant ($P<0.05$) treatment effects (by ANOVA), means in rows followed by the same letter are not significantly different by LSD.

Table 2. Correlation coefficients greater than 0.5 between canopy arthropod taxa at the H. J. Andrews Experimental Forest in western Oregon in 1992. Probabilities of coefficients = 0 range from 0.005 for r = 0.50 to <0.0001 for r = 0.65

Taxon/Taxon	W. spruce budworm	Sawflies	Misc. Lepidoptera	Kellogg scale	Pine needle scale	Black pineleaf scale	Adelgids	Giant conifer aphids	Misc. Homoptera	Thrips 1	Neuroptera	Predaceous Hemiptera	Bdellid	Anyphaenid spiders	Aranid spiders	Philodromid spiders	Jugatala sp. 1	Jugatala sp. 2	Scapheremaeus
Pine needle scale		0.50																	
Black pineleaf scale		0.56						0.56											
Predaceous Coleoptera			0.52																
Neuroptera		0.60																	
Lestodiplosus	0.68							0.52											
Predaceous Hemiptera											0.59								
Parasitic Hymenoptera												0.63							
Erythraeid mites									0.96										
Aranid spiders														0.62					
Philodromid spiders										0.58									
Salticid spiders			0.51					0.57						0.53	0.65				
Psocoptera													0.55						
Camisia										0.75						0.50			

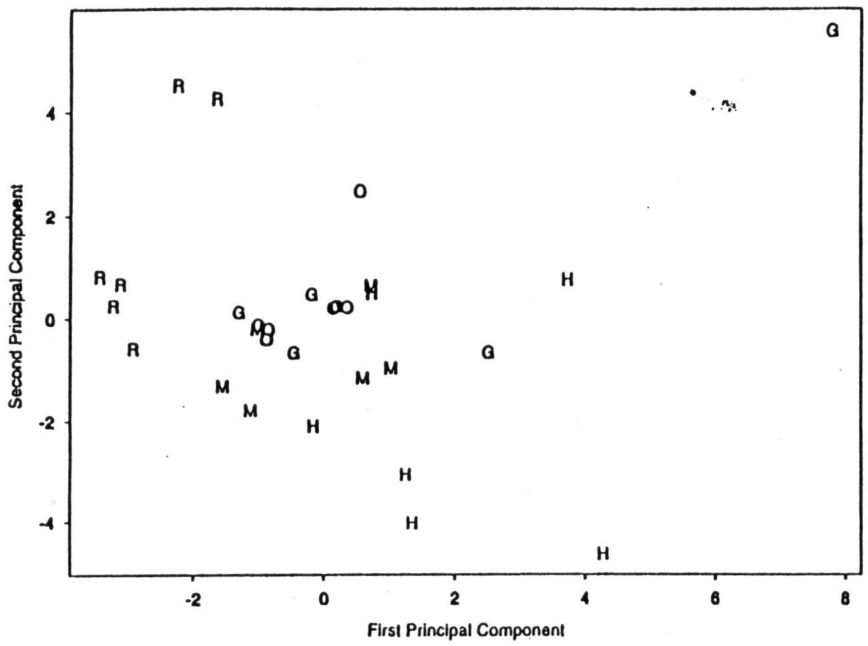
Table 2 continued

Jugatala sp. 1				0.72		0.55				
Scapheremaeus				0.59				0.63		
Podurids				0.78		0.54		0.75		0.68
Entomobryids	0.50		0.94							
Seed insects	0.50						0.58		0.59	
Wood borers										0.57
Aquatic insects					0.51					
Other Coleoptera		0.59								

Figure Captions

Figure 1. Principal components 1 vs. 2-5 for canopy arthropods in old-growth (O), mature (M), partial harvest/green tree retention (G) and regenerating plantation (R) Douglas-fir and old-growth hemlock (H) treatments at the H.J. Andrews Experimental Forest in western Oregon during 1992. Data are derived from Table 1.

Figure 2. Densities of arthropod functional groups by canopy treatments at the H.J. Andrews Experimental Forest in western Oregon during 1992. Data are derived from Table 1 and foliage biomass from Schowalter (1989) and S. Acker (unpubl. LTER data).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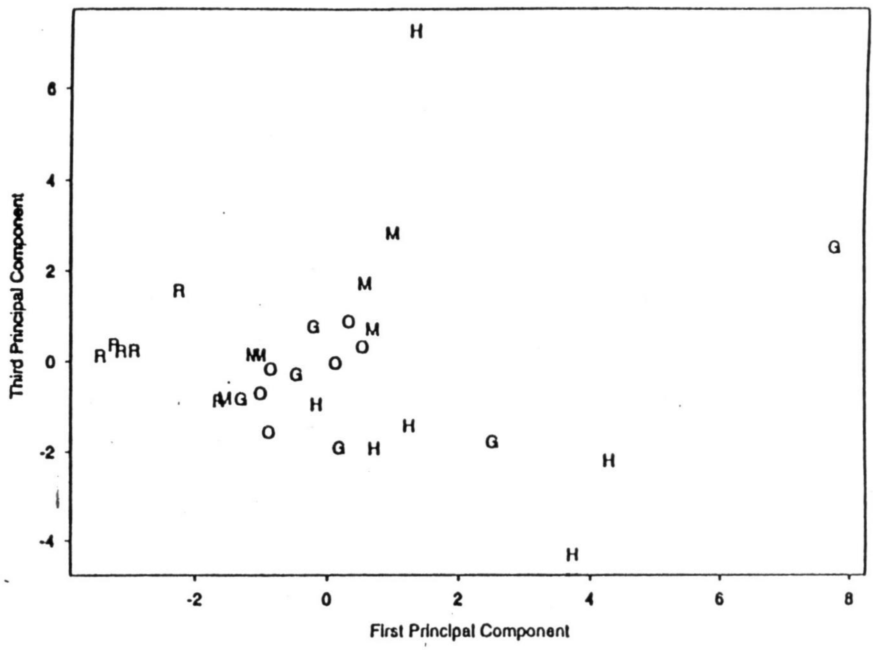
-2
-4
-2
0
2
4
6
8
First Principal Component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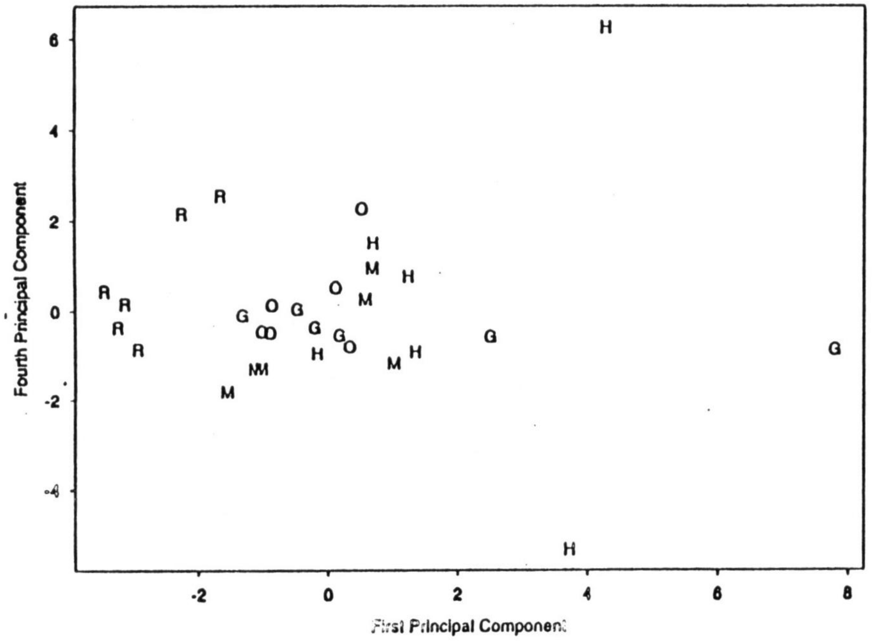
4
6
8
First Principal Component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6
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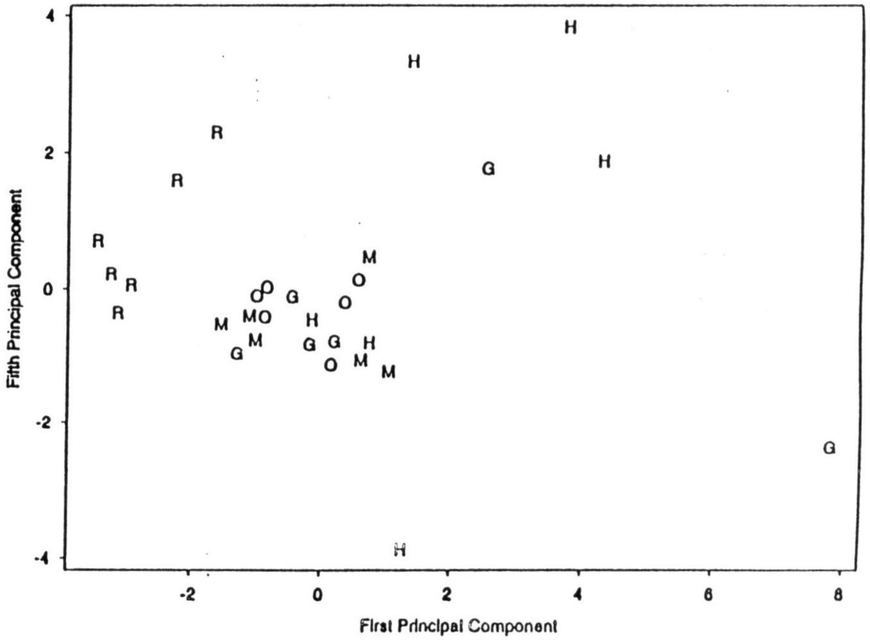
First Principal Component


Fifth Principal Component
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4
6
8
First Principal Component

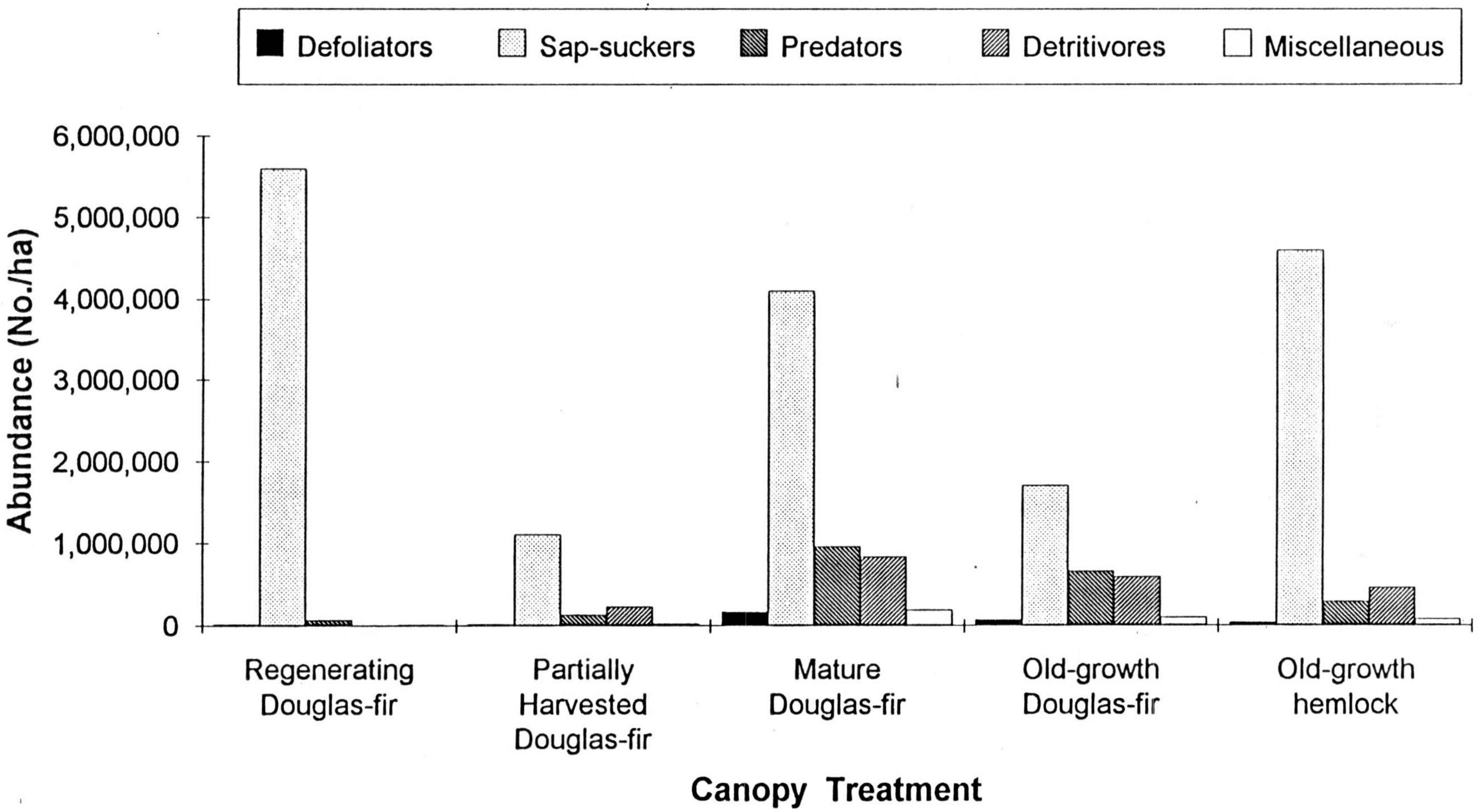
■ Defoliators
▨ Sap-suckers
▨ Predators
▨ Detritivores
☐ Miscellaneous
6,000,000
5,000,000
4,000,000
3,000,000
2,000,000
1,000,000
0
Abundance (No./ha)
Regenerating Douglas-fir
Partially Harvested Douglas-fir
Mature Douglas-fir
Old-growth Douglas-fir
Old-growth hemlock
Canopy Treatment

Fig 2