AN ABSTRACT OF THE DISSERTATION OF

Hoonbok Yi for the degree of Doctor of Philosophy in Forest Science presented on September 22, 2003.

Title: Response of Arthropods to Different Intensities of Thinning in Oregon

Abstract approved:

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Andrew R. Moldenke

The process of silvicultural thinning has become very controversial recently with regards to fire protection and management for old-growth conditions and biodiversity. Therefore, an unthinned control stand and 3 different thinning intensities were examined for their effects on the abundance, species richness, and diversity of arthropods in thinning treatments of silvicultural practices. Study sites were 40-50 year-old young stands of typical plantation Douglas-fir forests in the Willamette National Forest, Oregon. Shrub-, ground-, and litter-dwelling arthropods were collected with a bagging technique, pitfall traps, and Berlese extraction during 2000 and 2001.

Abundance of shrub-dwelling arthropods decreased with the thinning intensity for deciduous foliage, but did not show any response for conifer foliage. Species richness and diversity of shrub-dwelling arthropods showed higher values in the conifer foliage types. Functional group composition for the two foliage types revealed consistently different proportions; the deciduous foliage type had a higher proportion of plant suckers and the conifer foliage type had higher proportion of predators and detritivores. NMS ordination (Non-metric Multidimensional Scaling)

showed a very distinct difference between the species inhabiting the two contrasting foliage types.

Abundance and diversity of ground-dwelling arthropods were higher in Heavy Thin and Light Thin with Gap treatments than the Control and Light Thinning treatments. Five groups of arthropods with relatively high abundance (such as Formicidae (ants), Araneae (spiders), Carabidae (ground-beetles), Gryllacrididae (camel-crickets), and Polydesmida (millepedes)) permitted in depth analysis. Four groups (i.e., ants, spiders, camel-crickets, and millipedes) were more abundant in the more intense thinning treatment areas. However, the abundance of Carabidae (ground-beetles), the third most abundant group, was higher at the unthinned control than in any thinning treatments; densities were much higher during the wet season than dry season. NMS ordination showed that seasonal effects outweighed the thinning effects. Though the disturbance associated with thinning would be expected to decrease populations and density of fauna, I hypothesize that the principal effect of the thinning disturbance was to increase habitat heterogeneity and subsequently species richness.

Abundance of litter-dwelling arthropods decreased in proportion to the thinning treatments. The litter-dwelling fauna was primarily correlated with seasonal moisture and secondarily positively correlated with thinning intensity. The proportion of predators decreased with the advancing seasons.

Response of Arthropods to Different Intensities of T hinning in Oregon

by
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APPROVED:

Major Professor, representing Forest Science

Head of Department of Forest Science

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Hoonbok Yi, Author

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Chapter 1

INTRODUCTION

1.1. Overview

Over the past half-century, several million acres of mature and old-growth forests have been harvested in western Oregon and Washington and converted to young stands. Over time, the proportion of older forests in the landscape has steadily decreased, while the amount of young managed forests has vastly increased (Hunter 1993); therefore, silvicultural knowledge pertinent to young stand ecosystem management has become a significant part of the prospective forest management plan in the Pacific Northwest (PNW). The US Forest Service's Young Stand Thinning and Diversity Study and the US Bureau of Land Management's Density Management Study are designed to determine how different thinning treatments can accelerate the development of late-successional habitat, a primary requirement of the PNW Forest Plan (Han and Kellogg 2000).

The overall long-term goals of the multidisciplinary Young Stand Thinning and Diversity Study are to determine to what extent these management strategies will: (1) accelerate the return of old-growth characteristics in younger managed stands; and (2) promote more biologically diverse young forests (Hunter 1995, 2001). Forest management through the application of thinning protocols can alter species composition and stand structure (Graham 1999). Thinning can also create more disease- and insect-resistant stands (Berryman 1986).

Both young unmanaged and young managed forest ecosystems show variation in structure and composition. The greatest difference between unmanaged and managed stands is the lower density and volume of large snags and logs in managed plantations (Spies and Cline 1988, Spies *et al.* 1988, Spies 1991, Spies and Franklin 1991, Hunter 1993).

Thinning young stands may provide growing conditions that more closely approximate those historically found in developing old-growth stands (Tappeiner *et al.* 1997). Thinning can move stands out of the closed-canopy competitive stage and accelerate the development of conditions found in late seral forests (McComb *et al.* 1993; Bailey 1996; Carey and Curtis 1996; Hayes *et al.* 1997).

1.2. Arthropod diversity

Arthropods are one of the most speciose groups on earth, accounting for more than 50 % of all described species. They represent the vast majority of recognized species in terrestrial ecosystems. The diversity of arthropod species largely reflects an equivalent variety of physiological and behavioral adaptations to environmental conditions. The capacity for rapid response to environmental change makes arthropods useful indicators of change, as well as major engineers and potential regulators of ecosystem conditions (Schowalter 2000).

Interpreting the responses of a diverse arthropod community to multiple interacting environmental factors in integrated ecosystems requires new approaches, such as multivariate statistical analysis and modeling (Gutierrez 1996, Liebhold *et al.* 1993). Such approaches may benefit from avoidance of species-level resolution, using instead the combination of species into phylogenetic or functional groupings. An ecosystem approach provides a framework for integrating

insect ecology with the changing patterns of ecosystem structure and function. Stork (1988) and Stork and Brendell (1990) reported that 24 % of the total arthropod fauna inhabited canopy while 70% of arthropods inhabited the soil and leaf litter in the rainforest ecosystem in southeast Asia. Similar percentages of foliage-dwellers and soil-dwellers are reported by Southwood (1987) for temperate forests in Europe.

1.3. Response of arthropods to changing ecosystems

Taxa representing many functional groups have shown significant responses to silvicultural treatments (Progar *et al.* 1999). Reduced predator diversity in certain treatments with changing tree density may increase the probability that herbivores with potential rapid population responses to environmental change will escape population regulation by the surviving predators (Kruess and Tscharntke 1994, Schowalter 1994, 1995a). Reduction of host tree density should have strong direct effects on herbivore populations due to changes in microclimate, host plant condition, and the proximity of new hosts (Lorio 1980, Schowalter *et al.* 1986, Amman *et al.* 1988, McMillin and Wagner 1993). The effect of host density reflects a combination of accessibility and intraspecific competitive stress of closely spaced hosts and favorable microclimate for herbivores. Herbivores are sensitive to tree spacing and show reduced abundance in thinned stands (Mitchell *et al.* 1983, Amman *et al.* 1988, Schowalter and Turchin 1993).

Understory growth is usually stimulated after partial harvest by the increased availability of light, water and nutrients (Walker *et al.* 1986, Tappeiner and Alaback 1990); therefore, arthropods associated with understory plants should

also change in abundance and composition. Although difficult to predict on the basis of individual species, density and richness of herbivorous species should generally increase as host density and biomass increase. Evaluating trends in arthropod populations associated with understory plant species may be important in understanding changes in diversity and dynamics of the communities (Progar *et al.* 1999). That is, the distribution and physical structure of vegetation might directly influence the spatial patterns of insect herbivore populations. For example, increased vegetational diversity may indirectly encourage predators by providing heterogeneous shelter or increased numbers of alternative prey (Hodkinson and Hughes 1982).

Shrub-dwelling forest understory arthropods are a diverse and functionally important component of forest ecosystems (Schowalter *et al.* 1986; Erwin 1995, Stork *et al.* 1997, Schowalter and Ganio 1998). The response of shrub-dwelling understory arthropods to changing environmental conditions may have significant effects on forest productivity and nutrient cycling processes (Schowalter *et al.* 1986). We need, however, to know far more about how arthropods respond to changing forest conditions and management practices. Studying these responses is very difficult because of the taxonomic complexity of arthropods and the unreplicated nature and costs of systematic forest treatments. Previous studies have compared arboreal arthropod communities in stands of different age or disturbance histories (Schowalter 1995a; Simandl 1993). Current concerns over the protection of biological diversity and forest health under alternative management scenarios require that quantitative data from replicated plots be available for the assessment of understory arthropod responses to changing environmental conditions (Schowalter 1995a).

Forest thinning affects the litter layer on the forest floor. The forest floor includes surface litter, the partially decomposed layer beneath it, and the humus layer. Litter production depends primarily on the productivity of the plant community at the site and exhibits seasonal patterns varying with vegetation type and latitude. Chemical and physical degradation, heterotrophic consumption and decomposition reduce litter accumulation on the surface (Facelli and Picket 1991). Litter plays a major role in the transfer of energy and nutrients in the forest ecosystem and litterfall data have been used to quantify the overall productivity of the ecosytem (Toky and Singh 1983, Ananthakrishnan 1996).

Litter catabolism in soil depends primarily on the exoenzymatic activity of microorganisms, with the soil faunal elements tending to act as catalysts enhancing energy and nutrient influxes. The feeding activities of fauna increase the surface area of the substrate exposed to microbial attack. Arthropod diversity in litter depends on the type of litter and the complex microbial components coupled with the heterogeneity of the litter. Species richness is higher in natural forest litter than in the monoculture of forest plantations (Ananthakrishnan 1996). Seasonal abundance of soil fauna varies with seasonality of rainfall (Ananthakrishnan 1996; Moldenke and Fichter 1987).

1.4. Hypotheses

Although previous studies of arthropod responses to thinning apply to a wide range of 20 to 120 year-old stands, there is a lack of insect community data for 45 to 60 year-old managed Douglas-fir forests (Schowalter 1995a). For this study, four thinning treatments were applied to young stands of 40- to 60-year-old

plantations. The four treatments were: Control (CN), Light thin (LT), Light thin with Gap (L/G) and Heavy thin (HT) (Hunter 1993).

The purpose of this study is to determine the diversity and abundance of the arthropod community in the young stands which were subjected to the thinning treatments.

Hypotheses:

H1. Even though the understory should respond to thinning with increased growth, the abundance and richness of plant feeders in the understory of this particular experiment should *decrease* (defoliators and bark beetles), because in this experiment (5-6 years after treatment), understory shrubs were specifically decreased to improve competitive conditions for conifers. The predators which feed upon the herbivores should therefore *decrease* as well, since their resource has likewise been decreased.

H2. After the copious slash is added to the forest floor and the biomass of deciduous foliage increases, the abundance of ground-dwelling arthropods will *increase*. The response will be detected most easily in the detritivorous arthropods and secondarily in the fungivores and predators.

H3. The response of the forest floor community will be seasonally specific. General increases in all faunal components will be found in the moist spring or early summer. During the summer dry season

characteristic of the West Coast of the United States, contrasting moisture conditions will make the resultant arthropod response difficult to predict. In the litter, thinning will promote dehydration and a consequent *decrease* in entomofauna. However, in the rooting zone, thinning will increase available soil moisture due to the lack of transpiration, and entomofauna should *increase*.

In general, the three forms of thinning treatments should produce a graduated response in the entomofauna, since none are especially severe treatments. The effects of gaps are minimized in this research because sampling is confined to the circumference of the gaps, and not within the gaps *per se.*

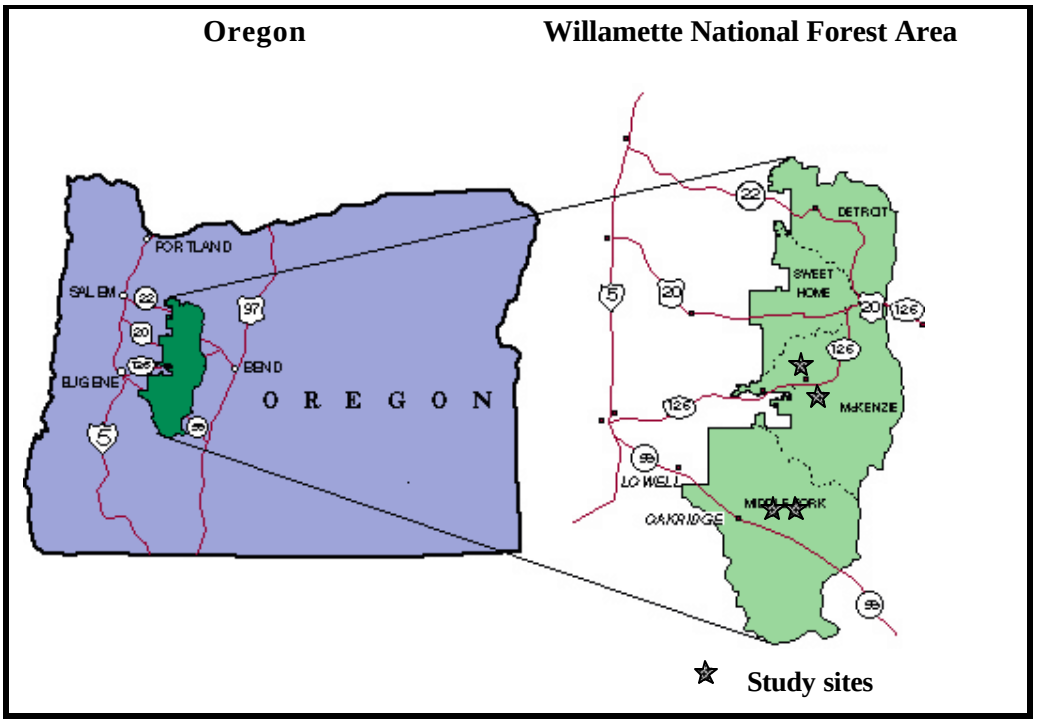


Fig. 1. Map of 4 study sites (stars); TAP, MILL, FLAT, WALK, in Willamette National Forest in Oregon.

Chapter 2

MATERIALS AND METHODS

2. 1. Study Sites

This study was conducted during 2000 and 2001 at 4 study sites located in the Blue River, McKenzie and Oakridge Ranger Districts in the Willamette National Forest (44°07' 30" N, 122°15' 00" W) on the western slope of the Cascade Mountain Range, approximately 80 km east-southeast of Eugene, Oregon, USA (Fig. 1). This region receives approximately 2000 to 4000 mm of rainfall annually, with only 5 % falling between July and October. The average yearly temperature is 10.1°C with 1.6 °C in January and 18.9 °C in July. Soils are generally well developed on a tertiary volcanic substrate (Zobel *et al.* 1976). The forest overstory in the region is dominated by two conifer species, Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Franklin and Dyrness 1973). The regional climate of the typical northwestern mesic forest zone is Mediterranean, with dry hot summers and wet relatively warm winters.

The age of the dominant conifer trees at the research site is 30 to 50 years old and their height is 18 to 27m. Stands of greater than 10 cm in DBH (Diameter Breast Height) averaged about 610 trees per hectare (tph). Deciduous trees average about 7% of the canopy cover (Bohac *et al.* 1997). The L/G treatment was the same as LT except that about 20% of the stand consisted of 0.2 hectare openings (Fig. 2). Treatment areas were selected for homogeneity of stand age, soil class, size, dominant tree species, slope, and elevation. Each of the four stand treatments was implemented in close proximity to one another within four separate blocks.

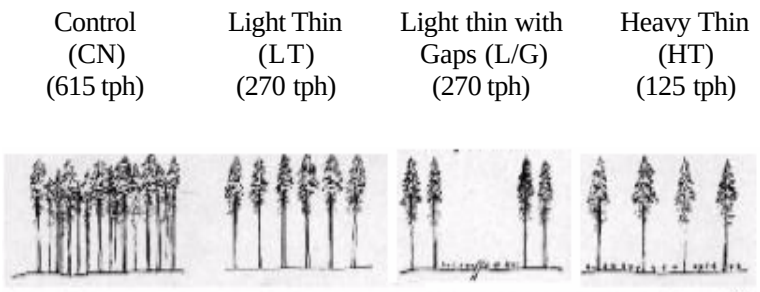


Fig. 2. A schematic of four thinning treatments

Table 1. Thinning Treatments Area Stand Characteristics were determined from an examination of trees greater than 13 cm in Diameter Breast Height (DBH) before commercial thinning; the commercial thinning occurred between October of 1994 and December of 1997. CN; Control, LT; Light Thin, L/G; Light thin with Gap, HT; Heavy Thin (Bohac *et al.* 1997, Soil resource inventory 1994).

Soil Type of surface soils and subsoils;

A.100 % of thin shotty loams/clay loams, silty clay loams, and clays

B. 50% of thin shotty loams/clay loams, silty clay loams, and clays , 50% of thin loams silty clay loams, clay loams/clay loams, silty clay loams, and clays

C. 50% of thin shotty loams/clay loams, silty clay loams, and clays , 50% of thin gravelly loams and sandy loams/thick gravelly cobbly loams

D. 100% of thin loams, sandy loams, and loamy sands/very thick, gravelly to very gravelly cobbly sandy loams

E. 60% of thin shotty loams and silt loams/thick silt loams, silty clay loams, and clay loams, 40% of thin shotty loams/clay loams, silty clay loams, and clays

F. 100 % of thin shotty loams and silt loams/thick silt loams, silty clay loams, and clay loams

G. 60% of thin gravelly loams/thick gravelly loams, silt loams, and silty clay loams, 40% of thin shotty loams/clay loams, silty clay loams, and clay

Block	Treatment	Area (Ha)	Elevation (m)	Slope (%)	Aspect	Date of Harvest	Stand Age	Dominant Plant Association	Soil Type
TAP	CN	30	804	18.8	E	N/A	40	TSHE/GASH	**A**
	LT	37	609	17.1	E	1995	38	TSHE/BENE	**B**
	L/G	15	792	16.0	E	1995	40	TSHE/BENE	**B**
	HT	19	792	24.0	ENE	1995	40	TSHE/BENE	**B**
MILL	CN	53	902	21.1	SSEE	N/A	42	TSHE/BENE	**C**
	LT	37	524	20.0	SE	1995	43	TSHE/BENE	**C**
	L/G	20	438	8.9	S	1996	42	TSHE/BENE	**D**
	HT	35	658	22.9	SSW	1996	42	TSHE/BENE	**E**
FLAT	CN	31	877	6.2	SE	N/A	39	TSHE/BENE	**F**
	LT	32	902	5.3	SE	1997	39	TSHE/BENE	**F**
	L/G	39	905	5.3	SE	1995-96	40	TSHE/BENE	**F**
	HT	20	905	0.0	SSEE	1996-97	36	TSHE/BENE	**F**
WALK	CN	51	634	11.4	N	N/A	37	TSHE/ RHMA-GASH	**G**
	LT	22	646	21.8	NW	1995	33	TSHE/ RHMA-GASH	**G**
	L/G	30	670	14.5	NNE	1994-95	39	TSHE/ RHMA-GASH	**G**
	HT	19	652	16.0	N	1995	35	TSHE/ RHMA-GASH	**G**

The area of treatments averaged 30.4 hectares in size (Table 1). The WALK block is somewhat more mesic than the others due to its north-facing aspect, and thus dominated by *Rhododendron macrophyllum* and *Gaultheria shallon*.

2.2. Vegetation

Vegetation analysis one year after thinning revealed that canopy cover was: CN = 82% (± 10%), LT = 57% (± 18%), L/G = 31% (± 24%), and HT = 34% (± 20%). Canopy covering L/G and HT were not significantly different because the between-tree interval of the remaining trees of the L/G actually was 13% greater than expected. The largest alteration in vegetation was the significant decrease in both moss and tall shrub (*Acer, Rhododendron, Vaccinium*) cover in all thinning treatments relative to the CN (Bohac *et al.* 1997).

No plant species was lost during thinning, and species richness increased (Bohac *et al.* 1997). This increase was largely due to additional pioneering herbaceous species. *Epilobium* spp, *Senecio sylvaticus, Collomia heterophylla,* and *Cirsium* spp., which were rarely encountered in control plots, formed a significant presence in thinned sites (Table 2). The more heavily thinned treatments, L/G and HT, consistently had higher frequency values for these species than did the LT. Average cover and frequency values were tabulated for some key indicator species and exotic invader species. Several invasive species appeared or increased their presence in thinned plots, most likely due to colonization (Table 2). Several species important in vegetation zone classification decreased in cover percentage in thinned areas compared to the CN: *Berberis nervosa, Acer circinatum, Polystichum munitum, Chimaphila menziesii, Achlys triphylla, Adenocaulon bicolor* and *Viola sempervirens.* However, *Vancouveria hexandra, Trillium ovatum,*

Table 2 Species Cover and Frequency (Freq) one year after thinning (adapted from Bohac *et al.* 1997)

Species	CN		LT		L/G		HT	
	Cover	Freq	Cover	Freq	Cover	Freq	Cover	Freq
Tall Shrubs								
Acer circinatum	37.8	70.4	5.6	72.2	10.7	91.3	8.5	92.6
Rhododendron macrophyllum	2.3	23.9	0.9	29.6	2.8	55.4	4.5	48.2
Vaccinium parvifolium	0.8	56.3	0.1	85.2	1.0	77.1	0.7	89.4
Low Shrubs								
Berberis nervosa	11.6	62.0	4.3	88.9	6.5	97.2	7.0	100
Chimaphila menziesii	*	43.7	*	33.3	*	10.3	*	24.2
Chimaphila umbellata	*	25.4	*	7.4	*	24.7	*	16.7
Gaultheria shallon	5.0	59.2	2.5	90.7	7.3	88.1	4.1	96.8
Linnaea borealis	2.5	56.3	0.6	68.5	1.4	67.8	0.9	84.1
Rubus nivalis	0.3	33.8	*	3.7	0.1	18	*	9.5
Rubus ursinus	2.8	62.0	1.8	92.6	3.9	97.2	1.8	100
Whipplea modesta	0.9	46.5	0.3	40.7	0.7	74.8	0.3	63.8
Ferns								
Polystichum munitum	5.1	56.3	3.6	96.3	3.5	88.6	2.3	89.6
Pteridium aquilinum	1.4	46.5	1.9	72.2	1.1	66	1.4	86.4
Herbs								
Cirsium vulgare (I)	*	1.4	*	1.9	*	38.1	*	39.9
Collomia heterophylla	-	0	*	38.9	0.1	25	0.1	37.7
Epilobium paniculatum	-	0	-	0	*	56.5	*	17.9
Epilobium watsonii	-	0	*	20.4	*	34.5	*	61.4
Gallium triflorum	*	23.9	0.2	70.4	0.3	82.7	0.2	81.1
Trillium ovatum	*	54.9	*	35.2	*	31.7	*	70.7
Senecio sylvaticus (I)	*	1.4	*	44.4	0.3	84	0.1	77.1
Vancouveria hexandra	*	35.2	*	31.5	0.1	51.3	0.1	53.7
Viola sempervirens	0.6	56.3	0.2	68.5	0.1	69.4	0.2	86.4

(I) = Introduced * Value less than 0.5, - No presence detected

Rubus ursinus, and *Whipplea modesta,* common species in the *Tsuga heterophylla* zone, showed no significant change in cover percentages between treatments and control. For all growth forms the CN plots had the highest cover estimates, with a ratio of 5.0 : 2.5 : 1.0 for tall shrub: low shrub: herb cover. The overall architecture of the understory remained mostly the same (albeit with lower cover values) in the HT treatments with a 4.1 : 2.3 : 1.0 ratio. Low shrubs in the LT had the greatest difference from the CN of all the treatments, 57% lower, decreasing from 23.5% to 10.2% cover. The HT showed no significant difference from any of the groups for low shrubs. Tall shrub cover was reduced greatly in all treatments. The LT showed the greatest reduction at 25% of the control value. L/G and HT treatments were reduced by 58% and 43% respectively. Though there was a reduction in herb foliage cover in the treatments (range: 9.3% in CN, 5.6% in L/G), significant herb layer changes did not occur according to ANOVA analysis (alpha = .05) (Table 3). The L/G had a canopy component ratio of 3.4 : 3.7 : 1.0 and the LT had only 1.5 : 1.4 : 1.0, nearly even coverage for all growth forms. The increase of understory growth following thinning is generally expected for both shrubs and herbs but the treatment had not yet had sufficient time to respond by the first year post-thin (adapted from Bohac *et al.* 1997). Fifth-year post-treatment shrub data are starting to reveal treatment effects, but the results are not yet significant (Puettmann, unpub. data).

Table 3. Overstory and understory mean cover (%) for each thinning treatment (adapted from Bohac *et al.* 1997)

Treatment	Overstory	Tall shrubs	Low shrubs	Herbs	Moss
CN	82.0	45.4	23.5	9.3	22.1
LT	57.0	11.5	10.2	7.5	11.3
L/G	32.0	19.1	20.6	5.6	3.4
HT	34.0	25.7	14.4	6.2	3.4

2.3. Arthropod Sampling

2.3.1. Shrub-dwelling understory arthropods

Shrub-dwelling arthropods were collected from shrub branches in June (late spring), August (dry season), and October (early wet fall) in 2000 and June and August in 2001 to assess the importance of seasonal changes in arthropod communities. The samples were collected at the edge of the gaps for the L/G treatment to minimize as much of the effect of gaps, as possible. In the other treatments, samples were collected haphazardly within the center of the treatment block, avoiding special microhabitat types; *i.e.*, fallen logs, tree stumps, and shrub thickets.

To represent the understory, sapling individuals of two conifer tree species (Douglas-fir, *Pseudotsuga menziesii*, and western hemlock, *Tsuga heterophylla*) and one deciduous tree species (vine maple, *Acer circinatum*) were haphazardly chosen within each plot. Three vine maples for deciduous foliage type and two Douglas-fir and two western hemlock for conifer for coniferous foliage type were sampled from each treatment.

A bagging technique was employed for collecting arthropod samples within the shrub canopy. The sampling was applied to four replicates of four treatments. One 50 liter plastic bag was sufficient to enclose all of the foliage on one branch (approximately 0.5 meter wide by 0.5 meter long) of an understory sapling tree. One foliage-bearing branch (about 50 cm in length at crown level of the understory trees) was quickly enclosed in the plastic bag, the branch was clipped from the tree; and the bag was then sealed (Schowalter 1995b, Schowalter and Ganio 1998). Although this sampling technique may not collect all of the most highly mobile or the nocturnal invertebrates, the resident fauna of functional concern is largely

sedentary and therefore the samples were quite likely representative of the density and biomass of relevant invertebrates.

Invertebrate samples were preserved in cold storage at 5 ^{o}C until processing. Arthropods were sorted and identified to the finest possible taxonomic resolution. Branches were removed sequentially from the cooler and examined for invertebrates. Each branch was examined quickly for mobile arthropods, then examined microscopically for smaller or less mobile arthropods. Finally, plant debris in each bag was examined microscopically for any remaining invertebrates. Larvae were reared to facilitate identifications. This bagging method allowed organisms to be maintained alive, but inactive, until processing, reducing the likelihood that dead arthropods were subsequently overlooked. All arthropod taxa were combined at a family or ecological guild level (functional groups: e.g., defoliatiors, plant feeders, predators, detritivores, and miscellaneous) to allow a thorough statistical analysis of abundance patterns (Schowalter and Ganio 1998; Schowalter 2000).

The collected plant materials were dried at 50 ^{o}C to a constant weight and then weighed to estimate plant biomass. Invertebrate numbers were divided by plant biomass to obtain a standard unit of comparison (intensity = number/ kg plant biomass) among tree species and treatment (Schowalter 1995b, Schowalter and Ganio 1998). The total list of arthropods collected appears as Appendix A.

2.3.2. Ground-dwelling arthropods

Ground-dwelling arthropod sampling on forest floors using pitfall traps was conducted from June 15 to June 29 (warm wet season) and July 27 to August 11 (hot dry season) in 2000, and June 18 to July 3 and August 2 to August 18 in 2001

in order to quantify seasonal changes in arthropod communities. Each pitfall trap consisted of two plastic cups (12.5 cm in diameter by 8 cm deep) stacked and buried flush to the ground. The upper cup containing propylene glycol as a preservative was used for trapping while the bottom cup remained in place to reduce local soil disturbance between collection dates. Each trap was covered by a metal cover (13 cm x 13 cm) to prevent rain from diluting the preservative supported by four nails, leaving a space of about three centimeters between the cover and the rim of the cup, which was at ground level. Five pitfall traps per treatment were maintained for two weeks per sampling period. To minimize the edge effect of each thinning treatment, each trap was located close to the center of each treatment with five-meter intervals between each trap.

Traps were left open for a period of fourteen days and closed during non-sampling periods using the lid of a big plastic cup. The metal roofing of each trap was pushed down on the lid of the cup when not in use (Lemieux and Lindgren 1999, Villa-Castillo and Wagner 2002). All samples collected from each treatment site were taken to the lab and identified under a dissection microscope. The identified sample data were pooled to compare abundance and diversity of arthropods under the separate treatments. All samples were identified to family level. However, the Carabidae, widely employed in biodiversity studies, were keyed out to species level. Separate analyses were performed on (1) total taxa, (2) Coleoptera, and (3) Carabidae.

2.3.3. Litter-dwelling arthropods

Two 0.5 m X 0.5 m combined litter and humus samples were collected from each treatment unit on October 14, 2000 (late-growing season), June 18, 2001

(early-growing season) and August 2, 2001 (mid-growing and dry season). The samples were collected at the edge of the gaps in the L/G to minimize the effect of gaps. In the other treatments, samples were collected within the center of the treatment block, avoiding special microhabitats (*i.e.*, fallen logs, tree trunks, shrub thickets, etc.) in order to represent the typical forest condition. All samples were chilled at 5 ^{o}C until they were processed in a Berlese funnel (30 cm in diameter and 50 cm deep).

In order to extract arthropods from the litter samples, the two litter depths from each treatment were combined in one Berlese extractor and allowed to dry for at least two weeks in the Berlese funnel under 65 watt bulbs (Macfadyen 1961, 1962, Southwood 1978, Moldenke 1994). Litter arthropod samples were identified to the lowest possible taxonomic level with the available expertise. For comparison among treatments (Appendix A), the arthropod number divided by sample size provided a standard unit (intensity = number/m^2). As with the foliage-dwelling arthropods, all taxa excluding mites and Collembolla, were combined by family and ecological guilds (e.g. functional groups: defoliatiors, plant feeders, predators, detritivores, and miscellaneous) for statistical analyses of abundance patterns (Schowalter and Ganio 1998).

To measure moisture content (%) of the litter, five sub-samples of litter (about 20g) were chosen from each treatment. Litter samples were dried at 50 ^{o}C to a constant weight and then weighed.

All specimens were verified against H.J. Andrews Long-Term Ecological Research Collection and the Oregon State University Arthropod Collection at Corvallis, Oregon. Voucher arthropods were deposited at the Oregon State University Arthropod Collection.

2.4. Statistical Analyses

Species diversity was determined as alpha, beta and gamma diversity measures. To calculate beta diversity, the total number of species was divided by the average number of species per each thinning treatment, relative to the CN. The Shannon-Weiner Diversity Index was calculated, with evenness included, as well as the Simpson Diversity Index.

Analyses of variance (ANOVA) were performed to test the hypothesis of there being no difference among thinning treatments. A Proc Mixed ANOVA test from the SAS program was used to obtain F-statistics with species abundance as a response variable including sites, treatments, dates and interactions (SAS Inc. 1982). The arthropod samples collected from shrub understory, pitfall traps, and litter samples at each treatment were separately pooled for all sampling seasons and years to compare the abundance and diversity of the samples. The pair-wise comparison method on graphs and tables was performed by Tukey-Kramer procedure (SAS Inc. 1982).

The pooled data were analyzed with the PC-ORD version 4.28 for multivariate analyses (McCune and Mefford 1999, McCune and Grace 2002). The pooled main matrices for each arthropod sample had high beta diversity, moderate to extreme row and column skewness, and a high coefficient of variation among the sums of the columns (species) in the matrix. To reduce these characteristics and to increase the interpretability of the results, a data transformation was executed. First, rare species which occurred in less than 5 % of the number of samples were deleted. Then logarithmic transformation was used. The relativization by column (species) maximum was performed to equalize the weights between abundant and

less abundant species. The Sorensen distance measure was used for all analyses. The transformed data were used for ordination analysis at this point.

To detect outliers, various distance measures (Sorensen, Relative Sorensen, Euclidean, Relative Euclidean, Chi-square) were used and ordinations (PCA, NMS, RA, and DCA) were carried out. After finding and discarding only a single outlier, I ran Bray-Curtis Ordination to find variables with strong positive or negative correlations. This result was examined along with Row and Column summary statistics to determine in what ways the sample unit was an outlier.

Non-metric Multidimensional Scaling (NMS) (Mather 1976, Kruskal 1964, Clarke 1993) is an iterative method based on rank distances between sample units. It is useful for ecological gradient studies because of its general robustness and lack of assumptions about the distribution or type of data. Therefore, NMS was used to determine the number of factors structuring the complex arthropod community structure and to qualitatively summarize the overall distribution of species assemblages across the gradients of different thinning levels. NMS was used in lieu of other ordination methods because it avoids the "zero-truncation problems" of Beals (1984). Sorensen distances were used in species space.

The analysis of indicator species by Dufrene and Lengendre's (1997) method provided a simple, intuitive solution for identifying which species might serve as indicators of a particular environmental condition. This method calculated the proportional abundance of a particular species in a particular group relative to the abundance of that species in all groups. Then the method calculated the relative abundance of a certain species in a certain group and calculated the proportional frequency of the species in each group. These percentages were regarded as the faithfulness or constancy of presence within a particular group. The 2 proportions

were then multiplied to yield a percentage, used as an indicator value for each species in each group. Because the component terms are multiplied, both indicator criteria must be high for the overall indicator value to be high. The highest indicator value for a given species across groups is saved as a summary of the overall indicator value (IV) of that species and evaluated by a Monte Carlo method with randomly reassigned SUs (sample units) to groups 1000 times. The probability of type I error was the proportion of times that the IV from the randomized data set equals or exceeds the IV from the actual data set. The null hypothesis is that IV is no larger than would be expected by chance (McCune and Grace 2002).

Table 4. ANOVA table on understory arthropod intensity among thinning treatments during 2000 and 2001

Source	DF	Type III SS	Mean Square	F Value	Pr > F
Treatment (T)	3	4678910	1559637	0.97	0.4081
Foliage type (F)	1	80066195	80066195	49.63	<.0001
Season (S)	2	1750056	875028	0.54	0.5817
T*F	3	4836572	1612191	1.00	0.3928
T*S	6	28905262	4817544	2.99	0.0071
F*S	2	3571134	1785567	1.11	0.3314
T*F*S	6	22458128	3743021	2.32	0.0321

Chapter 3

RESULTS

3. 1. Shrub-dwelling understory arthropods

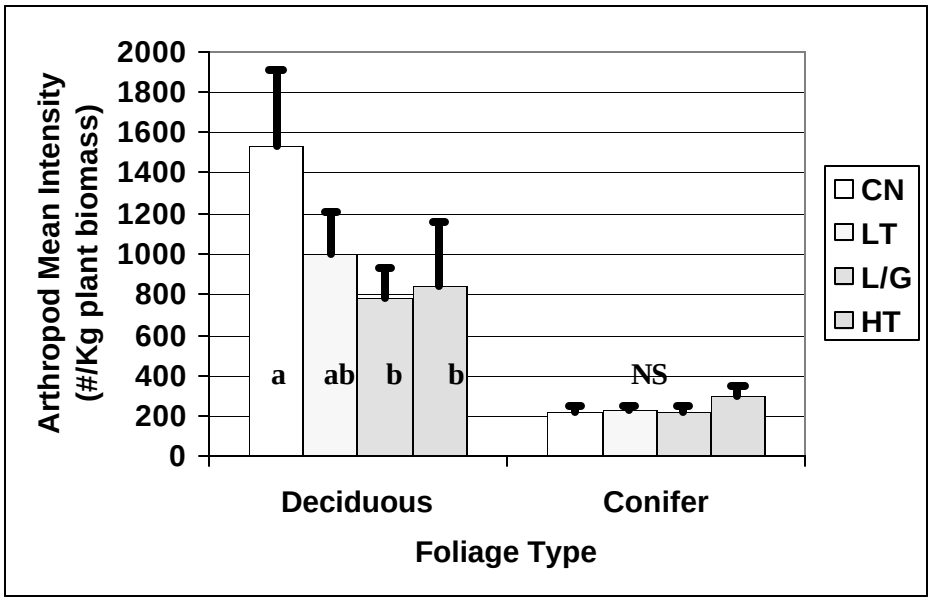
3. 1. 1. Arthropod intensity

Table 4 reveals that arthropod intensity (number of captures per kg foliage) was most affected by foliage type. Approximately four times as many arthropods were found on deciduous foliage as were found on coniferous foliage (Fig. 3A).

Average arthropod population intensities representative of the different thinning treatments are shown in Fig. 3B, with data pooled across foliage type and season. Although the abundance of shrub-dwelling arthropods does not show a statistically significant difference among the thinning treatments, there is a significant decreasing trend on deciduous foliage with thinning intensity, but no comparable trend on coniferous foliage type (Fig. 3A).

Since foliage types are significantly different (Table 4), I separated my results relative to the two foliage types. There is also a statistically significant difference with the treatment x season interaction term. Arthropod intensity is consistently higher on deciduous foliage for the entire year (Fig. 4C). There are no significant treatment effects on coniferous foliage either in general or separated by season (Fig. 4B). Deciduous foliage, on the other hand, supports a significantly higher intensity of arthropods during both spring and summer within the control plots (Fig. 4A). Variability within the data is too large to statistically support the apparent visual trend of decreasing arthropod intensity with thinning severity on

A



B

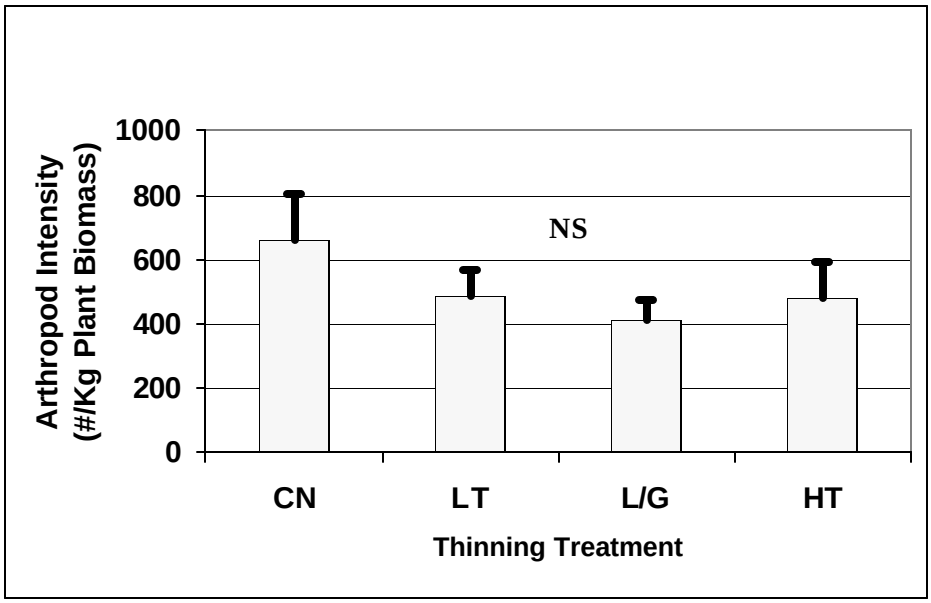
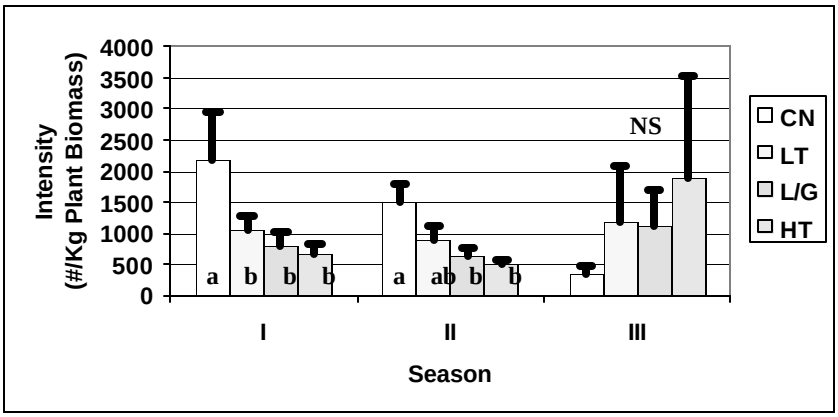
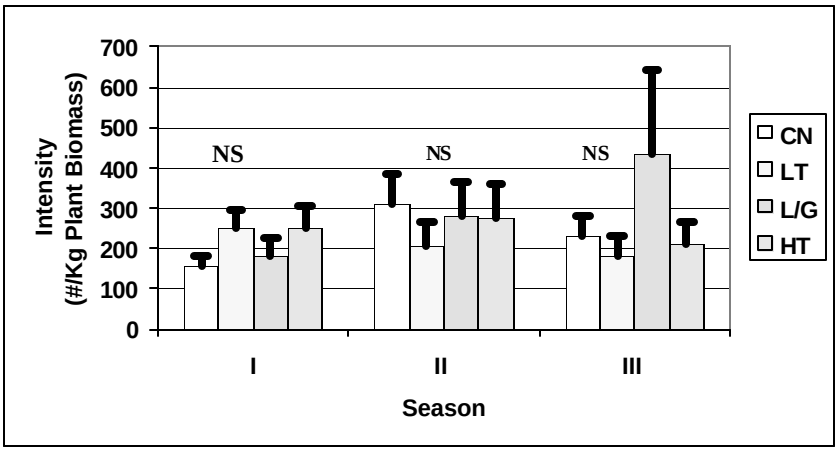


Fig 3. Mean arthropod intensity (# / Kg Plant Biomass) by thinning treatments with standard errors (SE) for: A) separate deciduous and coniferous foliage types and B) pooled foliage data. "a" and "b" indicate statistically significant differences and "ab" indicates no statistical difference between a and b. NS indicates no statistically significant difference.

A. Deciduous Foliage Type



B. Coniferous Foliage Type



C. Seasonal Abundance

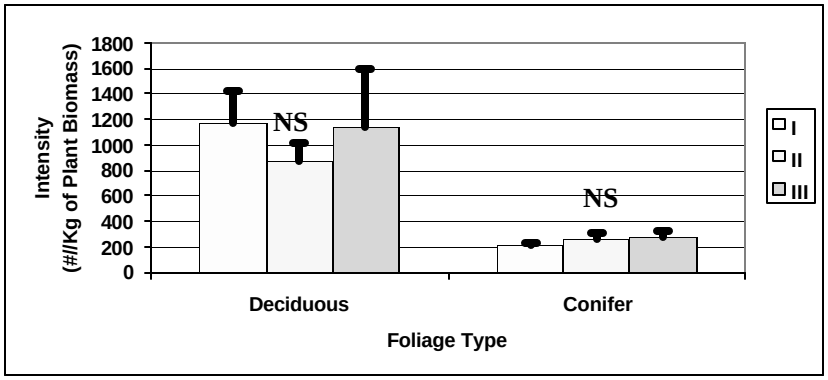


Fig. 4. Mean abundance of arthropods: A) Deciduous foliage type and thinning treatments B) Coniferous foliage type and thinning treatments C) seasonal abundance for foliage types, deciduous and conifer trees, in 2000 and 2001. (CN: Control, LT: Light Thin, L/G: Light with Gap, HT: Heavy Thin, I: June, II: August, III: October). "a" and "b" indicate statistically significant differences and "ab" indicates no statistical difference between a and b. NS indicates no statistically significant difference.

deciduous foliage. The effect of thinning apparently is reversed in fall (but no statistical difference) as the maple leaves drop more quickly in the most severe thinning, artificially increasing the density of arthropods on those few remaining leaves (Fig. 4A).

3. 1. 2. Species diversity and richness

Species diversity indices (alpha, beta, gamma, Shannon-Wiener, and Simpson) are shown in Table 5 for deciduous and coniferous foliage types within the thinning treatments. There is no apparent trend in diversity values for the deciduous foliage type with thinning. However, for the coniferous foliage type, α increases and β decreases with thinning intensity (both significantly).

The lowest average species richness (α) was recorded in LT with deciduous foliage type and the highest average species richness was recorded in HT on the coniferous foliage type. Beta diversity, in contrast, was highest in LT (11.1) with the deciduous foliage type and was lowest in HT (7.7) with the coniferous foliage type. Shannon-Wiener diversity (H') and Simpson diversity (D') were higher with the coniferous foliage type than with the deciduous foliage type.

3. 1. 3. Community composition

On the other hand, the proportions of arthropod abundance within functional groups showed a different community structure between deciduous and coniferous foliage types (Fig. 5). For the deciduous foliage type, defoliators (DF) and plant feeders (PF) comprised the dominant functional group (61%) while predators (PR) comprised 28% and detritivores (DT) only 9% (Fig. 5A).

Table 5. Average species richness (α) and its standard error, beta ($\beta = \gamma/\alpha$), Shannon-Wiener Diversity (H') and Simpson (D`) Diversity Indices of shrub-dwelling arthropods at each thinning treatment (N = 80 trees at deciduous and N=78 trees at conifer trees). "a" and "b" indicate statistically significant differences and "ab" indicates no statistical difference between a and b. NS indicates no statistically significant difference from Tukey multiple comparison

Thinning Treatment	Foliage type							
	Deciduous (tree species=1)				Conifer (tree species=2)			
	$(\alpha \pm SE)^{NS}$	β	H'	D'	$\alpha \pm SE$	β	H'	D'
CN	7.8 ± 0.9	$(8.6)^{b}$	1.39	0.64	$(8.4 \pm 0.8)^{a}$	$(10.8)^{a}$	1.67	0.73
LT	6.1 ± 0.6	$(11.1)^{a}$	1.05	0.50	$(10.9 \pm 0.7)^{b}$	$(8.3)^{ab}$	1.96	0.80
L/G	7.0 ± 0.6	$(9.6)^{ab}$	1.30	0.59	$(10.4 \pm 0.8)^{ab}$	$(8.7)^{ab}$	1.86	0.77
HT	7.3 ± 0.7	$(9.2)^{ab}$	1.28	0.57	$(11.7 \pm 0.7)^{b}$	$(7.7)^{b}$	1.79	0.73

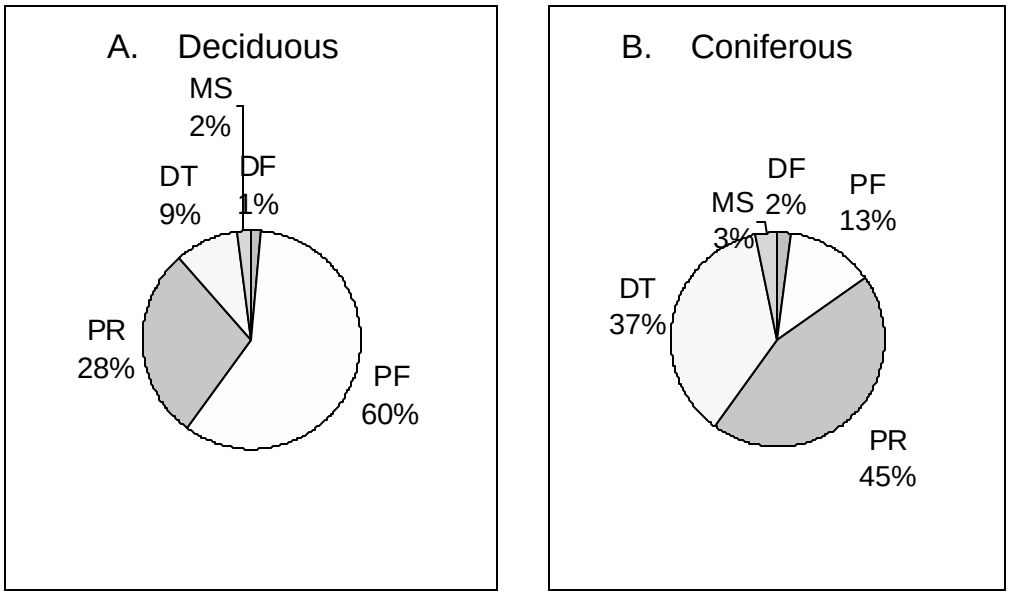


Fig 5. The proportion of arthropod abundance belonging to different functional groups (DF=defoliators, PS=plant suckers, PR=predators, DT=detritivores, MS=miscellaneous) in deciduous and coniferous foliage types.

For the coniferous foliage type, DF and PF combined were only 15%, PR was the dominant functional group (45%), and DT was very abundant (37%) (Fig. 5B). Similar patterns of functional groups were observed with each of the four thinning treatments.

Three factors, thinning treatment (T), foliage type (F), season (S) and their interactions were compared amongst functional groups of shrub-dwelling taxa (Table 6). Abundances of only 7 taxa varied significantly among the thinning treatments; five of these instances were also significant by T x F interaction. Fourteen taxa differed significantly by foliage type, 64% of which were also significantly different in the F x S interaction. Abundances of 17 taxa varied significantly among the sampling dates. Abundances of 5 taxa were affected by T x S interaction (Table 6).

Defoliators/leaf miners consisted of Coleoptera (Cerambycidae, Chrysomelidae, Curculionidae, Elateridae, Mordellidae, Scolytidae), Diptera (Anthomyiidae, Cecidomyiidae), Hymenoptera (Diprionidae-Sawflies), and all Lepidoptera (Geometridae, Noctuidae, and other moths). No defoliator showed differences due to treatment, foliage type or sampling season.

Plant suckers consisted of Diptera (Tephritidae), Heteroptera (Berytidae, Rhopalidae, Thyreocoridae), Hymenoptera (Halictidae, Tenthredinidae), Homoptera (Aphididae, Cercopidae, Cicadellidae, *Chionaspis*, *Nuclaspis* and *Straminaspis* scales and other Homoptera), Thysanoptera (yellow, black, and red thrips), and Heteroptera (Pentatomidae, Tingidae).

Plant suckers responded mostly frequently to foliage type (66%), which reflects a basic specialization within most taxa between coniferous versus deciduous foliage. Seasonal population responses were observed in 40% of the

Table 6. Effects of thinning treatment, foliage type, season, and their interactions and thinning degree (L; CN and LT, H; L/G and HT) on abundances of canopy arthropods in western Oregon during 2000 and 2001

GROUP	Thinning treatment (T) df = 3	Foliage type (F) df = 1	Season (S) df =2	(TXF) df = 3	(TXS) df=6	(FXS) df=2	Thinning degree (L and H) df=1
Defoliators/Leaf Miners							
Coleoptera	-	-	-	-	-	-	-
Diptera	-	-	-	-	-	-	-
Sawflies	-	-	-	-	-	-	-
Lepidoptera	-	-	-	-	-	-	-
Plant Suckers							
Diptera	-	-	-	-	-	-	-
Heteroptera	-	-	-	-	-	-	-
Aphids	-	****	0.0002***	-	0.0297*	0.0002***	-
Black Aphids	0.039*	0.0103*	0.0003***	0.0095**	-	-	-
Periphyllus	-	****	****	-	-	****	0.0463*
Cicadellidae	-	0.0014*	0.0018**	-	-	0.0118*	-
Cinara	0.0143*	0.0025*	-	0.0131*	-	-	0.0006***
Homoptera-scale	-	0.0065*	-	-	-	-	-
Other Homoptera	-	-	-	-	-	-	-
Yellow Thrips	-	0.0002***	0.0002***	-	-	****	-
Black Thrips	-	-	-	-	-	-	-
Red Thrips	-	0.0495*	-	-	-	-	-
Predators/Parasites							
Cantharidae	0.0359*	0.0052**	****	-	-	0.0088**	0.0211*
Coccinellidae	-	-	-	-	-	-	-
Other Coleoptera	-	-	-	-	-	-	-
Lestodiplosis	-	0.0317*	0.03*	-	-	0.0146*	-
Diptera	-	-	-	-	-	-	-
Heteroptera	-	-	-	-	-	-	-
Chalcidoidea	-	-	-	-	-	-	-
Formicidae	-	-	-	-	-	-	-
Ichneumonidae	0.0291*	-	-	-	0.0036**	-	0.0213*
Other Hymenoptera	-	-	-	-	-	-	-
Chrysopidae	-	-	-	-	-	-	-
Spiders	0.0002***	-	****	0.0013***	0.0251**	-	0.001**
Anystid mites	-	-	0.0243*	-	-	-	-
Erythraeid mites	-	-	-	-	-	-	-
Phytoseiid mites	-	****	****	-	-	****	-
Detritivores/Fungivores							
Coleoptera	-	-	-	-	-	-	-
Diptera	-	0.0002***	****	-	-	****	-
Heteroptera	-	-	-	-	-	-	-
Psocoptera	-	-	****	-	-	-	-
Collembola	-	-	0.0141*	-	-	-	-
Diplopoda	0.0362*	-	****	-	0.0341*	-	-
Camisia mite	-	0.0006***	-	-	-	-	-

Table 6. Continued

GROUP	Thinning treatment (T) df = 3	Foliage type (F) df = 1	Season (S) df =2	(TXF) df = 3	(TXS) df=6	(FXS) df=2	Thinning degree (L and H) df=1
Jugatala mite	-	-	0.0068**	0.0026**	-	-	0.0245*
Other mites	-	-	-	-	-	-	-
Miscellaneous							
Coleoptera	-	-	-	-	-	-	-
Diptera	-	0.001**	-	-	-	0.0042**	-
Heteroptera	-	-	0.0204*	-	0.0116*	-	-
Hymenoptera	0.013*	-	-	0.0455*	-	-	-
Thysanura	-	-	-	-	-	-	-
Miscellaneous mites	-	-	0.0017**	-	-	-	-

**** **< 0.0001,** *** **P < 0.001,** ** **P < 0.01,*** **P < 0.05,** - **Not Significant**

taxa. Only 2 species of aphids exhibited a treatment response (both also significant in the treatment by foliage type interaction).

Predators/parasites consisted of Coleoptera (Cantharidae and Coocinellidae, Lampyridae, Pselaphidae, Staphylinidae), Dermaptera (Forficulidae), Diptera (Acroceridae, Culicidae, Hippoboscidae, *Lestodiplosis*, Sciomyzidae, Syrphidae, Tachinidae, Tipulidae), Heteroptera (Nabidae), Hymenoptera (Braconidae, Chalcidoidea, Encyrtidae, Eulophidae, Eupelmidae, Erytomidae, Formicidae, Ichneumonidae, Perilampidae, Pteromalidae, Vespidae, Sphecidae), and Neuroptera (Chrysopidae, Hemerobiidae). Predators exhibited species-specific seasonal differences (33% of fauna), foliage type differences (20%), and treatment differences (two of which also differed significantly by treatment x season and one by treatment x foliage type interaction).

Detritivores/fungivores consisted of Coleoptera (Scarabaeidae), Diptera (Chironomidae, Mycetophilidae, Phoridae), Heteroptera (Aradidae), Psocoptera, Diplopoda (Polydesmida), Collembolla (Entomobryidae, Sminthuridae), and Acarina (*Camisia, Phauloppia, Platyliodes, Jugatala, Scapheremaeus*). Five species (55%) of fungivores differed seasonally, 2 by foliage type (22%), and only Diplopoda differed by treatment.

When the CN and LT treatments (CN + LT) and the L/G and HT are contrasted (Table 7), no entire feeding guilds show any effect of treatment. The only individual species to demonstrate a treatment effect from combining the treatment intensities are: Plant suckers - *Periphyllus Cinara* , Predaceous – Cantharidae, Ichneumonidae, and spider; Fungivores – *Jugatala* (Table 6).

Therefore, in summary, although Defoliators/Leaf Miners showed no significant differences for any factor or their interactions, Plant suckers showed

Table 7. Effects of thinning treatment, foliage type, season, and their interactions and thinning degree (L: CN and LT, H: L/G and HT) on functional groups of canopy arthropod abundances in western Oregon during 2000 and 2001

Functional Groups	Thinning treatment (T) df = 3	Foliage type (F) df = 1	Season (S) df =2	(TXF) df = 3	(TXS) df=6	(FXS) df=2	Thinning degree (L and H) df=1
Defoliators/Leaf Miners	-	-	-	-	-	-	-
Plant Suckers	-	****	0.0302*	-	0.0191*	0.0294*	-
Predators/Parasites	-	0.0079**	****	0.0018**	–	****	-
Detritivores/Fungivores	-	0.0269*	****	-	–	-	-
Miscellaneous	-	-	-	-	-	-	-

**** **P < 0.0001,** *** **P < 0.001,** ** **P < 0.01,** * **P < 0.05,** - **Not Significant**

significant differences for foliage type ($p<0.0001$ from F-test), season ($p<0.0302$), thinning treatment by season interaction ($p=0.02$), foliage type by season interaction ($p<0.0294$). Predators/Parasites showed significant differences for foliage type ($p<0.0079$), season ($p<0.0001$), thinning treatment by foliage type interaction ($p=0.0018$), and foliage type by season interaction ($p<0.0001$). Detritivores and Fungivores showed significant differences for foliage type ($p=0.0269$) and season ($p<0.0001$). Miscellaneous showed no significant differences for any factor or their interactions (Table 7).

The distinctiveness of the arthropod communities on the different foliage types is shown in Fig. 6. This NMS plot was rotated to -60^{o} and Axis 1 and Axis 3 explained 23% and 26 % of the variance (cumulatively 49%: p-value = 0.196 from the Monte Carlo test). The Monte Carlo tests were based on 50 randomizations.

3. 1. 4. Indicator species analysis

Indicator species analysis was applied to the shrub-dwelling arthropods of both foliage types (Table 8). Eight taxa for deciduous foliage type and seven taxa for coniferous foliage type were significant indicators. Three taxa for the deciduous foliage type, [*Periphyllus* aphid (IV=78.7), phytoseiid mite (IV=56), and yellow thrips (IV=29.8)] and two taxa for coniferous foliage type, [spiders (IV=54.3) and *Camisia* (IV=36.1)] have especially low p-values (0.001).

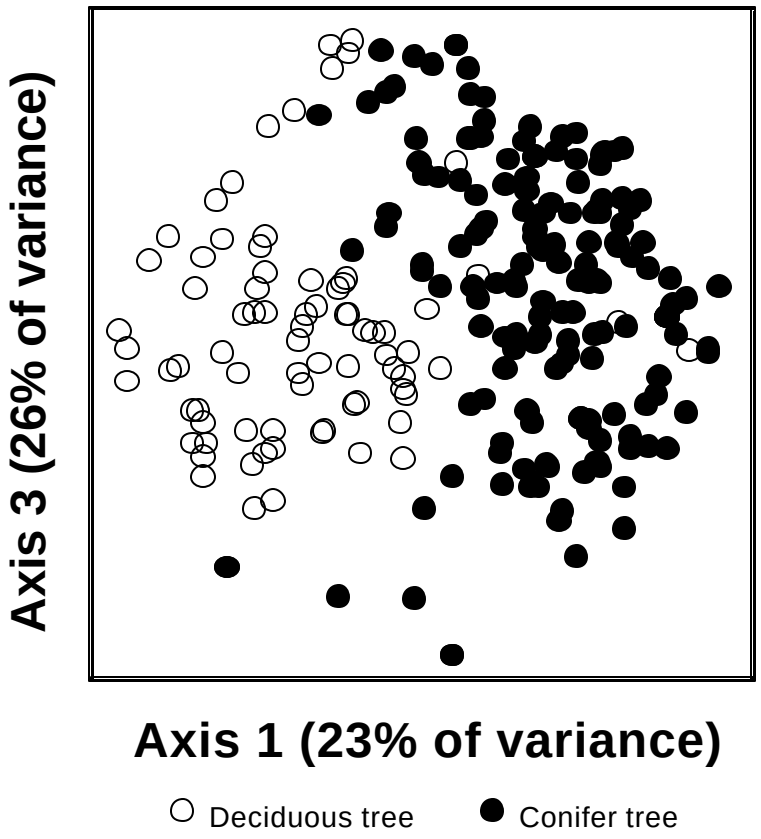


Fig. 6. Non-metric Multidimensional Scaling (NMS) plot of the deciduous (n=80) and conifer (n=78) shrub-dwelling arthropod communities in June, August, and October during 2000 and June and August during 2001. Open circle indicates deciduous foliage type (vine maple) and closed circle indicates coniferous foliage type (Douglas-fir and Western Hemlock trees). (Minimized final stress; 20%, Final instability; 0.0003)

Table 8. Monte Carlo Test of Significance level of Indicator values (IV) for indicator species with p-value across the deciduous and coniferous foliage types and the degree of thinning (Light; CN and LT, Heavy; L./G and HT) in western Oregon for across sampling years

	Foliage Type		Thinning Degree	
Taxa	Deciduous	Conifer	Light	Heavy
Cantharidae	13.4*	-	-	-
Chironomidae	5.2*	-	-	-
Mycetophilidae	16.1**	-	11.6*	-
Periphyllus	78.7**	-	-	-
Cicadellidae	14.8**	-	-	-
Cinara	13.5**	-	16.1**	-
Yellow Thrips	29.8**	-	-	-
Phytoseiid mites	56.0**	-	-	-
Ichneumonidae	-	-	7.8*	-
Coccinelidae	-	-	-	9.5*
Berytidae	-	6.4*	-	6.7*
Straminaspis	-	10.3**	-	-
Diprionidae	-	8.3*	-	-
Psocoptera	-	38.8**	-	-
Spiders	-	54.3**	45.3*	-
Camisia	-	36.1**	-	-
Jugatala	-	27.0*	-	28.4*

** **= P < 0.01;** * **= P < 0.05;** - = **Not Significant**

3. 2. Ground-dwelling arthropods

3. 2. 1. Thinning treatment and seasonal effects on arthropod species abundance

The mean abundance of captured arthropods was significantly directly correlated to thinning intensity during the wet season, but there was no consistent treatment effect during the dry season (Fig. 7). The mean abundance of the warm wet season was higher than for that of the hot dry summer for all treatments.

Season (S) and thinning treatment (T) each proved statistically significant for all taxa ($p<0.0001$) and Carabidae ($p<0.0001$), but their interaction effect was not statistically significant for all taxa ($p=0.128$), while it was significant for the Carabidae ($p=0.0021$) (Table 9).

To quantify how much the thinning treatments differ, a pair-wise comparison was conducted (Table 10). It was found that there was a significant difference between L/G and HT treatments relative to both CN and LT, respectively. However, there is no evidence of a difference in abundance in LT treatment relative to CN nor for any significant difference between L/G and HT. I also examined separately the five dominant taxa: Formicidae (ants), Araneae (spiders), Carabidae (ground-beetles), Gryllacrididae (camel-crickets), and Polydesmida (millepedes) (Fig. 8). The first and second groups, Formicidae and Araneae, (Fig. 8B and 8C) show higher mean abundance during the wet season. The mean abundance for both taxa generally increased with the intensity of thinning during both seasons but not significantly for ants. The third most abundant group, Carabidae, shows a higher mean abundance during the wet season, however its mean abundance decreased with the intensity of thinning (Fig. 8D). Gryllacrididae shows higher abundance during the dry season and Polydesmida

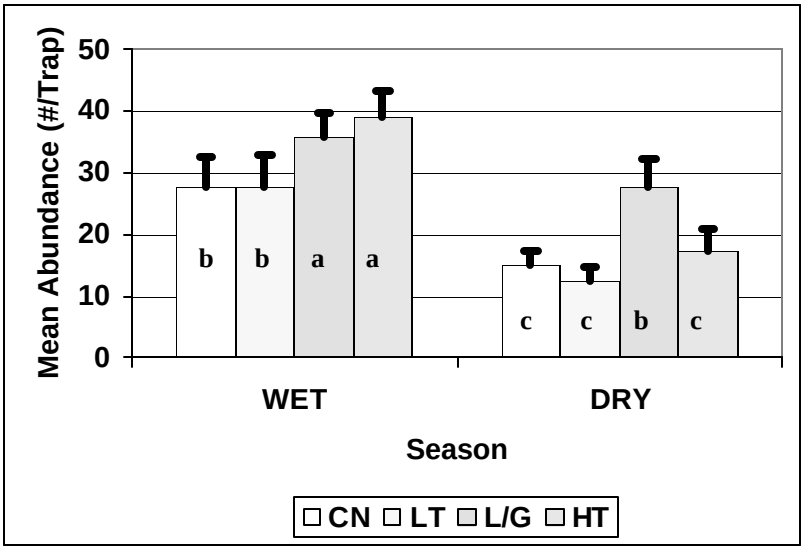


Fig. 7. Mean abundance and standard error of ground dwelling arthropods at each treatment during wet and dry seasons in 2000 and in 2001. “a”, “b”, and “c” indicate statistically different values.

Table 9. ANOVA table for season and thinning treatments. The number in parenthesis indicates degrees of freedom (DF)

Taxa \ Effect	Season (S) (1)	Treatment (T) (3)	S X T (3)
All taxa	<0.0001***	<0.0001***	0.128
Carabidae	<0.0001***	0.0001***	0.0021**

*** = **P < 0.001;** ** **= P < 0.01**

Table 10. Pair-wise comparison of thinning treatments for ground dwelling arthropods in 2000 and 2001. (the numbers are p-values)

	CN	LT	L/G	HT
CN		0.5819	<.0001***	0.0062**
LT			<.0001***	0.0011**
L/G				0.1766
HT				

*** = **P < 0.001**; ** = **P < 0.01**

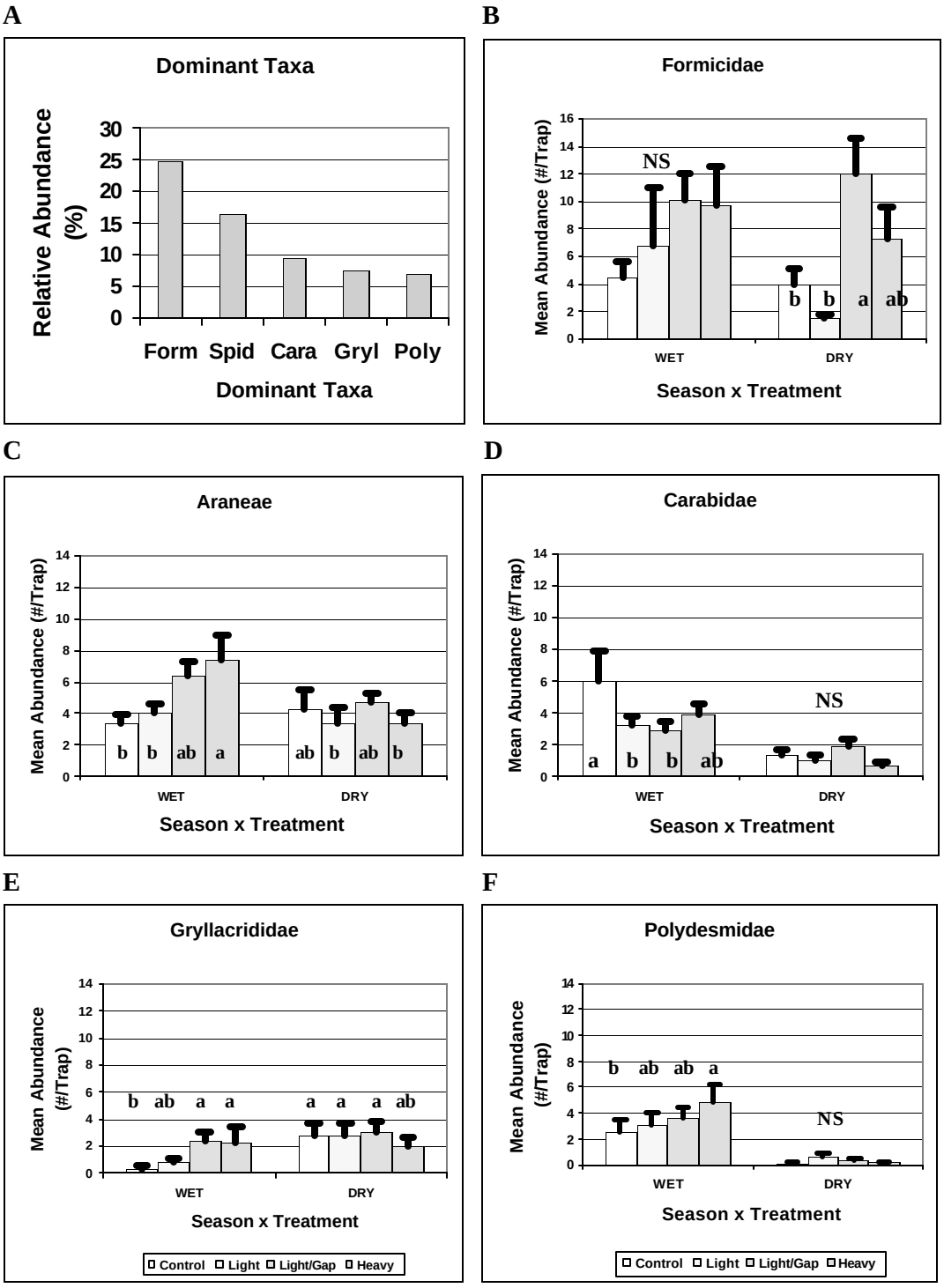


Fig. 8. Relative abundance of dominant taxa. The five dominant taxa comprise over 67% of all taxa. Mean abundance with standard error bars of each taxa , shown separately both seasons, w arm wet spring and hot dry summer, with four thinning treatments in 2000 and 2001. “a” and “b” indicate statistically significant differences and “ab” indicates no statistical difference between a and b. NS indicates no statistically significant difference.

show a higher mean abundance during the wet season (Fig. 8D - 8F); both the Gryllacrididae and Polydesmida showed a weak positive correlation with thinning intensity during the wet season.

3. 2. 2. Species diversity and richness

Mean species richness of arthropods increased with the intensity of thinning (CN = LT < L/G = HT) (Table 11). Mean beta diversity decreased with thinning intensity (CN, LT < L/G, HT). Values for Shannon and Simpson diversity were all too similar to reveal any differences correlated with thinning.

3. 2. 3. Community response of arthropods

The patterns generated by NMS in overall arthropod community composition revealed that both season (Wet (W) and Dry (D)) and thinning treatment (L (CN and LT) and H (L/G and HT)) were highly significant (Fig. 9). The NMS result revealed 4 separate clouds of points, with moisture dominating thinning along Axis 2, which explains 40% of the variance.

In this NMS ordination, Axis 1 and Axis 2 explained 19% and 40% of the variance between sampling points ($p=0.02$ from the Monte Carlo test based on 50 randomizations). Both Axis 1 and Axis 2 were weakly positively correlated to litter moisture and negatively correlated to stand age (Table 12). It is likely that litter moisture was sensitive to both season and thinning intensity. The dominant taxa, Formicidae were negatively associated with Axis 1 ($r = -0.572$), Araneae were negatively associated with Axis 2 ($r = -0.418$), Carabidae were negatively associated with Axis 2 ($r = -0.722$), Gryllacrididae were positively associated with

Table 11. Abundance (S) and species richness (α) and standard error (SE), Shannon, and Simpson diversity of ground-dwelling arthropods for thinning treatments in 2000 and 2001 (total species, γ= 73). Mean arthropod abundance from each pitfall trap cup (no./cup) was used. (CN; Control, LT; Light Thin, L/G; Light with Gaps, HT; Heavy Thin).). "a", "b", and "c" indicate statistically significant differences. NS indicates no statistically significant difference

Season	Treatment	$S \pm SE$	$(\alpha \pm SE)^{NS}$	H'	D'
June	CN	$(27.83 \pm 4.92)^{b}$	20.13 ± 1.72	2.17	0.79
	LT	$(27.78 \pm 5.13)^{b}$	20.50 ± 1.85	2.23	0.81
	L/G	$(35.78 \pm 3.92)^{a}$	21.63 ± 1.74	2.17	0.81
	HT	$(38.98 \pm 4.37)^{a}$	23.13 ± 1.36	2.19	0.82
August	CN	$(15.20 \pm 2.15)^{c}$	13.38 ± 1.89	1.82	0.75
	LT	$(14.68 \pm 1.29)^{c}$	14.38 ± 1.44	2.03	0.80
	L/G	$(27.78 \pm 4.56)^{b}$	16.63 ± 1.66	1.92	0.76
	HT	$(17.43 \pm 3.37)^{c}$	15.25 ± 1.31	1.91	0.76

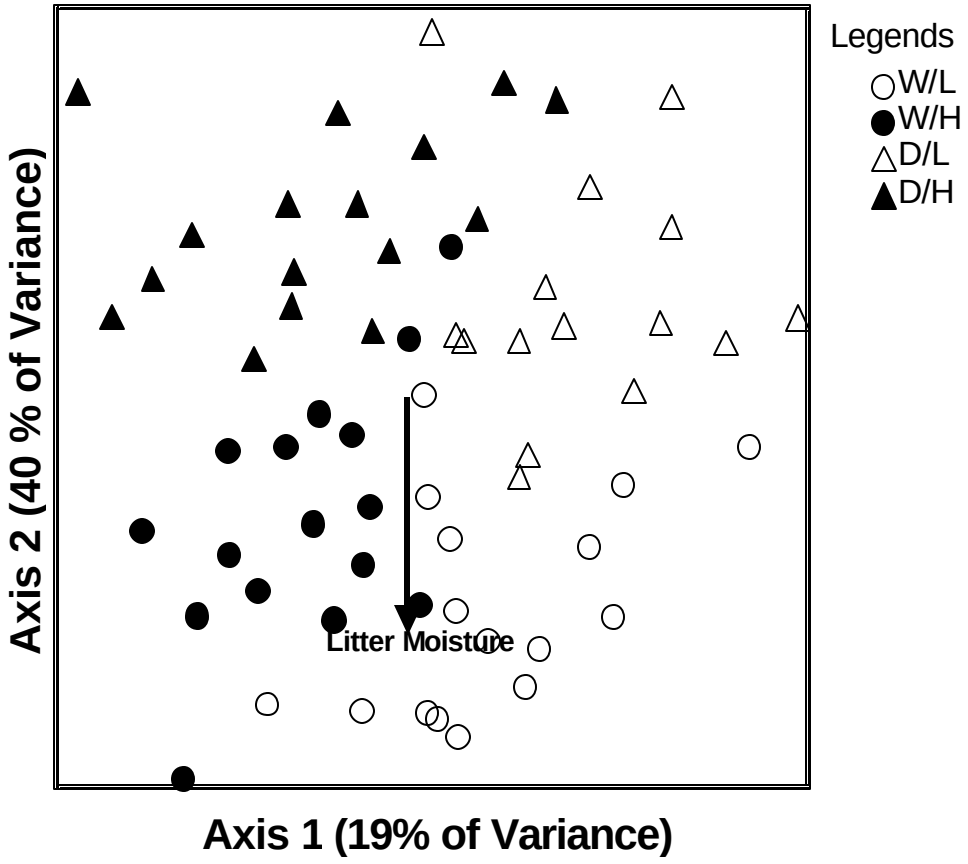


Fig. 9. NMS ordinations of pitfall arthropod samples for season (W=wet, D=dry) and thinning treatments (L= CN and LT; H= L/G and HT) in 2000 and 2001. (Minimized final stress; 26%, Final instability; 0.00002)

Table 12. Correlations between each of the variables used in the multidimensional scaling (NMS) analysis

Variables	Axis 1		Axis 2	
	r	r-sq	r	r-sq
Stand age (years)	-0.380	0.144	-0.317	0.100
Litter Moisture (%)	0.449	0.202	0.319	0.102

Axis 2 (r =0.516), and Polydesmida were negatively associated with Axis 2 (r = -0.745).

3. 2. 4. Indicator Species Analysis

Dufrene and Lengendre's (1997) indicator species analysis examined the responses of individual species to both thinning treatments and seasonal abundance (Table 13). As a general rule, treatment effects only occurred when seasonal effects were absent (10 out of 15 examples). Heavier thinning favored Lampyridae, Scarabaeidae, Lygaeidae*, Nabidae*, Cicadellidae, Thomisidae, Acrididae*, Scolopendromorpha, Thomisidae and miscellaneous spiders (the asterisk mark (*) is an indicator species of early succession – Moldenke, pers. comm.) Less intense thinnings favored mollusks, Curculionidae, Diprionidae, Aphidae and Julidae.

Nineteen arthropod groups were chosen as indicators for the June wet season (all have high IV, all p-values < 0.05). Four families were indicator species for the August dry season: Nabidae, Cicadellidae, Hodotermitidae, and Gryllacrididae (Table 13). The June wet season was characterized by 3.5 times as many indicator taxa as the August dry season.

One of the dominant families, Carabidae, was analyzed by thinning intensity and season but there were no carabid indicator species for thinning intensity. There were 6 indicator species, *Cychrus tuberculatus*, *Omus dejeani*, *Promecognathus crassus*, *Pterostichus lama*, *Scaphinotus angulatus*, and *S. marginatus*, for the wet season (Table 13).

Table 13. Monte Carlo Test of Significance level of Indicator values for All Taxa and Carabidae across the degree of thinning (Light; CN and LT, Heavy; L/G and HT) and season (W=wet and D=dry) in 2000 and 2001 in western Oregon young stands

	Thinning Degree		Season	
Taxa	Light	Heavy	W	D
All Taxa				
Carabidae	-	-	75.5**	-
Clambidae	-	-	40.6**	-
Curculionidae	54.3*	-	63.9**	-
Elateridae	-	-	25.0*	-
Lampyridae	-	18.7*	-	-
Scarabaeidae	-	21.1*	-	-
Staphylinidae	-	-	60.3**	-
Lygaeidae	-	56.9**	-	–
Nabidae	-	28.1**	-	23.8**
Aphididae	37.5**	-	-	-
Cicadellidae	-	57.7**	-	48.0**
Diprionidae	35.6*	-	36.5*	-
Formicidae	-	69.5**	-	-
Hodotermitidae	-	-	-	18.7*
Acrididae	-	37.5**	-	-
Gryllacrididae	-	-	-	65.0*
Lepismatidae	-	-	27.8*	-
Chordeumatida	-	-	60.7**	-
Julidae	16.1*	-	-	-
Polydesmida	-	-	89.4**	-
Sprirobolida	-	-	44.4**	-
Scolopendromorpha	-	35.3**	–	-
Geophilomorpha	-	-	18.7*	-
Lithobiomorpha	-	-	67.4**	-
Thomisidae	-	34.3*	41.8**	-
Other spiders	-	58.3*	-	-
Snails	46.6**	-	-	-
Carabidae				
Cychrus tuberculatus	-	-	41.8**	-
Omus dejeani	-	-	65.7**	-
Promecognathus crassus	-	-	40.6**	-
Pterostichus lama	-	-	55.8**	-
Scaphinotus angulatus	-	-	20.8*	-
S. marginatus	-	-	21.9*	-

*** **= P < 0.001;** ** **= P < 0.01;** * **= P < 0.05;** - = **Not Significant**

3.3. Litter-dwelling arthropods

3.3.1. Abundance / Density

Mean density (#/m^2 of sampling area) of litter-dwelling arthropods showed thinning treatments effects during both the mid- and late-seasons (Fig. 10). Mid-growing season had the highest mean abundance and late-growing season had the lowest mean abundance at each thinning treatment.

The relative seasonal abundance of litter-dwelling arthropods among the functional groups is shown in Fig. 11. Predaceous arthropods (PR) were the dominant group and were relatively the most abundant at the mid-growing season (72%) and the lowest at the early-growing season (51%). Detritivores/fungivores (DT) were the second most abundant group and decreased in abundance according to the growing season. The main predators were ants, spiders, and geophilomorph centipedes. The main detritivores were Diplopoda. It should be stressed that this sampling technique did not enumerate Collembola and Acari, which are largely fungivorous, and represent the prey base for the predators that were collected.

Generally, abundance of litter arthropods decreased relative to thinning intensity (Fig. 10 and 12). The number of ants in a single sample of HT (Mill, August 2001) seriously affects the overall trend of the treatment comparison (Fig. 12); because of the clumped distribution of ant colonies, single samples with disproportionate ant abundances are usually excluded from these types of analyses. Though not significant, a parallel decrease in detritivores with thinning severity is suggestive.

As a dependent variable, litter-dwelling arthropod abundance was used with moisture content for ANOVA analysis. Moisture was statistically significant

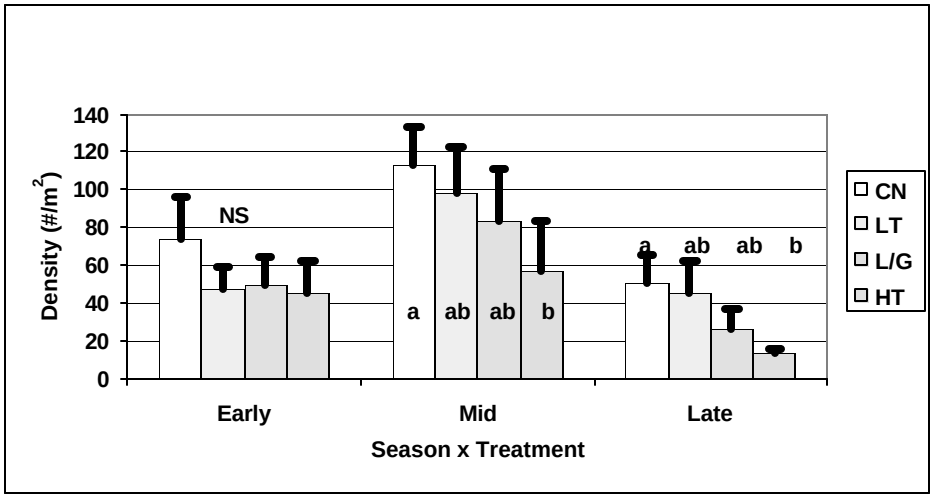
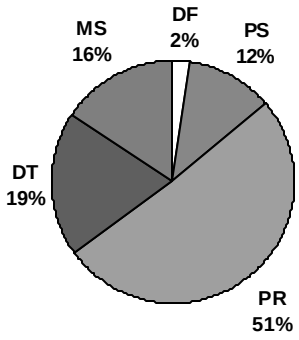
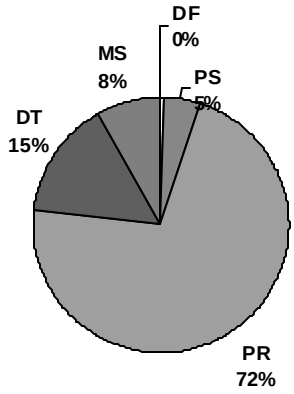


Fig. 10. Mean density of litter-dwelling arthropods between the different growing seasons and thinning treatments. CN, Control; LT, Light Thin; L/G, Light with Gap; HT, Heavy Thin. Early, 6/19/01; Mid, 8/15/01; Late, 10/15/00. "a", "b" and "c" indicate statistically significant differences and "ab" and "bc" indicate no statistical differences between a and b and b and c. NS indicates no statistically significant difference.

A. Early-growing season



B. Mid-growing season



C. Late-growing season

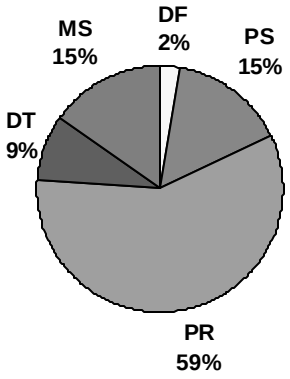


Fig. 11. Relative seasonal abundance of litter-dwelling arthropods collected at young stand study sites by functional groups. DF=defoliators, PS=plant suckers, PR=predators, DT=detritivores, MS=miscellaneous. **A**. Early-growing season; 6/19/01, **B**. Mid-growing season; 8/15/01, **C**. Late-growing season; 10/15/00.

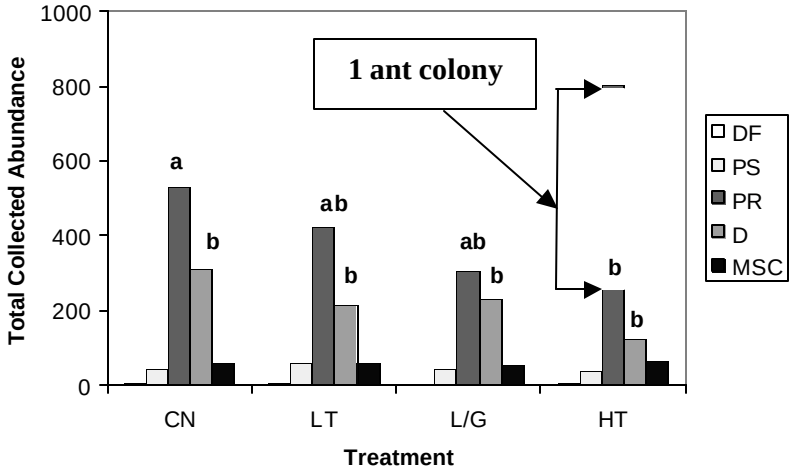


Fig. 12. Total abundance (excluding Collembola and mites) of functional groups of litter arthropods at each thinning treatment. DF=defoliators, PS=plant suckers, PR=predators, DT=detritivores, MS=miscellaneous. “a” and “b” indicate statistically significant differences and “ab” indicates no statistical difference between “a” and “b”.

(p=0.036) but the thinning treatment only approached significance at p=0.091 (Table 14). The positive relationship between log arthropod abundance and log moisture was revealed in the scatter plot in Fig. 13.

A pair-wise comparison of arthropod abundance by treatment was examined (Table 15). We found that there was a significant difference between HT treatment relative to CN and LT after accounting for site and season (two sided p-value=0.02 (for CN) and <0.04 (for LT) from regression analysis); however, there was no evidence of a difference in abundance between LT (two-sided p-value = 0.6 from regression analysis) relative to CN, after accounting for site and season.

3. 3. 2. Species diversity and richness

Litter moisture content decreased with increasing thinning intensity (Table 16). Moisture content of CN (43.7%) was the highest and that of HT (31.7%) was the lowest. Species diversity was directly correlated with pooled litter moisture content (Table 16).

Species richness (α), Shannon-Weiner diversity (H'), and Simpson diversity (D') decreased with the intensity of thinning, but beta diversity (β) increased with thinning intensity. Moisture content was examined during the three growing seasons (spring: 36.6%; summer: 13.2%; fall: 62.5%), but the seasonal moisture content was not directly correlated with the species diversity. Seasonal effects on species diversity showed the highest diversity at the early-growing season, and the lowest diversity at mid-growing season, however, within any one season, lower thinning intensity shows a higher species diversity at all times (Table 16).

3. 3. 3. Community composition

Analysis of litter arthropod communities using 48 litter samples (four sites X four thinning treatments X three seasons), using nonmetric multidimensional

Table 14. ANOVA table to determine treatment, season, and moisture effects and their interactions

Source	DF	F Value	Pr > F
Treatment (T)	3	2.24	0.0906
Season (S)	2	1.45	0.2422
Moisture (M)	1	4.54	0.0364

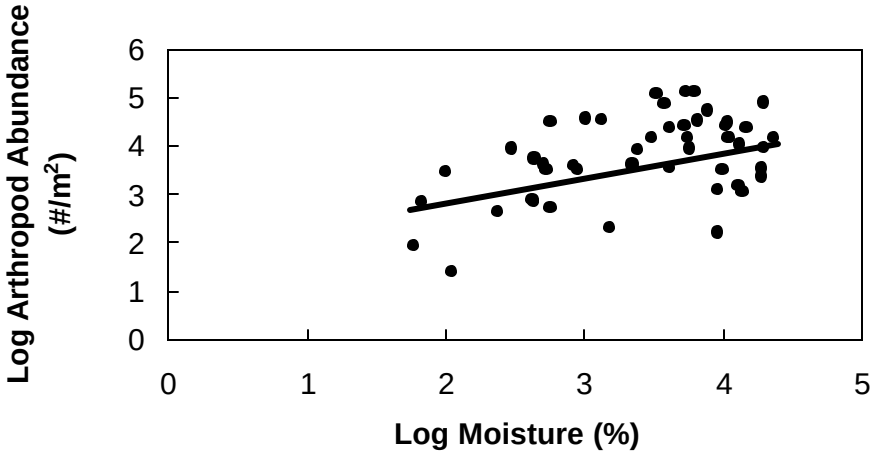


Fig. 13. Scatter plot for moisture and abundance as a log scale (y = 0.419x + 2.419, r = 0.485).

Table 15. Pair-wise comparison (Tukey) of thinning treatments in litter arthropod samples

	CN	LT	L / G	HT
CN		0.5696	0.1310	0.0160*
LT			0.3063	0.0381*
L / G				0.2598
HT				

* **= P < 0.05**

Table 16. Average species richness per thinning treatment and the standard error, beta ($\beta = \gamma / \alpha$), gamma diversity (total species richness, $\gamma = 61$), Shannon diversity and Simpson diversity of litter arthropods and litter moisture (%) at Willamette National Forest in 2000 and 2001. Growing season (I; Early growing season (6/19/01), II; Mid growing season (8/15/01), III; Late growing season (10/15/00)). "a" and "b" indicate statistically significant differences and "ab" indicates no statistical difference between "a" and "b". NS indicates no statistically significant difference from Tukey multiple comparison

Growing season		Thinning Treatments (Mean litter moisture)			
(Mean litter moisture)	Diversity	CN (43.7%)	LT (38.6%)	L/G (35.8%)	HT (31.7%)
I (36.6%)	α	$(11.1 \pm 0.6)^{a}$	$(9.8 \pm 0.6)^{ab}$	$(10.9 \pm 1.1)^{b}$	$(7.1 \pm 1.3)^{b}$
	β	$(5.9)^{b}$	$(6.6)^{b}$	$(6.0)^{b}$	$(9.2)^{a}$
	$(H)^{NS}$	1.9	1.8	1.8	1.5
	$(D')^{NS}$	0.8	0.8	0.7	0.6
II (13.2%)	α	$(8.1 \pm 0.9)^{a}$	$(6.9 \pm 1.2)^{a}$	$(3.4 \pm 0.8)^{b}$	$(4.0 \pm 0.9)^{b}$
	β	$(8.0)^{b}$	$(9.4)^{b}$	$(19.1)^{a}$	$(16.3)^{a}$
	H	$(1.7)^{a}$	$(1.4)^{a}$	$(0.8)^{b}$	$(0.8)^{b}$
	D'	$(0.8)^{a}$	$(0.6)^{ab}$	$(0.4)^{b}$	$(0.4)^{b}$
III (62.5%)	$(\alpha)^{NS}$	8.5 ± 1.2	6.4 ± 0.9	5.8 ± 0.9	6.0 ± 1.1
	β	$(7.7)^{b}$	$(10.2)^{a}$	$(11.2)^{a}$	$(10.8)^{a}$
	$(H)^{NS}$	1.5	1.5	1.2	1.3
	$(D')^{NS}$	0.7	0.7	0.6	0.6

scaling (NMS) with 11 variables, showed that arthropod community structure responds primarily through litter moisture content (Fig. 14). Moisture correlated to Axis 1 at 0.777 and to Axis 2 at 0.479. Other variables had exceedingly weak correlations (Table 17). Axis 1 explains 48 % of variance and Axis 2 explains 22 % of variance. In total, 70% of variance was explained on the NMS plot with 190^{o} rotation. The plot shows the distinct point clouds among growing seasons (early, mid and late) (Fig. 14); surprisingly the fall season is the most distinctive. Final stress was 22.99 and real data were 20 runs; the randomized data of the Monte Carlo test were 50 runs (p-value = 0.196).

3. 3. 4. Indicator Species Analysis

Results of the Monte Carlo test of significance for indicator values (IV) were summarized with the distinct growing seasons in Table 18. Table 18 shows only significant taxa with p-value less than 0.05.

Early-growing season has 11 statistically significant taxa; among those 11 taxa, the mid-growing season had only one taxon, Thomisidae, and the late-growing season had 2 taxa, Chilopoda and Lepismatidae. For the early growing season, I found many indicator taxa. However, there were no indicator species for the thinning treatments.

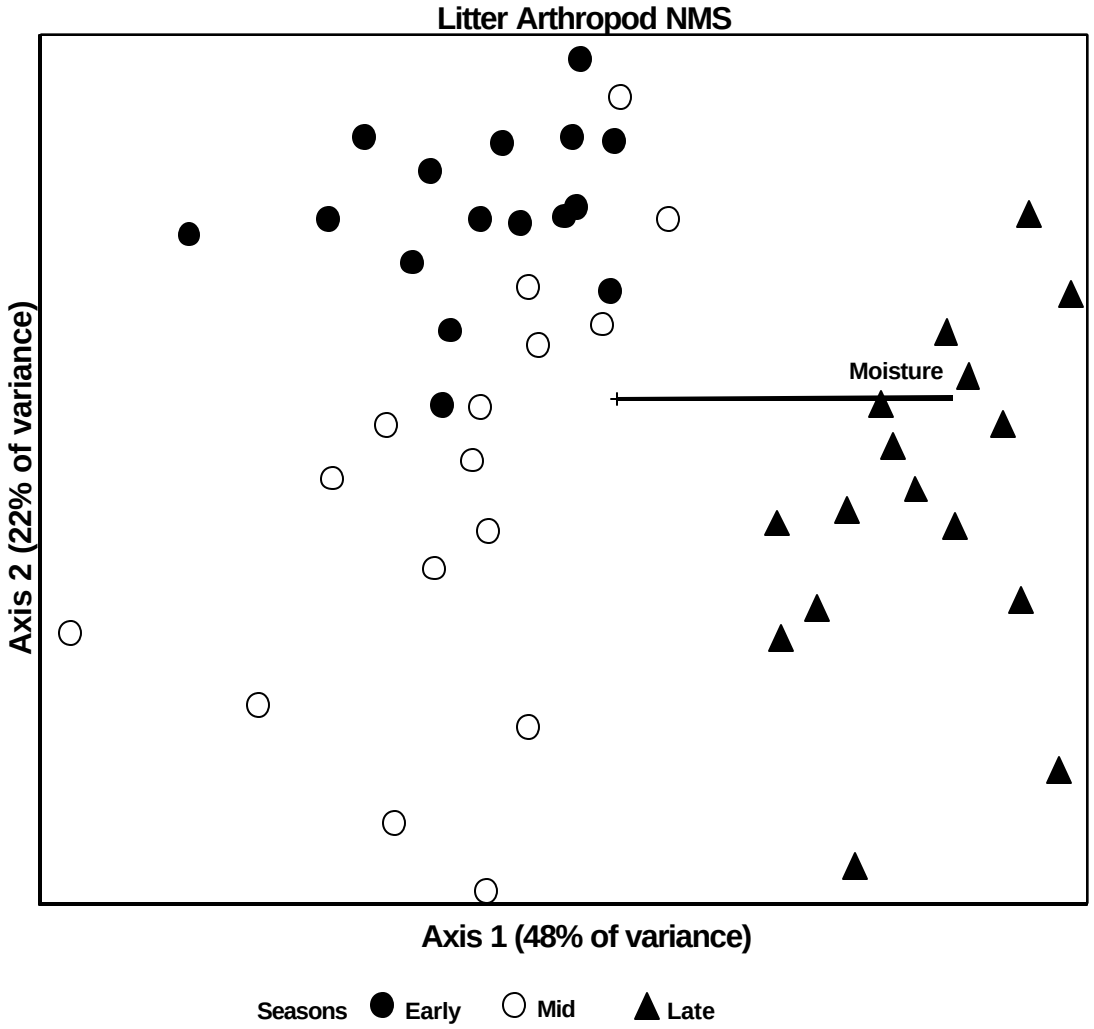


Fig. 14. Nonmetric Multidimensional Scaling (NMS) plot of the litter arthropods according to the growing seasons (early, mid, and late) in 48 litter samples from the thinning treatments. Growing seasons represented the sampling times during 2000 and 2001. (Minimized final stress; 19%, Final instability; 0.00001)

Table 17. Pearson (r) and Kendall (tau) Correlations between variables used in the multidimensional scaling (NMS) analysis describing litter moisture and other environmental factors

Variables	Axis 1		Axis 2	
	r	tau	r	tau
Moisture(%)	0.772	0.596	0.479	0.241
Elevation (m)	-0.141	0.020	-0.124	-0.127
Slope (%)	0.094	0.009	0.102	0.236
Area (acre)	0.095	0.009	0.077	0.186
Stand (age)	0.128	0.016	0.147	0.128

Table 18. Monte Carlo test of significance level of indicator values (IV) for all taxa, across growing seasons in 2000 and 2001

Growing Season	TAXA	IV
Early	Geophilomorpha	85.5**
	Pselaphidae	51.3**
	Dipluran	50.9**
	Lithobiomorpha	48.8**
	Other Diplopoda	47.7*
	Scolopendromorpha	42.2**
	Chalcidoidea	34.2*
	Dipteran larva	34.1*
	Carabidae	33.7*
	Other Homoptera	28.3*
	Polydesmida	25.0*
Mid	Thomisidae	33.3**
Late	Chilopoda	82.8**
	Lepismatidae	25.0*

* **P < 0.05** ** **P < 0.01**

Chapter 4

DISCUSSION

My study shows the effects of different silvicultural thinning intensities on the abundance of the three groups of arthropods (shrub-dwelling, ground-dwelling, and litter-dwelling). The responses of the arthropods are likely to be the result of differences in microclimate, plant productivity or diversity, and habitat structural diversity created by forestry thinning management (Greenberg and McGrane 1996).

4.1. Species richness (a diversity) and thinning effect

For the shrub-dwelling arthropods, coniferous foliage type supports higher average species richness than deciduous does, as a whole. This is contrary to the results from Hammond and Miller (1998) who only examined defoliators. In my study, all functional groups are assessed. These different arthropod communities may be due to a difference in plant physiology, but more likely reflect a difference in the permanence of the habitat type.

Although there is no apparent trend in diversity values on the deciduous foliage type with thinning intensity, coniferous foliage type shows higher average species richness at the heavier thinning intensity (L/G and HT) than at the lighter thinning intensity (CN and LT). It is known that microclimatic effects of light and air temperature under moderate thinning are very minimal at 1 m height in Pacific Northwest conifer forests (Chan *et al.* 2002). While average species richness of

ground-dwelling arthropods increases at heavier thinning intensities than at the lighter thinning intensities, species richness of litter-dwelling arthropods decreases with thinning intensity. The increased disturbance associated with heavier thinning seems to open up more possible niches for ground-dwelling arthropods and increases the heterogeneity of their habitats. The litter-dwelling arthropods, on the other hand, are more closely dependent on the moisture condition of litter. Litter moisture content decreases with thinning intensity and species richness appears to be directly related to litter moisture content. Chen *et al.* (1993) reported that various forest practices altered the surface thermal properties near the ground due to the removal of forest canopy and ground materials. They found more intense forest thinning practices received more direct solar radiation and precipitation, lost more outgoing long-wave radiation, and showed higher rates of evapotranspiration. There was typically a sunnier, warmer, windier, and drier environment outside the unthinned forest than inside the forest during summer days (Geiger 1965, Wales 1967, Lee 1978, Ghuman and Lal 1987) and a cooler and wetter environment at night (Chen 1991).

Litter-dwelling mesoarthropods extracted with a Berlese would be expected to decline with decreasing soil moisture since they are composed primarily of predators whose food base of fungivorous microarthropods has been documented to decline with decreasing soil moisture (Moldenke 1994), as does total soil metabolic activity (Griffiths 1999). However, the relationships among soil moisture, litter moisture, and richness of total arthropods have been little studied (Coleman *et al.* 1996). Deeper soil moisture was not measured in this study, so that the relationship between soil moisture and litter moisture or deeper soil moisture

and species richness cannot be directly addressed by this study. This relationship should be worthy of future investigation.

4.2. Species abundance and thinning effect

Arthropod abundance is apparently not coupled with species richness or diversity, at least in this local study. Although abundance of arthropods is significantly greater on the deciduous foliage than the coniferous foliage, the species richness of coniferous foliage is higher than on the deciduous foliage. Considering this contrasting relationship between abundance and species richness, it is perhaps significant that predators are proportionately more abundant on the coniferous foliage type (Doolittle 2001).

The abundance of shrub-dwelling arthropods does not show a statistically significant difference among thinning treatments. In terms of species richness, coniferous foliage has higher values at the heavier thinning intensity than at the lighter thinning intensity.

Heavier thinning is associated with a higher abundance of ground-dwelling arthropods than lighter thinning, regardless of season. This trend parallels species richness and it might be simply explained by an increase in resources or habitat heterogeneity. The abundance of two dominant taxa, Formicidae and Araneae, are both higher in the heavier thinning treatment. The problem is that it is not easy to quantify the total number of potential habitats or niches under comparative conditions. Ecologists usually assume that higher species richness requires a greater number of microhabitats; proving the causality is daunting when arthropod diversity is analyzed. It would be possible, however, to determine if total food

resources are greater for either the litter-dwelling predators (*i.e.*, total Collembola and Oribatida) or the herbivorous shrub dwellers (total plant biomass).

For the litter-dwelling arthropods, both abundance and richness decrease with the thinning intensity. Total arthropod abundance and abundance of each of the main taxa showed positive relationships with litter moisture for each thinning treatment. In these results, the decrease of spider abundance at the lighter thinning with more litter moisture, cannot be directly compared with Huhta *et al*'s study (1967), since the relationship of deeper soil moisture and litter moisture was not assessed in this study.

4.3. Seasonal effects on thinning

As was expected, seasonal differences in species abundance are very large for the arthropods from each of the 3 forest strata. Seasonal abundance for shrub-dwelling arthropods is not different on coniferous foliage, which is consistent with the evergreen multi-year nature of the coniferous foliage. However, the fauna on the deciduous foliage shows distinct seasonal abundance patterns.

The seasonal abundance of deciduous foliage-dwellers steadily declines with thinning intensity. However, the fall season (October), did not show the same trend for deciduous foliage. The deciduous foliage of that season reveals obvious withering and discoloration, thus arthropod abundance cannot be meaningfully compared across thinning treatments

4.3.1. Ground-dwellers:

The abundance of ground-dwelling arthropods reveals strong differences between two seasons, warm wet season and hot dry season. Arthropod abundance

of the wet season is higher than that of the dry season. However, although a seasonal trend in total abundance of arthropods captured was apparent, it is difficult to explain the difference in terms of the distribution of individual taxa among treatments (Greenberg and Thomas, 1995; Greenberg and McGrane 1996). In this study, the dominant predaceous taxa (*eg*., Formicidae and Araneae) have higher abundances in wet season than in dry season and they drive the entire faunal response.

The abundance of ground-dwelling arthropods is higher during both seasons in the heavier thinning conditions. Thinning appears to affect ground-dwelling arthropods almost as strongly as season. That is, the ground-dwelling fauna seem to be affected more by altered habitat heterogeneity than by microclimate for any season.

4.3.2. Litter-dwellers:

Litter moisture changes both with season and thinning intensity. Changes in litter moisture content do produce significant differences in the epigeic macroarthropod community. However, seasonal changes in litter/humus moisture far exceed thinning-induced changes on the richness and abundance of litter-dwelling arthropods.

Species richness of litter-dwelling arthropods is lowest at both L/G and HT intensities of mid-growing season. However, the highest abundance occurs at CN condition of early-growing season. Early-growing season has the highest species richness but mid-growing season has the highest abundance and lowest species richness. During each growing season, the control undisturbed forest has the highest abundance and HT has the lowest abundance. Presumably this result is

correlated with increased radiation from the sun and active evaporation. Large canopy opening areas reveal significant differences of maximum and minimum temperature and seasonal irradiance correlated with the size of canopy opening. Carlson and Groot (1997) reported that the radiation regime was affected by season and sky conditions. In open areas, the air temperature was higher during the day and lower at night than in the forest interior. Soil temperatures of depths of 5 cm and 20 cm rose with the larger openings. In general, the largest canopy openings experienced greater heat sums at the two depths (Carlson and Groot 1997).

Open- and closed-canopy sites differed with respect to microclimate factors (Matlack 1993). The open-canopy sites had more variable environmental factors that likely affected the abundance of arthropods (Thiele 1977). Peltonen *et al.* (1997) and Koivula (2002) found that canopy gaps of small diameter did not affect insect diversity, but larger gaps did. Chen *et al.* (1993) also reported that mean daily air temperature, mean daily soil temperature, and mean daily soil temperature differences were higher in the canopy opening area than in the forest interior. Mean daily average relative humidity increased from the border of the open-canopy area into the forest. Mean soil moisture was highest at the edge and lowest within the open canopy area in the Pacific Northwest (Chen *et al.* 1993). In this study, both the HT and LG treatments share similarities with the open site treatment and should be characterized by significantly different environmental values.

4.4. Taxonomic composition

The deciduous and coniferous foliage types differ greatly in the proportion of arthropods belonging to different functional groups. The deciduous foliage has

much higher proportion of plant-suckers and leaf-chewers than does the coniferous foliage because of the high abundance of Homoptera (especially Aphididae) and Lepidoptera. However, the coniferous foliage has relatively higher numbers of predators and detritivores than the deciduous foliage. Arthropod on the coniferous foliage consists of only 13% plant suckers, compared to 45% predators, and 37% detritivores. This proportion is similar to Showalter and Ganio's (1998) results on other coniferous trees. My percentage of plant suckers was lower than that documented Winchester's (1997) for Sitka spruce in western Canada. Stork (1987) documented similar guild frequencies in a tropical forest: phytophagous (40%), predator (40%) and parasitoid (10%). Moran and Southwood (1982) reported a higher proportion of plant suckers for temperate forests than occurred in this study, but the results for predators were similar. Predators and parasitoids are higher than levels reported by Moran and Southwood (1982).

In these studies, only a few shrub-dwelling taxa showed significant thinning treatment effects, but many taxa of plant suckers (aphids and thrips), predators (mites) and detritivores (Diptera and *Camisia* mites) showed significant differences between the foliage types. It is quite apparent (i.e., NMS results) that the foliage-dwelling arthropod fauna is much more closely tied to differences in foliage-type than to differences in thinning intensity. Since there has not yet been a deciduous foliage release subsequent to thinning in this particular experiment, it is logical to assume that the total foliage-dwelling fauna has remained nearly the same on a site-scale. However, in the normal expected successional sequence, it seems very likely that a great majority of any foliage-related responses would be primarily due to the altered percentage composition of deciduous foliage present.

The Indicator Species Analysis (ISA) of shrub-dwelling arthropods documents two distinct foliage-type faunas, deciduous and coniferous. For the former, Cantharidae, *Periphyllus* aphids, yellow thrips, and phytoseiid mites are the main indicator taxa; herbivores have high indicator values, and predators and detritivores have relatively lower indicator values. For the latter, Psocoptera, spiders, *Camisia,* and *Jugatala* are the indicator taxa; herbivores have low indicator values, and predators and detritivores have relatively high indicator values.

NMS for ground-dwelling arthropods documents a thinning response that is much less than that for season. Even though the thinning treatment relatively weak, many of the species which invade the HT are unique and are normally found in an open-canopy situation (and never in the denser forests). Thus, far more species were indicators of the heavy than of the light thin.

Among the Carabidae, Lindroth (1969) and Work (2000) reported edge effects for many forest-dwelling taxa. While distribution of these species may be due in part to microclimate changes resulting from tree harvest effects, they may also indirectly reflect prey availability across the gradient (Parsons *et al.* 1991). Parsons *et al.* also indicated the role prey availability plays in the presence of *Scaphinotus angusticollis, S. marginatus,* and *Promecognathus crassus*. In this present study, the prey of the different species of Carabidae are not well understood. However, *P. crassus* and its prey (Polydesmida) are correlated and both are tied to soil moisture

4.5. Management implications

This study was conducted in large stands that have received operational thinning. The gaps created by L/G and HT are influenced by direct sunlight and the drying effect of winds, and thus these treatments cause the most severe and rapid effects on the forest-arthropod fauna, which are most often detected by an increase of open-habitat species (Koivula 2002).

The Northwest Forest Plan envisions that the total harvested forest area in the landscape will probably stay constant, with a constant volume of trees logged. Widely applied small-scale logging within a forest mosaic increases edge boundaries in the landscape. The application of small-scale logging results in much less intact forest core. Many ecologists emphasize the importance of the edges around gaps or forest boundaries because these areas have changing microclimate environments (Geiger 1965, Wales 1967, Ranney 1977, Chen *et al.* 1993). The increased amount of edges has consequences on the spatial distribution of species (Koivula 2002). The impact of both gaps and edges on arthropods deserves further study.

In my study, shrub-dwelling, ground-dwelling, and litter-dwelling arthropods have all demonstrated different species compositions with forest thinning effects.

4.6. Broader generalizations with vertebrates

4.6.1. Shrub understory

Because so little is known about the distribution of arthropod diversity and biomass across the forested landscape, data collected from the control unthinned stands contributes substantially to the beginnings of a baseline. This information is

significant not only for the study of arthropod ecology, but also insofar as it estimates the abundance, temporal presentation and diversity of food items available for vertebrate predation.

I have found that the abundance of arthropods/kg of foliage is significantly greater on deciduous shrubby foliage than on understory saplings. This holds not only for totals for the entire year but for each season independently. At first glance, this is not surprising for it is probably generally assumed that coniferous foliage is less palatable due to the presence of terpenes which serve as well-documented anti-herbivory substances that protect the plant's investment in multi-year evergreen leaves. The ratio of the biomass of deciduous foliage to coniferous foliage is variable in stands of the different types of forest of the Pacific Northwest, but the value probably never exceeds 15% of the total biomass (which includes both canopy and understory) ; even so, deciduous foliage is not difficult to locate by potential arthropod herbivores, since it is the primary component of the shrub and herbaceous layer of forest structure throughout (Tappeiner *et al.* 2001, Muir *et al.* 2002, Halpern and Spies 1995)

In direct contrast to the abundance results, I have documented significantly greater arthropod species richness on coniferous foliage than on deciduous foliage, a feature which holds up under all the intensities of thinning. The explanation for this apparent discrepancy is revealed by the analysis of relative feeding guild composition. Though both types of foliage support high relative species richness of predators (30-45% of species totals), coniferous foliage supports many species of detritivores/fungivores (nearly 40% total species richness), whereas, by contrast, deciduous foliage supports larger numbers of herbivores (more than 60% of species). The long-lived leafy structures on the branch tips of conifers provide

habitats for the growth of algae and fungi (especially during the moist 8-month winter season. These microhabitats support large populations of mites and springtails during the entire year (Andre and Voegtlin 1981). Most of these microarthropods are well below the threshold size limit for direct vertebrate predation (Hagar 2003), though they are correlated with a significantly higher abundance and diversity of predaceous spiders on coniferous foliage (Halaj *et al.* 1998) which do contribute directly to the vertebrate food base. The larger density and diversity of spiders on coniferous foliage was also documented by Moldenke *et al*. (1987, and unpub. data). Most of the vertebrate predation on understory foliage, however, is upon the herbivores (review of literature in Hagar, 2003). I have shown that the number and diversity of arthropod herbivores was significantly greater on deciduous relative to coniferous foliage.

Therefore, if deciduous leaves are a significantly greater food resource for foliage-gleaning birds and mammals than are the more omnipresent conifer branches, it becomes important to monitor what happens to both deciduous foliage density and arthropod foliage-dwellers as a result of different forest thinning intensities. Many studies on forest management practices in the Northwest have focused on understory vegetation (Tappeiner *et al.* 1991, Tappeiner and Zasada 1993, Huffman *et al.* 1994, O'Dea *et al.* 1995, Halpern and Spies 1995, Thomas *et al*. 1999, Sullivan *et al.* 2001, Muir *et al.* 2002, Bailey and Tappeiner 2002). They have shown that shrub response to canopy removal is a complex and highly variable outcome depending on forest type, logging technique, degree of ground disturbance, use of herbicides or fire, etc. However, in general, shrub growth and standing crop are usually distinctly decreased for several years after canopy removal due to the direct effects of physical disturbance. Subsequently, shrub

response then exceeds the growth of seedling conifers for 1-2 decades, but ultimately becomes shaded out by the reestablishing conifer canopy. The fact that the trajectory of shrub response varies so much following canopy removal makes it very important to specify under which conditions correlative experiments on arthropod abundance are undertaken. These studies were conducted during the initial stage of recovery from thinning, while the growth response of the shrubs was depressed due to the initial physical disruption (no chemicals or fire were applied to this study design; Bohac *et al.* 1997).

All the different thinning intensities in this experiment supported significantly less arthropod intensity (#/kg foliage) on the deciduous foliage than the control did. These treatment effects were slight, much smaller in amplitude than the basic differences in abundance between coniferous and deciduous foliage. Though richness was not adversely affected by thinning on deciduous foliage, it was upon coniferous foliage (with the heavy thinning intensity producing the greatest decrease in richness). Though this particular study does not address the question, it appears from similar studies by Hagar (2003) conducted 15-years post-thinning, that the abundance and biomass of potential arthropod food for vertebrates increases as a long-term response to thinning correlated with an increase in deciduous foliage in the understory.

Therefore, these experimental results agree with those of others, in that we recommend that positive deciduous understory management be a specified aspect of forest management practices that seek to affect changes in the biodiversity of forest stands (arthropods: Hammond and Miller 1998, Jokimaki *et al.* 1998, Humphrey and Hawes 1999, Miller 2002; herpetofauna: Gomez and Anthony 1996; birds: Willson and Comet 1996, Hagar *et al.* 1996, Hagar and Starkey 2002,

Hagar 2003, Hayes *et al.* 2003; mammals: Yahner 1986, Carey 1995, Carey and Harrington 2001, Carey and Johnson 1995, Hayes and Larson 2001, Larson 2001, Sullivan *et al.* 2001; all vertebrates: Raphael 1988; Garman 2000, 2001a, 2001b).

Gomez and Anthony (1996) found the highest richness of amphibians and reptiles where the deciduous overstory and understory were most prominent in Oregon forests; Welsh and Lind (1991) found similar results for large hardwoods only. Brush and Stiles (1986) found that insect abundance was even better than plant structure at predicting bird diversity in New Jersey. However, the effect of plant structure can interact with available arthropod food biomass, such that an increase in arthropod biomass on certain resources can alter the time spent foraging on any particular plant structure (Whelan 1989). The amount of deciduous understory subsequent to a management practice such as thinning can be manipulated relatively easily and economically through the precise choice of techniques utilized during overstory removal (Klinka *et al.* 1996); likewise, deciduous understory vegetation has both a direct effect on arthropod diversity and an indirect effect on vertebrate biomass. Hence, it seems logical to maximize understory deciduous vegetation in at least some portions of the heterogeneous landscape (more so than has been the case for the past several decades; Muir *et al.* 2002).

Specific studies quantifying the response of vertebrates to the intensity of thinning are limited. Hayes *et al.* (2003) found 9 species of birds that decrease relative to thinning intensity, 8 that increase and 5 that evidence no change. Most of these changes were noticeable only 1-year post-treatment, but Pacific-slope flycatchers decreased and Warbling vireos increasedprogressively. Hagar and Starkey (2002) found 6 bird species correlated with old-growth, 2 with unthinned

forests, 3 with thinned forests and 3 that showed no difference; overall they found that bird species richness was correlated with the deciduous components of the flora.

Larson (2001) found 3 species of mammals that increased with thinning, 1 that decreased and 5 that showed no change; the one decrease was due to arboreal microhabitat removal, the 3 that increased were perhaps correlated with low shrub density and small branches on the ground surface. Hooven and Black (1976) found that shrews and chipmunks decreased in clearcuts (and presumably in gap formation as well), but that deer mice and creeping voles increased. Sullivan *et al.* (2001) observed an immediate post-thinning decrease in mammal diversity, followed by 6 years of increase. In the most thorough examinations to date of forest structure and mammal response in the Pacific Northwest, Garman (2000, 2001a) found few consistent changes in mammal richness with thinning (*i.e.*, flying squirrel decreased, deer mice increased). In Garman (2001b) flying squirrels decreased and creeping voles increased; however, in these studies no attempt was made to separate a resident breeding population from total incidental captures of mammal species. By separating resident breeding populations from non-residents, Sullivan (1979) was able to show that during successive years the same stands could serve either as dispersal sources or sinks. Arthropod biomass and physical structure are not the only things to change, of course, with thinning. Gunther *et al.* (1983) demonstrated that in forests, small mammals fed mostly on arthropods; whereas in burned clearcuts, epiphytic lichens, fungi and conifer seeds were the principal dietary items driving the shift in species abundances.

Arthropod richness and biomass may not be responding only to the scale of the thinning treatments (20-60 hectares). Both Rosso (2002) and Peterson and

McCune (2001) found that richness of the bryophyte and lichen floras was more closely associated with "hot spots" of particular environmental microhabitats than it was to the thinning treatments *per se*. It is very likely that arthropod guilds with limited mobility will respond more interactively to the scale of such limited microsites (10-100m^2) than they will to the usual scale of forest management.

A deciduous understory is relevant to vertebrate biomass and richness not only as a food source, but also in providing a habitable feature of the environment (Holmes and Schultz 1988). Studies by Enge and Marion (1986) in Florida have shown changes in reptile species richness primarily due to the elimination of forest structure with management practices; even though diversity was altered with clear-cutting, no change in reptile biomass occurred.

Research by Jokimaki *et al.* (1998) and Helle and Muona (1985) raises a caveat about interpreting the results of the arthropod species richness reported in this study. All of the samples from the L/G treatment were obtained from under the forest canopy adjacent to the gap. The Finnish conifer forest study documented that there was a significant decreasing gradient in insect diversity with increasing distance from the gap edge into the forest. This change was presumably due to the decreasing admixture of open-canopy species along the gap boundary. Though not directly quantifying this effect in these studies, no doubt the same phenomenon occurs in Oregon as well. (This is the reason that I took samples in the manner I did.) Both Jokimaki *et al.* (1998) and Martin and McComb (2001) document that richness within the gap itself is diameter dependent.

Though most people (even ecologists) tend to de-emphasize patterns of arthropod species diversity, this may be more a result of the imprecise knowledge scientists have of these diversity patterns than it is a conscious judgment about its

ultimate significance. When arthropod diversity can be carefully documented, as in the studies of Hammond and Miller (1998), its significance is obvious to everyone. Their documentation showed that even though deciduous foliage is a minimal component in coniferous forests of the Pacific Northwest, more than 90% of the species richness of the enormously diverse Order Lepidoptera and more than 80% of the total abundance of leaf-feeding caterpillars was dependent on deciduous foliage.

Different species of birds and mammals feed within the different strata of the forest, and it is logical to conclude that each species has a differential dependence upon deciduous vegetation (Holmes and Schultz 1988, Brush and Stiles 1986). Though it is apparent from the previously cited studies that forests with a prominent deciduous understory support a higher richness of terrestrial vertebrate species, it is not clear whether a larger component of deciduous understory can increase the total biomass of all resident vertebrate species. It would be fascinating to determine whether a predominantly conifer forest at the same latitude in the USA would support less bird biomass and diversity than a deciduous forest. Willson and Comet (1996) found that deciduous (*Alnus*) forests supported more bird richness than conifer forests in Alaska; they speculated that bird richness was correlated with understory vegetation structure and foliage-dwelling arthropod abundance.

4.6.2. Forest floor

Pitfall trapping revealed that the biomass of large arthropods was greater during the warm wet spring season than during the dry summer for all treatments. These results parallel those of Moldenke (unpub) for forest floor in the Pacific

Northwest (Brenner 2000, Heyborne *et al.* 2003) and contrast with results from clearcuts, which reveal highest densities and richness during the dry summer. The pitfall results of higher spring abundances hold for all component taxa (mostly predators), except for the Gryllacrididae (herbivore-omnivores). Moldenke (unpub. data) found that clearcut pitfall trappping yields higher densities in the summer due to increasing populations of herbivorous Orthoptera and Heteroptera.

Epigeic macroarthropods (the species caught in pitfall traps) responded to thinning with increased abundance. The heavy thinning was similar to the thinning with gaps, both of which were significantly greater in arthropod abundance than the light thin or the control (true, as well, for most individual taxa during the wet season). Species richness appeared to follow the same trend but was not significant. Abundance of epigeic macroathropods was directly correlated with soil moisture and NMS ordination revealed that species composition was strongly affected by thinning intensity. Indicator species analysis revealed that the species characteristic of the heavy thinning intensities were typically encountered by Moldenke (unpub. data, Parsons unpub. data) in clearcuts.

Soil mesofauna sampled by Berlese extraction revealed that the wet warm season soils supported more arthropods than those of the wet cool season, and in turn those of the dry hot season were the most depauperate. NMS ordination revealed a very strong difference between the mesofaunas of the 3 successive seasons. Indicator species analysis revealed that many species were unique to the coolest early spring season. Detritivores (mostly millipedes) decreased in abundance with the onset of summer, predators (many groups) increased. All of these seasonal decreases in abundance and species activity were significantly correlated with decreasing soil moisture content. That soil mesofaunal activity

decreases with seasonal soil moisture content is not surprising. Lowered soil moisture during the dry summer is itself a limiting factor, and since the majority of the taxa collected are predators of the microfauna (nematodes, springtails and mites -- excluded from these studies) which have been shown to decrease during the dry season (Moldenke and Fichter 1988), it is logical to expect declines in this fauna as the season progresses.

The soil mesofauna shows a strong negative thinning treatment response (highly significant during the mid- and late-growing season only). Species richness of mesofauna also decreases with thinning intensity (significant for all three seasons; significant for Shannon-Weiner and Simpson diversity measures during the mid- and late-seasons as well). It should not be surprising that of all 3 faunal elements assessed in this research (foliage-dwelling, macro-epigeic, litter-dwelling mesoarthropods) the soil mesofauna showed the strongest treatment effects. Madson (1998) documented a similarly enhanced mesofaunal response relative to the epigeic macrofauna in a thinning study in southern Oregon. This mesofauna is most strongly tied to a physical environmental variable that is directly affected by thinning, *i.e.*, soil moisture.

The response of soil moisture to thinning procedures is not well understood and doubtless varies with soil type and annual precipitation pattern. In general, it is broadly hypothesized that moisture availability (leaving aside physical trauma to the soil during the harvest process) should increase following canopy removal since transpiration from the canopy trees which have been removed is eliminated. In the case of gaps, the total transpiratory draw-down by the dense succeeding herbaceous/shrub growth is presumed to be far less than the transpiratory loss by whatever trees were there beforehand. Surprisingly, in the particular instance of

this study, thinning intensity was directly correlated with increased soil drying. It is likely that this was due to the preceding initial disturbance of logging, during which the shrub cover was adversely affected in order to stimulate understory conifer growth. As a general rule, under the canopy it would be expected that both the soil mesofauna and microfauna would increase after thinning (in direct proportion to thinning intensity) since the soil moisture content would increase and additional leaf litter (as a food resource) would have been created during the thinning process. This rate would decrease as the litter was removed by decomposition, but should be counterbalanced somewhat by an increased deciduous annual litter deposition rate.

Therefore, under most situations the litter-dwelling fauna would be expected to significantly increase following thinning, which would in turn provide additional food resources for ground-feeding vertebrates. That it didn't in this study, I consider an anomaly. I hypothesize that the increase in the pitfall-trapped macroinvertebrate fauna is related to the increase in the amount of slash and ground disturbance caused by the logging. This increases the heterogeneity of the environment greatly and provides refuges for the larger species (mostly predators) to hide successfully from their own predators. This increase in heterogeneity is obvious to anyone visiting the plot, but is very hard to quantify in a meaningful manner for arthropods whose limiting factors are imprecisely known. Mammologists cite the same factor as a limiting factor for small mammals, but seldom can successfully correlate it directly to abundance patterns (Garman 2001b); whether this means that the generally held hypothesis of limiting refuges is incorrect or that the appropriate descriptors have not been utilized is unknown.

Chapter 5

CONCLUSION

In conclusion, the effects of thinning on the arthropod fauna of NW forests are complex. Since the arthropod fauna changes seasonally, it is critical to quantify treatment effects within a given season as well as to compare treatment effects at different times of the year. Seasonal effects on arthropods are always very large and expected to exceed treatment effects since, in general, the species active in the dry season are vastly different from those active in the wet season. Between-seasonal comparisons can be facilitated by analysis at the functional guild or higher taxonomic level.

The litter-dwelling fauna is most closely tied to seasonal moisture. Even though seasonal differences are large, the indirect treatment effects of thinning on litter moisture seem to significantly decrease both abundance and diversity proportional to thinning. The epigeic ground-dwelling fauna also demonstrate greater seasonal effects than treatment effects. Thinning increases the abundance while simultaneously increasing richness and diversity of the epigeic fauna. I hypothesize that the disturbance and openness probably increases the prey base, while compensating with far greater habitat heterogeneity. The foliage-dwelling fauna reveals little seasonal difference on coniferous foliage, but significant differences on deciduous foliage. In this instance, treatment effects are limited, but all evidence indicates that, subsequently, once increased successional response of deciduous foliage to more intensive thinning occurs, the arthropod faunal response will be large.

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APPENDICES

APPENDIX A: Mean arthropod intensities (#/Kg of Plant Biomass) with standard error (SE) by thinning treatment and foliage type (deciduous and coniferous trees) at Willamette National Forest in western Oregon during 2000 and 2001

Foliage Type	Deciduous				Conifer			
Thinning Treatment / Groups	CN	LT	L/G	HT	CN	LT	L/G	HT
Defoliators/Leaf Miners								
Coleoptera	2 (2)	1 (1)	0	2 (2)	1 (0)	4 (2)	2 (1)	6 (3)
Diptera	0	1 (1)	0	0	0	0	0	0
Sawflies	0	1 (1)	0	1 (1)	1 (1)	2 (1)	3 (3)	3 (2)
Lepidoptera	33 (24)	2 (2)	5 (3)	5 (3)	6 (2)	5 (2)	1 (1)	3 (1)
Plant Feeders								
Diptera	0	0	1 (1)	0	1 (1)	1 (1)	0	1 (1)
Heteroptera	1 (1)	1 (1)	16 (15)	2 (2)	0	1 (1)	2 (1)	3 (1)
Aphids	249 (215)	227 (181)	189 (139)	373 (324)	14 (4)	13 (3)	7 (2)	6 (2)
Black Aphids	23 (14)	3 (3)	15 (8)	1 (1)	1 (1)	2 (2)	5 (3)	3 (3)
Periphyllus	768 (252)	368 (121)	289 (95)	259 (78)	0	0	0	0
Cicadellidae	6 (4)	21 (13)	12 (10)	19 (8)	2 (1)	1 (1)	3 (1)	2 (1)
Cinara	45 (16)	44 (29)	1 (1)	1 (1)	4 (2)	1 (1)	3 (2)	2 (2)
Homoptera-scale	0	0	0	0	5 (3)	7 (4)	1 (1)	7 (4)
Other Homoptera	4 (3)	0	0	4 (4)	0	2 (1)	0	1 (1)

APPENDIX A: Continued

Yellow Thrips	30 (11)	14 (5)	25 (11)	20 (8)	0	1 (1)	3 (3)	3 (2)
Black Thrips	5 (4)	0	4 (3)	1 (1)	1 (0)	0	1 (1)	1 (1)
Red Thrips	0	0	0	0	0	0	1 (1)	0
Predators/Parasites								
Cantharidae	21 (8)	7 (4)	6 (3)	2 (2)	3 (2)	2 (1)	1 (0)	2 (1)
Coccinellidae	2 (2)	1 (1)	1 (1)	7 (4)	0	1 (1)	2 (1)	1 (0)
Other Coleoptera	3 (2)	2 (2)	1 (1)	0	0	0	1 (1)	1 (1)
Lestodiplosis	3 (2)	15 (13)	0	1 (1)	8 (5)	10 (5)	12 (7)	58 45)
Diptera	0	1 (1)	0	0	1 (1)	0	1 (1)	0
Heteroptera	0	0	0	0	0	1 (1)	0	0
Chalcidoidea	14 (5)	12 (4)	14 (5)	7 (2)	6 (2)	10 (5)	16 (8)	8 (4)
Formicidae	9 (6)	9 (7)	6 (3)	2 (1)	2 (2)	4 (2)	2 (1)	1 (1)
Ichneumonidae	3 (3)	3 (2)	1 (1)	0	2 (1)	2 (1)	0	0
Other Hymenoptera	1 (1)	8 (6)	21 (17)	0	3 (2)	5 (3)	4 (3)	5 (3)
Chrysopidae	6 (5)	3 (2)	3 (2)	1 (1)	4 (2)	5 (1)	2 (1)	2 (1)
Salticidae	8 (4)	7 (3)	7 (3)	6 (4)	4 (2)	8 (2)	14 (6)	4 (1)
Thomisidae	3 (3)	8 (6)	4 (2)	2 (1)	4 (2)	4 (2)	3 (2)	3 (1)

APPENDIX A: Continued

Other spiders	90 (29)	21 (9)	15 (7)	17 (6)	41 (10)	40 (7)	31 (4)	27 (3)
Anystid mites	1 (1)	0	3 (2)	3 (2)	2 (1)	2 (1)	2 (1)	2 (1)
Erythraeid mites	0	0	0	0	0	0	0	1 (1)
Phytoseiid mites	79 (25)	139 (39)	73 (29)	55 (16)	12 (10)	1 (0)	3 (2)	6 (3)
Detrivores/Fungivores								
Coleoptera	0	0	1 (1)	0	0	0	0	0
Diptera	32 (13)	28 (16)	20 (9)	5 (2)	2 (1)	2 (1)	2 (1)	2 (1)
Heteroptera	0	0	0	0	0	0	0	1 (1)
Psocoptera	25 (12)	19 (9)	22 (6)	25 (7)	29 (7)	41 (12)	35 (16)	47 (13)
Collembola	2 (2)	8 (7)	7 (6)	1 (1)	4 (1)	2 (1)	7 (3)	4 (2)
Diplopoda	0	2 (2)	0	1 (1)	0	0	0	1 (1)
Camisia	5 (3)	5 (3)	2 (2)	4 (2)	43 (16)	30 (11)	14 (4)	22 (11)
Jugatala	27 (16)	14 (6)	8 (4)	5 (2)	9 (3)	7 (3)	30 (11)	48 (15)
Other Mites	5 (4)	3 (3)	1 (1)	4 (3)	1 (1)	2 (1)	3 (2)	2 (1)
Miscellaneous								
Coleoptera	0	0	1 (1)	0	2 (1)	0	1 (1)	0
Diptera	9 (3)	3 (2)	6 (2)	5 (3)	2 (1)	1 (1)	2 (1)	3 (2)

APPENDIX A. Continued

Heteroptera	6 (4)	0	0	0	2 (2)	1 (1)	1 (1)	0
Hymenoptera	5 (3)	0	0	1 (1)	1 (1)	0	0	0
Thysanura	0	0	1 (1)	0	0	0	0	1 (1)
Mites	7 (4)	0	3 (2)	2 (1)	2 (1)	3 (1)	2 (1)	2 (1)

Numbers in parentheses are one standard error of the mean

APPENDIX B: Lists of all arthropod taxa collected for the Young Stand Diversity Study along the different collecting methods in 2000 and 2001

Different-Dwelling Arthropods	Year	Shrub	Ground	Litter
Collecting Date or Period	2000	06/15/00 07/27/00 10/14/00	06/15/-06/29 07/27-08/11	10/14/00
	2001	06/18/01 08/02/01	06/18-7/03 08/02-8/18	06/18/01 08/02/01
Taxa \ Sampling methods	**Code**	Leaf and Branch	Pitfall Trap	Litter Samples
Archaeognatha				
Machilidae	**Mach**	-	124	3
Coleoptera				
Cantharidae	**Cant**	1028	-	1
Carabidae				
Cychrus tuberculatus	**Cytu**	-	25	-
Harpalus spp.	**Harp**	-	7	-
Metrius contractus	**Meco**	-	9	-
Notiophilus sylvaticus	**Nosy**	-	4	-
Omus dejeani	**Omde**	-	91	-
Promecognathus crassus	**Prcr**	-	10	-
P. herculaneus	**Pthe**	-	204	-
P. inopinus	**Ptin**	-	18	-
P. lama	**Ptla**	-	80	-
P. spp.	**Ptsp**	-	2	-
Scaphinotus angulatus	**Scan**	-	7	-
S. angusticollis nigripennis	**Scann**	-	1	-
S. marginatus	**Scma**	-	20	-
S. rugiceps	**Scru**	-	28	-
Zacotus mathewsii	**Zama**	-	19	-
Other *Carabidae* spp.	**Casp**	-	2	27
Cerambycidae	**Cera**	48	-	-
Chrysomelidae	**Chry**	92	-	-
Timarcha intricata	**Tiin**	-	9	-
Clambidae	**Clam**	-	603	1
Cleridae	**Cler**	-	1	2
Coccinellidae	**Cocc**	404	-	2
Curculionidae	**Curc**	102	136	80
Dermestidae	**Derm**	-	-	3
Elateridae	**Elat**	253	16	4
Endomychidae	**Endo**	-	2	-
Lampyridae	**Lamp**	86	5	-

APPENDIX B: Continued

Lucanidae	**Luca**	-	3	1
Mordellidae	**Mord**	38	1	-
Pselaphidae	**Psel**	-	12	39
Scarabaeidae	**Scar**	28	9	4
Scolytidae	**Scol**	57	4	1
Staphylinidae	**Stap**	105	49	52
Tenebrionidae	**Tene**	-	6	58
Zopheridae				
Phrellopsis poncata LeC	**Prpo**	-	8	-
Small Zopheridae	**Zoph**	-	1	-
Misc or Larva	**CoMS**	151	85	214
Dermaptera				
Forficulidae	**Forf**	7	-	-
Diptera				
Acroceridae	**Acro**	37	-	-
Anthomyiidae	**Ant**	35	-	-
Cecidomyiidae	**Ceci**	420	-	11
Chironomidae	**Chir**	228	-	3
Culicidae	**Culi**	29	-	-
Hippoboscidae	**Hipp**	21	-	-
Lestodiplosis	**Lest**	3907	-	14
Mycetophilidae	**Myce**	1258	-	2
Phoridae	**Phor**	27	-	3
Sciomyzidae	**Scio**	9	-	-
Syrphidae	**Syrp**	14	-	-
Tachinidae	**Tach**	19	-	-
Tephritidae	**Teph**	45	-	-
Tipulidae	**Tipu**	247	-	-
Nematocera	**Nema**	149	-	1
Brachycera	**Brac**	83	-	1
Cyclorrhapha	**Cycl**	12	-	-
Misc or Larva	**DiMS**	302	-	11
Heteroptera				
Aradidae	**Arad**	29	2	-
Coreidae	**Core**	-	4	-
Berytidae	**Bery**	131	-	-
Lygaeidae	**Lyga**	-	46	40
Miridae	**Miri**	155	1	-
Nabidae	**Nabi**	37	12	-
Pentatomidae	**Pent**	122	2	-
Rhopalidae	**Rhop**	41	-	-

APPENDIX B: Continued

Thyreocoridae	**Thyr**	310	2	-
Tingidae	**Ting**	41	8	29
Misc or Larva	**HeMS**	119	-	1
Homoptera				
Aphididae				
Aphids	**Aphi1**	22320	9	3
Black aphids	**Aphi2**	1296	-	-
Periphyllus	**Perip**	33677	-	-
Cercopidae	**Cerc**	224	2	-
Cicadellidae	**Cica**	1496	28	3
Cinara	**Cina**	2268	-	-
Membracidae	**Memb**	-	2	-
Chionaspis	**Chio**	250	-	-
Nuclaspis	**Nucl**	20	-	-
Straminaspis	**Stra**	553	-	-
Misc or Larva	**HoMS**	80	-	21
Hymenoptera				
Chalcidae	**Chal**	45	-	-
Chalcidoidea	**Chalc**	2571	-	53
Diprionidae	**Diap**	400	22	-
Encyrtidae	**Ency**	9	-	-
Eulophidae	**Eulo**	360	-	-
Eupelmidae	**Eupe**	240	-	-
Eurytomidae	**Eury**	11	-	-
Formicidae-ant	**Form**	875	996	1221
Halictidae	**Hali**	32	-	-
Ichneumonidae	**Ichn**	329	-	1
Perilampidae	**Peri**	54	-	-
Pteromalidae	**Pter**	283	-	-
Tenthredinidae	**Tent**	17	-	-
Torymidae	**Tory**	32	-	-
Vespidae	**Vesp**	136	-	-
Wasps	**Wasp**	33	-	-
Misc or Larva	**HyMS**	148	-	4
Isoptera				
Hodotermitidae	**Hodo**	-	6	-
Lepidoptera				
Geometridae	**Geom**	305	2	4
Misc or Larva	**LeMS**	261	-	12
Moth/Butterfly	**Moth**	643	-	7
Noctuidae	**Noct**	247	2	-

APPENDIX B: Continued

Black Head bud worm	**Budw**	57	-	-
Neuroptera				
Chrysopidae	**Chrys**	746	4	1
Hemerobiidae	**Heme**	8	-	-
Myrmeleontidae	**Myrm**	-	-	-
Opiliones	**Opil**	42	-	4
Orthoptera				
Acrididae	**Acri**	-	44	-
Gryllacrididae	**Gryl**	-	313	1
Psocoptera	**Psoc**	7944	15	4
Raphidioptera	**Raph**	-	-	1
Thysanoptera				
Yellow Thrips	**Thri1**	2076	-	-
Black Thrips	**Thri2**	297	-	-
Red Thrips	**Thri3**	74	-	-
Other Thysanoptera	**Thys**	-	-	2
Lepismatidae	**Lepi**	53	7	5
Collembola				
Entomobryidae	**Ento**	882	-	—
Sminthuridae	**Smin**	135	-	-
Protura	**Prot**	-	-	1
Diplura				
Dipluran	**Dipl**	-	-	42
Diplopoda				
Chordeumatida	**Chor**	-	20	3
Julida	**Juli**	-	15	1
Polydesmida	**Poly**	147	365	9
Spirobolida	**Spri**	-	22	8
Other Diplopoda	**Diplo**	-	-	165
Chilopoda				
Geophilomorpha	**Geop**	-	4	256
Lithobiomorpha	**Lith**	-	115	38
Scolopendromorpha	**Scolo**	-	21	28
Other Chilopoda	**Chil**	-	1	56
Crustacea				
Isopoda	**Crus**	-	-	2
Pseudoscorpiones	**Pseud**	-	6	75
Scorpiones				
Vejovidae	**Vejo**	-	3	-
Araneae				
Salticidae	**Salt**	1785	-	3
Thomisidae	**Thom**	875	21	27

APPENDIX B: Continued

Other Spider	**Spid**	8370	633	157
Acari				
Anystid mites	**Anys**	473	-	-
Camisia	**Cami**	4672	-	-
Erythraeid mites	**Eryt**	24	-	-
Immature Oribatida	**OribIm**	71	-	-
Phauloppia	**Phau**	113	-	-
Phytoseiid mite	**Phyt**	7840	-	-
Platyliodes	**Platy**	11	-	-
Jugatala	**Juga**	4857	-	-
Scapheremaeus	**Scap**	286	-	-
Ommatocepheus	**Omme**	86	-	-
Miscellaneous mites	**MiMS**	599	-	-
Snails	**Snail**	-	39	-
Column Total		122006	4395	2826