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Folivory of Vine Maple in an Old-growth Douglas-fir-Western Hemlock Forest

Abstract

Folivory of vine maple was documented in an old-growth Douglas-fir-western hemlock forest in southwest Washington. Leaf consumption by lepidopteran larvae was estimated with a sample of 450 tagged leaves visited weekly from 7 May to 11 October, the period from bud break to leaf drop. Lepidopteran taxa were identified by handpicking larvae from additional shrubs and rearing to adult. Weekly folivory peaked in May at 1.2%, after which it was 0.2% to 0.7% through mid October. Cumulative seasonal herbivory was 9.9% of leaf area. The lepidopteran folivore guild consisted of at least 22 taxa. Nearly all individuals were represented by eight taxa in the Geometridae, Tortricidae, and Gelechiidae. Few herbivores from other insect orders were observed, suggesting that the folivore guild of vine maple is dominated by these polyphagous lepidopterans. Vine maple folivory was a significant component of stand folivory, comparable to ~ 66% of the folivory of the three main overstory conifers. Because vine maple is a regionally widespread, often dominant understory shrub, it may be a significant influence on forest lepidopteran communities and leaf-based food webs.

Introduction

Herbivory in forested ecosystems consists of the consumption of foliage, phloem, sap, and live woody tissue by animals. Typical insect-produced herbivory levels of 7.1% for temperate forests and 11.1% for shade-tolerant species in the humid tropics have been reported, based on leaf area loss (Coley and Barone 1996). In contrast, occasional folivore outbreaks of the western spruce budworm (*Choristoneura occidentalis*) (Tortricidae) (Brookes, 1987) or the western hemlock looper (*Lambdina fiscellaria lugubrosa*) (Geometridae) (Harris et al. 1982) in temperate conifer forest can produce defoliation approaching 100%. Herbivory also varies spatially, for example, from 1% to 54% along an elevation gradient in Australia (Lowman 1995). Studies are usually restricted to measuring holes produced by leaf chewing arthropods, and therefore describe folivory alone.

Old-growth conifer forests in the Pacific Northwest west of the Cascade Range crest tend not to have defoliator outbreaks (Perry and Pitman 1983). Exceptions are outbreaks of geometrids, such as the western hemlock looper. This moth occasionally produces patches of intense defoliation in old-growth stands dominated by western hemlock (*Tsuga heterophylla*) (Harris et al. 1982). In contrast to defoliator outbreaks, less is known about endemic populations of defoliators and low-level folivory.

Vine maple (*Acer circinatum*) is one of the dominant shrubs in forest communities in the zone of maritime climatic influence in Oregon and Washington from the crest of the Cascade Mountains to the Pacific Ocean (Franklin and Dyrness 1988), and in coastal British Columbia (Haeussler et al. 1990). The shrub typically grows in clumps that enlarge vegetatively through resprouting and layering, and persists through multiple disturbances and successional stages (Schoonmaker and McKee 1988, Haeussler et al. 1990, Tappeiner and Zasada 1993, O'Dea et al. 1995). Mature vine maples are usually several meters tall with irregularly shaped crowns that have foliage arranged in flattened irregular sprays (Haeussler et al. 1990, O'Dea et al. 1995).

Even though vine maple is a common species in the Pacific Northwest, little information has been published on its herbivory and insect herbivores. Known folivores are generalist feeders (Furniss and Carolin 1980, Miller 1995). One report states that herbivory is low (Taylor 1976). Reported folivores include the tussock moths (*Orgyia*) (Lymantriidae), the polyphemus moth (*Antheraea polyphemus*) (Saturniidae), and the brown day moth (*Hemileuca eglanterina*) (Saturniidae) (Taylor 1976). The western hemlock looper feeds on vine maple during outbreaks on its principle host,

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western hemlock (Furniss and Carolin 1980). Other maples have been better documented; for example, the herbivory of red maple, a common tree in eastern North America, has been reported at 2% to 10% (Reynolds and Crossley 1997).

The presence of a generalist folivore guild on vine maple can be predicted based on the common shrub's perennial growth form, likely chemical defenses against herbivory and common occurrence within its range. Long-lived, common plants typically have tannins, digestibility reducing phenolic compounds, as the main anti-herbivory chemicals (Feeny 1980, Rhoades and Cates 1976). Condensed tannins and lignins become more concentrated as leaves age, decreasing leaf palatability and digestibility, whereas labile hydrolysable tannins increase in response to herbivory (Rhoades 1979). Although the defensive chemistry of vine maple has not been reported, it is probably similar to several other maples for which a tannin and lignin based defense has been described (Bate-Smith 1977, Seastedt et al. 1983, Hunter and Lechowicz 1992, Shure and Wilson 1993, Shure et al. 1998). As maple leaves mature and age, greater lignin content increases leaf toughness, inhibiting folivory. Lepidopteran larvae may exhibit a spring feeding strategy to avoid these defenses (Hagen and Chabat 1985, Shure and Wilson 1993).

The purpose of this study was to quantify vine maple herbivory and describe the folivore guild. We described temporal and spatial folivory patterns in addition to producing an overall folivory estimate.

Methods

Study Site

Three study sites were selected in a 500 year-old Douglas-fir-western hemlock forest in the southern Washington Cascades, in and adjacent to the T. T. Munger Research Natural Area (the RNA), Gifford Pinchot National Forest. The RNA was established in 1934 for the study of forest dominated by Douglas-fir (*Pseudotsuga menziesii*), and it is the location of a stationary canopy access crane erected in 1995. One site was near the crane, and all were within 1.2 km of each other in the same stand.

The environment of the RNA reflects its submontane location just west of the crest of the Cascade Range, at an elevation of 360-380 m in the Trout Creek drainage (Franklin 1972, Shaw et al. 2001). Precipitation is 247 cm per year, occurring partly as snow, and average minimum and maximum temperatures are 0.5°C and 12.3°C. Soils underlying the sites are well drained because of volcanic tephra parent material, and are moderately fertile.

The stand is typical in structure for an old-growth conifer forest in the western hemlock zone dominated by Douglas-fir, western hemlock, and western red cedar (*Thuja plicata*) (Franklin 1972, Franklin and Dyrness 1988, Franklin and DeBell 1988, Parker 1997). The study sites were located in relatively dry western hemlock associations (Topik et al. 1986), described as the western hemlock/Oregon grape-salal, western hemlock/salal complex (Meyers and Fredricks 1993). Vine maple was widespread at each site, and had been estimated at 26.7% cover near one site (Shaw et al. 2001).

Herbivory in the RNA is low. Bark beetles have probably produced the largest herbivore impact, by periodically killing mature Douglas-fir and western white pine (*Pinus monticola*) (Franklin and DeBell 1988). Western hemlock looper outbreaks have not been observed in the RNA from the time it was established in 1934 (Franklin and DeBell 1988). Folivory estimates of 3% or less have been made for the three dominant conifer species in the 2.3 ha area accessed by the crane (Shaw and Baker 1996, Schowalter and Ganio 1998). Limited defoliation by the silver spotted tiger moth (*Lophocampa argentata*) has been observed in the upper crowns of Douglas-fir and western hemlock in this area (Shaw 1998).

Folivory

Folivory was estimated by repeated observations of 450 leaves to track intra-seasonal folivory. At each of the three sites, 10 leaves were tagged on each of 5 shrubs arrayed on 3 transects. Leaves were tagged on the petiole with a loop of dental floss and a small piece of flagging, and were observed 23 times from 7 May to 9 October 1999. Both shrubs and transects were approximately 50 m apart. Some shrubs were excluded that had less than 200 leaves.

Leaves were selected by dividing each crown into 10 equal sectors originating at a central point, and selecting the outer-most leaf in each. This approach was utilized to sample the irregular, planar, 3-5 m tall crowns systematically while seeking to avoid disturbance of resident arthropods. Because foliage was in flattened arrays along branches that were at multiple heights and had little vertical overlap, selected leaves were in a wide range of distances from shrub centers and the ground. However, leaves towards the centers of foliage planes may have been under-represented. Selected leaves varied in height from 8 to 430 cm, with a mean of 160.8 ± 2.8 cm., and varied in area from 11 to 96 cm^2, with a mean of 38 ± 0.7 cm^2.

Folivory estimates were based on percentage leaf area lost calculated for individual leaves, a method reported by Lowman (1984). Periodic and seasonal folivory estimates were means of leaf percentages. To estimate folivory on each leaf, the area consumed was visually measured with a clear plastic grid to an accuracy of 0.1 cm. Folivory was defined as the loss of leaf area for attached leaves. If an entire leaf and petiole were absent, no herbivory was recorded on the observation date. Sketches were made of leaf outlines and holes to aid in distinguishing new feeding. Holes were defined as the new areas consumed from one week to the next.

Folivore Guild

Sampling was limited to lepidopterans because populations of other orders were extremely low. Occasional aphids and leafhoppers (Homoptera: Aphididae and Cicadellidae) were observed, but leaf beetles were not (Coleoptera: Chrysomelidae).

Larvae were collected on separate transects 10 - 20 m away from each folivory transect. On each visit, a target number of five larvae were hand-picked from a new shrub on each transect. Ten collections were made between 1200 and 1700 hr from 18 May to 18 August.

Larvae were reared with vine maple leaves as food. At the end of the season, remaining pupae were refrigerated for one month at 4.5°C to complete the development of fall-emerging species. Species identifications based on larval anatomy were made with reference to Miller (1995); species identifications of larvae and pinned adults were confirmed by Jeffrey Miller and Paul Hammond, Department of Entomology, Oregon State University.

Statistical and Graphical Analysis

The similarity of the three sites was examined to justify pooling leaf consumption data for an overall folivory estimate. The arcsine transformation was applied to individual leaf percentages to normalize the data before statistical analysis (Seastedt et al. 1983, Zar 1999). Analysis of variance was performed to compare the percentage folivory among sites, with sites as the single random factor. Correlation among folivory and spatial variables (total leaf folivory, number of holes per leaf, leaf height, and size) was explored with the Spearman Rank test (Zar 1999).

Graphical analysis was used to assess sampling rigor. The mean and standard error of increasingly large subsets of leaf folivory were plotted over subset size, and repeated for multiple random orderings of the leaf folivory data. A range for the mean and standard error of a sample size less than the total could then be estimated.

Results

Folivory

Folivory was estimated within the entire foliated period for vine maple, based on phenological observations (Braun, 2002). Bud break occurred within several days of 1 May, and leaf expansion continued for almost 3 wk. Observations were ended on 11 October because many leaves were turning color, signaling the beginning of seasonal leaf drop.

Weekly folivory varied from 0.2 % - 0.8 % on 17 of 23 observation visits. It was below this range at the beginning and end of the seasonal observation period, and peaked in May at 1.2 ± 0.2 % (Figure 1).

The number of leaves observed did not remain constant over the 23 visits from 6 May to 11 October: of the original 450 leaves, 382 leaves (84.9%) remained on the last visit. The initial number of leaves was 438, because 12 leaves abscised before full expansion, precluding folivory estimation based on the area of fully expanded leaves.

Seasonal folivory was the product of up to 26 holes per leaf, with a mean frequency of 4.6 ± 0.2. Holes were most often on leaf edges (50.3%), followed by interior areas (43.3%), and areas adjacent to previous holes (6.2%). The amount of folivory was significantly correlated with holes

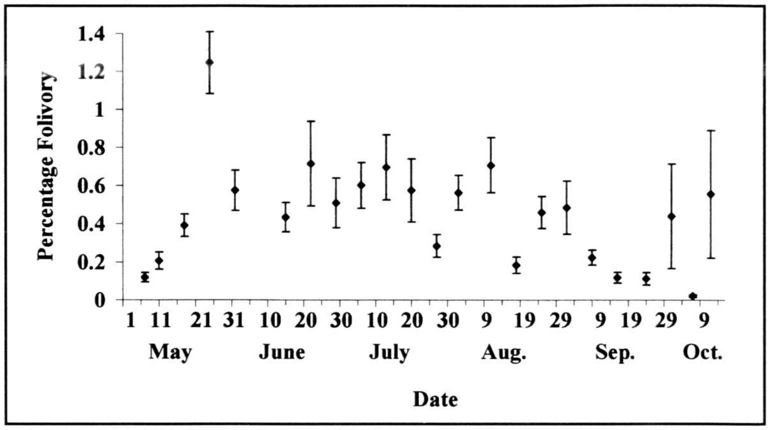

Figure 1. Weekly folivory produced by lepidopteran larvae from 7 May to 11 October 1999 feeding on tagged vine maple leaves. Data are the mean percentages of missing portions divided by fully expanded leaf area.

per leaf, but not with leaf size or leaf height. There was no significant correlation among holes per leaf, size, or height.

The validity of pooling folivory data was supported by the results of an analysis of variance comparing folivory among the sites. The sites were not significantly different from each other. Means for individual sites were 8.7% ± 1.0, 10.0% ± 1.2, and 10.9% ± 1.2.

The sufficiency of folivory sampling intensity was supported by the stability of the mean and standard error at less than the total sampling effort. Based on five random orderings of leaf folivory, these statistics became focused in narrow ranges beginning with about half the sample leaves (Figure 2a, b). Based on 50%, 90%, and 100% of leaves, mean folivory was 9.0% - 10.3% (SE 0.8 - 1.1), 9.9% - 10.2% (SE 0.7), and 9.9% (SE 0.7).

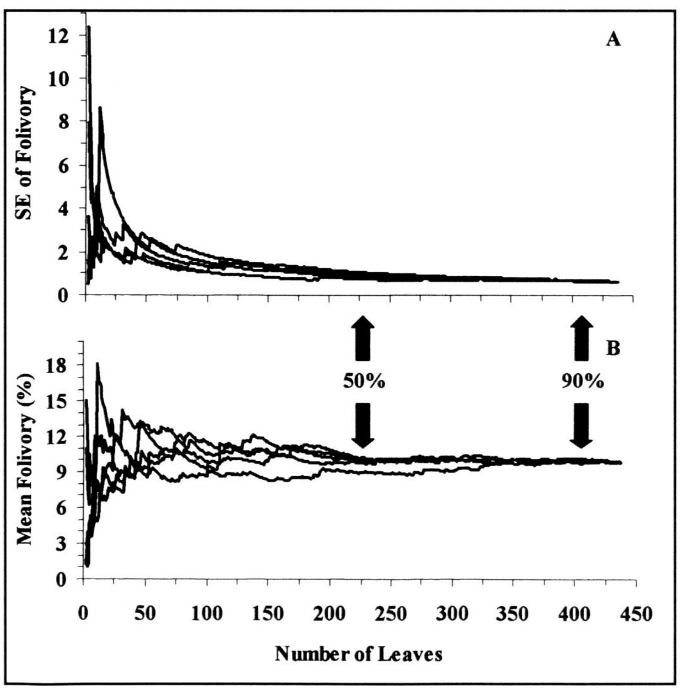

Figure 2. Plots of the mean (A) and the standard error (B) generated by cumulative resamples of the seasonal folivory of 2 to 438 vine maple leaves arranged in five random rankings.

Folivore Guild

Larval collection visits yielded 397 larvae of which 389 were assigned to taxa at the family level or below (Table 1). Thirteen taxa were distinguished at the species level, increasing the number of previously reported species known to feed on vine maple by 11.

Taxonomic identifications were based on reared adults, slides of larvae, and descriptive notes. Because only about 10% of the eight common taxa were successfully reared to adult, these were assigned to major groups based on family membership and temporal occurrence (Table 1). None of the less common taxa, represented by

TABLE 1. Lepidopteran larvae collected from vine maple in an old-growth Douglas-fir-western hemlock forest in 1999[1].

	May			June			July			August
	18	21	28	4	17	24	1	14	28	20
Major Groups:										
Early Geometridae	36	46	37	29	0	0	0	0	0	0
Tortricidae	0	0	0	5	5	0	1	1	0	1
Late Geometridae	0	0	0	0	31	45	28	2	1	0
Gelechiidae	0	0	0	0	0	1	8	38	32	20
Other Geometridae:										
Erannis tiliaria	0	0	0	0	0	2	0	0	0	0
Eupithecia sp.	0	0	0	0	0	0	1	0	0	0
Iridopsis emasculata	0	0	0	0	1	0	0	2	0	0
Per mizon	0	0	0	0	1	0	0	0	0	0
Geometrid 1	0	0	1	0	0	0	0	0	0	0
Geometrid 2	0	0	0	0	0	0	0	1	0	0
Geometrid 3	0	0	0	0	0	0	0	0	1	3
Noctuidae:										
Lithophane georgii	0	0	0	0	0	0	0	0	0	1
Amphipyra pyramidoides	0	1	1	1	0	0	0	0	0	0
Phlogophora periculosa	0	0	0	0	1	0	0	0	0	0
Zale sp.	0	0	0	0	0	0	1	0	0	0
Noctuid 1	0	0	0	3	0	0	0	0	0	0
Lasiocampidae:										
Phyllodesma americana	0	0	0	0	0	0	0	0	1	0
Saturniidae:										
Antheraea polyphemus	0	0	0	0	0	0	0	0	1	0
Total:	36	47	39	38	39	48	39	44	36	25

[1]Taxa of the Major Groups were as follows: early geometrids: *Operophtera bruceata*; tortricids: *Choristoneura rosaceana*, *Archips* sp., and *Acleris* sp.; late geometrids: *Itame plumosata*, *Lambdina fiscellaria lugubrosa*, and *Neoalcis californiaria*; gelechiids: one or more species.

three or fewer individuals, was successfully reared. However, because many taxa have distinctive larval characteristics, 13 of the 22 taxa were identified to species.

Four groups representing at least eight taxa made up the bulk of the collections (Table 1). The first group was present in May and early June and consisted solely of a geometrid, the Bruce spanworm (*Operophtera bruceata*). The second group was present from mid-June to early July and consisted of geometrids: the western hemlock looper, the brown-lined looper (*Neoalcis californiaria*), and *Itame plumosata*. The third group was present from June through August and consisted of at least three tortricids: the obliquebanded leafroller (*Choristoneura rosaceana*), and *Acleris* and *Archips* species. The fourth group, present from early July to late August, consisted of at least one species of a microlepidopteran family, the Gelechiidae.

Low numbers of individuals in at least 14 additional taxa were collected or observed (Table 1). Geometrid taxa consisted of the linden looper (*Erannis tiliaria*), *Eupithecia* sp., *Iridopsis emasculata*, *Pero mizon*, and three unknowns. Noctuid taxa consisted of *Lithophane georgii*, the copper underwing (*Amphipyra pyramidoides*), *Phlogophora periculosa*, *Zale* sp., and one unknown. One lasiocampid, the lappet moth (*Phyllodesma americana*) was collected. One saturniid, the polyphemus moth (*Antheraea polyphemus*) was observed in September on an herbivory transect but not collected; it was identified by its distinctive large size and coloration.

Discussion

The 9.9% folivory is similar to the level reported elsewhere for temperate broadleaved trees, including maples (Seastedt et al. 1983, Reynolds and Crossley 1997). This amount may be a significant portion of stand folivory. Based on the projected leaf area of vine maple relative to the conifers in the stand, 0.4 m^2 compared to 6.5 m^2 leaf area/m^2 forest floor (Thomas and Winner 2000), vine maple folivory represented ~66% of the amount of conifer leaf area consumed, if conifer folivory of 1% is typical.

All identified species were polyphagous (Brown 1962, Furniss and Carolin 1980, Carriere et al. 1995, Miller 1995), confirming our prediction of a lepidopteran community dominated by generalists. Three of the species also feed on conifers, reflecting wide host ranges; these are the western hemlock looper, the obliquebanded leafroller (Carriere et al. 1995), and *Neoalcis californiaria* (Furniss and Carolin 1980). The Bruce spanworm, the most commonly collected taxon in this study, feeds on a wide range of other broadleaved trees and shrubs: alder, apple, blueberry, cherry, hazel, maple, poplar, rose, serviceberry, and willow (Brown 1962, Troubridge and Fitzpatrick 1993, Carriere et al. 1995, Miller 1995). Because members of these host plant genera are common in the stand and greater Wind River drainage (Franklin and Dyrness 1988, Meyers and Fredricks 1993), the identified lepidopteran taxa may be as well.

The sequential nature of the common members of the community may represent adaptations to changes in food quality related to foliage age and folivore damage. In other maple species, leaf toughness and tannin content increase over time, decreasing food value for insect folivores (Hunter and Lechowicz 1992, Shure et al. 1998). Additional studies on food choice may distinguish the importance of host quality from other potential influences on folivore populations, such as competition with other lepidopteran folivores and the avoidance of predators and parasites.

Even though the observed folivores are polyphagous, host choice may shift with population level. During outbreaks, the hemlock looper feeds on western hemlock, its preferred host, and understory shrubs including vine maple (Furniss and Carolin 1980). We commonly found the hemlock looper on vine maple, even though there has not been a hemlock looper outbreak since at least 1934 in the RNA (Franklin and DeBell 1988), suggesting that vine maple may be a preferred host in endemic periods. This hypothesis could be addressed by monitoring the host choice of this looper in the stand.

Our description of a lepidopteran folivore guild containing 22 taxa is conservative. More intensive sampling and greater rearing success would have produced some additional species identifications. Because populations can be expected to vary from year to year, species we described as common may become less so, while others become more common. Multi-year studies in a range of forest communities and successional stages are justified to better understand the role of this shrub and its lepidopteran folivores in forest ecosystems.

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Literature Cited

Bate-Smith, E. C. 1977. Astringent tannins of *Acer* species. Phytochemistry 16:1421-1426.

Braun, D. M. 2002. Phenology of some common plants at the Wind River Canopy Crane Research Facility, 2000-2002. Unpublished report on file at the Wind River Canopy Crane Research Facility, Carson, Washington.

Brookes, M. H. 1987. Western spruce budworm. U. S. Department of Agriculture Technical Bulletin 1694. Washington, D. C.

Brown, C. E. 1962. The life history and dispersal of the Bruce spanworm, *Operophtera bruceata* (Hulst), (Lepidoptera: Geometridae). Canadian Entomologist 94:1103-1107.

Carriere, Y., S. Pare, and B. D. Roitberg, 1995. Oviposition preference of a polyphagous moth, the obliquebanded leafroller, *Choristoneura rosaceana* (Harris) (Lepidoptera: Tortricidae). Canadian Entomologist 127:577-586.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics 27:305-335.

Feeny, P. 1980. Biochemical evolution between plants and their insect herbivores. Pages 3-19 *In* L. E. Gilbert and P. H. Raven (editors), Coevolution of Animals and Plants, Symposium V, First International Conference of Systematic and Evolutionary Biology, University of Texas Press, Austin, Texas. Revised Edition.

Franklin, J. F. 1972. Wind River Research Natural Area. Federal research natural areas in Oregon and Washington—a guidebook for scientists and educators. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Franklin, J. F., and D. S. DeBell. 1988. Thirty-six years of population change in an old-growth *Pseudotsuga-Tsuga* forest. Canadian Journal of Forest Research 18:633-639.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Furniss, R. L., and V. M. Carolin. 1980. Western Forest Insects. Miscellaneous Publication No. 1339, USDA Forest Service, Washington, D.C.

Haeussler, S., D. Coates, and J. Mather. 1990. *Acer circinatum* (vine maple). Pages 12-17 *In* S. Haeussler, D. Coates, and J. Mather (editors), Autecology of common plants in British Columbia: a literature review. Forestry Canada and British Columbia Ministry of Forests, FRDA Report 158. Victoria, British Columbia.

Hagen, R. H., and J. F. Chabot. 1986. Leaf anatomy of maples (*Acer*) and host use by Lepidoptera. Oikos 47:335-345.

Harris, J. W. E., A. F. Dawson, and R. G. Brown. 1982. The western hemlock looper *Lambdina fiscellaria lugubrosa* in British Columbia, 1911-1980. BC-X-Canadian Forest Service, Pacific Forest Research Center, 234, Victoria, British Columbia.

Hunter, M. D., and M. J. Lechowicz. 1992. Foliage quality changes during canopy development of some northern hardwood trees. Oecologia 89:316-323.

Lowman, M. D. 1984. An assessment of techniques for measuring herbivory: Is rainforest defoliation more intense than we thought? Biotropica 16:264-268.

Meyers, A. P., and N. Fredricks. 1993. Thornton T. Munger Research Natural Area Management Plan, Gifford Pinchot National Forest, Wind River Ranger District. Unpublished Report on File at the Wind River Work Center, Carson, Washington.

Miller, J. C. 1995. Caterpillars of Pacific Northwest Forests and Woodlands. USDA Forest Service Technology Transfer Booklet FHM-NC-06-95. National Center of Forest Health Management, Morgantown, West Virginia.

O'Dea, M. E., J. C. Zasada, and J. C. Tappeiner II. 1995. Vine maple clone growth and reproduction in managed and unmanaged coastal Oregon Douglas-fir forests. Ecological Applications 5:63-73.

Parker, G. G. 1997. Canopy structure and light environment of an old-growth Douglas-fir/Western hemlock forest. Northwest Science 71:261-270.

Perry, D. A., and G. B. Pitman. 1983. Genetic and environmental influences in host resistance to herbivory: Douglas-fir and the Western Spruce Budworm. Zeitschrift fur Angewandte Entomologie 96:217-228.

Reynolds, B. C., and D. A. Crossley, Jr. 1997. Spatial variation by forest canopy arthropods along an elevation gradient. Environmental Entomology 26:1232-1239.

Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3-54 *In* Denno, R. F., and M. S. McClure (editors), Herbivores: Their Interactions with Plant Secondary Metabolites. Academic Press, New York.

Rhoades, D. F., and R. G. Cates. 1976. Towards a general theory of plant defense. Recent Advances in Phytochemistry 10:168-213.

Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Science 34:960-979.

Schowalter, T. D., and L. M. Ganio. 1998. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA. Bulletin of Entomological Research 88:633-640.

Seastedt, T. R., D. A. Crossley, Jr., and W. W. Hargrove. 1983. The effects of low-level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. Ecology 64:1040-1048.

Shaw, D. C. 1998. Distribution of larval colonies of *Lophocampa argentata* Packard, the silver spot tiger moth (Lepidoptera: Arctiidae), in an old growth Douglas-fir, *Pseudotsuga menziesii*/Western hemlock, *Tsuga heterophylla*, forest canopy, Cascade Mountains, Washington State. Canadian Field-Naturalist 112:250-253.

Shaw, D. C., and A. Baker. 1996. Elongation of branch tips and loss of new foliage within the lower, mid, and upper canopies of an old-growth forest. (Abstract). Supplement to the Bulletin of the Ecological Society of America 77:404.

Shaw, D. C., J. F. Franklin, J. Klopatek, K. Bible, S. Greene, and E. Freeman. 2001. Ecological setting of the Wind River old-growth forest. Unpublished report on file at the Wind River Canopy Crane Research Facility, Carson, Washington.

Shure, D. J., and L. A. Wilson. 1993. Patch-size effects on plant phenolics in successional openings of the southern Appalachians. Ecology 74:55-67.

Shure, D. J., P. D. Mooreside, and S. M. Ogle. 1998. Rainfall effects on plant-herbivore processes in an upland oak forest. Ecology 79:604-617.

Tappeiner, J. C., and J. C. Zasada. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. Canadian Journal of Forest Research 23:1775-1780.

Taylor, S. 1976. *Acer circinatum* Pursh. Davidsonia 7:32-37

Thomas, S.C., and W. E. Winner. 2000. Leaf area index in an old-growth Douglas-fir forest: an estimate based on direct structural measurements in the canopy. Canadian Journal of Forest Research 30:1-9.

Topik, C., N. M. Halverson, and D. G. Brockway. 1986. Plant Association and management guide for the Western Hemlock Zone, Gifford Pinchot National Forest. USDA Forest Service R6-ECOL-230A-1986. Pacific Northwest Region, Portland, Oregon.

Troubridge, J. T., and S. M. Fitzpatrick. 1993. A revision of the North American *Operophtera* (Lepidoptera: Geometridae). Canadian Entomologist 125:379-397.

Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

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