The Role of Disturbance in Creating Dead Wood: Insect Defoliation and Tree Mortality in Northeastern Oregon[1]

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Abstract

Knowledge of natural disturbance factors that influence ecosystems over large temporal and spatial scales is essential for understanding interactions among ecosystem processes. Repeated assessment of forest stand structure after disturbance events may aid in identifying ecosystem processes and components affected by disturbance that are not readily apparent until long after the disturbance event. In northeastern Oregon, conifer defoliation by phytophagous insects occurs over large temporal and spatial scales and often leads to tree mortality. The current composition and stand structure in mixed conifer stands were documented after two such disturbances: stands 23 years after defoliation by Douglas-fir tussock moth (*Orgyia pseudotsugata* McD.) in the Wenaha-Tucannon Wilderness, and stands 12 years after defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman) in the Starkey Experimental Forest. Assessment of these areas includes the density of snags, the density and size of down logs, and the change in associated vegetation. The research suggests that similar patterns of stand dynamics, including tree mortality and eventual conversion of standing dead to down logs, along with new seedling establishment, can result from defoliation events with vastly differing durations. This work provides valuable insights into the role of large insect outbreaks and the dynamics of dead wood in these mixed conifer stands.

Introduction

Knowledge of natural stand-replacement disturbances over large temporal and spatial scales is essential for understanding the interactions among ecosystem processes, such as nutrient cycling, plant competition and community development, and wildlife habitat and population dynamics. In the Blue Mountains of northeastern Oregon and southeastern Washington, natural stand-replacement disturbances in mixed conifer stands of grand fir *(Abies grandis* [Dougl. ex D. Don] Lindl.), Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and western larch *(Larix occidentalis* Nutt.) primarily occur as either wildfire (Agee 1993) or insect herbivory (Hessburg and others 1994, Wickman 1992). The largest Douglas-fir tussock moth *(Orgyia pseudotsugata* McD.) outbreak on record occurred in this area between 1972 and 1974, resulting in about 3,240 km^2 of defoliation (Brookes and Campbell 1978,

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Graham and others 1975, USDA 1978). Grand fir and Douglas-fir that were stripped of foliage for more than 90 percent of their crown length died (Wickman 1978). Patches of dead trees were scattered throughout the outbreak area. Federal and State land managers and private landowners initiated chemical control programs to reduce larval densities and salvage harvesting of timber to reduce fuels and capture tree volume. In the early 1980s, a western spruce budworm *(Choristoneura occidentalis* Freeman) outbreak began in northeastern Oregon. Stands throughout eastern Oregon and eastern Washington eventually were infested, resulting in about 28,300 km^2 of defoliation (USDA Forest Service 1988). Again, salvage harvesting of timber and aerial spray programs occurred throughout the two states.

Studying the long-term effects of natural disturbances such as Douglas-fir tussock moth or western spruce budworm outbreaks requires assessment of stand dynamics over several decades. It also requires assessment of stands that remain relatively undisturbed by human activities or management. After the recent Douglas-fir tussock moth and western spruce budworm outbreaks, managers were increasingly concerned about long-term ecological effects, especially the changes in stand structure and the accumulation of dead and down wood that may increase fire hazard. Many opportunities to evaluate long-term changes, however, were compromised by management activities, including harvesting and aerial spraying. Two areas in northeastern Oregon in which natural processes were not altered by management activities were recognized at the onset of the respective outbreaks and thus provide an opportunity for long-term assessment. A study site at Grizzly Bear Ridge, in the Wenaha-Tucannon Wilderness Area, Umatilla National Forest, was established in 1972 during the early phase of the Douglas-fir tussock moth outbreak. A similar site at Bally Mountain, in the Starkey Experimental Forest, Wallowa-Whitman National Forest, was established in 1983 at the beginning of the western spruce budworm outbreak. Both sites have a multi-century history of insect-caused defoliation (Swetnam and others 1995). The original study objectives at both sites were to assess host tree mortality and damage such as top-kill and growth loss, and stand dynamics and compositional changes including natural regeneration. The stands were examined annually for 10 years after the outbreaks.

Tree mortality after Douglas-fir tussock moth defoliation occurred over a 5-year period from 1973 to 1977 at the Grizzly Bear Ridge site. Tree mortality after western spruce budworm defoliation occurred over an 8-year period from 1984 to 1992 at the Bally Mountain site. Stands at both sites had similar extreme post-outbreak tree mortality, ranging from 40 to 90 percent tree mortality (Wickman and others 1986).[4] Ten years after the onset of the outbreak, natural regeneration was assessed at Grizzly Bear Ridge. About 1,230 new seedlings per hectare were counted, of which 60 percent were grand fir (Wickman and others 1986). Wickman and others (1986) suggested that, in the absence of fire, the stand structure would be conducive to supporting the next Douglas-fir tussock moth outbreak in 70 to 90 years.

With increasing recognition of the importance of snags and logs for wildlife habitat (Bull and others 1997, Maser and others 1979) and ecosystem processes, such as the role of nonsymbiotic nitrogen fixation in nutrient cycling, coarse woody debris in ectomycorrhizae relations, and long-term carbon storage (Harvey and others 1987, Jurgensen and others 1992), we expanded the original study objectives to include assessment of the dead wood component. In 1995, we re-examined stand structure at

[4] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

the Grizzly Bear Ridge site, focusing on natural regeneration, snag and log distribution, and plant community composition. This represented a 23-year postoutbreak assessment of stand conditions. In 1997, we re-examined stand structure at Bally Mountain, focusing on establishment of natural regeneration and snag and log distribution. This represented a 12-year postoutbreak assessment of stand conditions.

In this paper, we describe stand conditions at both Grizzly Bear Ridge and Bally Mountain, emphasizing the dead wood component. We believe these results have relevancy as individual case studies of typical Blue Mountain mixed-conifer stands subjected to extreme defoliation after which natural processes of mortality and down wood recruitment were allowed to proceed unhindered by management activities.

Study Area and Methods

Stand structure after Douglas-fir tussock moth defoliation was examined on Grizzly Bear Ridge in the Wenaha-Tucannon Wilderness *(fig. 1)*. The study site (latitude 45° 59' 45", longitude 117° 44' 30") is on a gentle south-facing slope and broad plateau at about 1,280 m elevation, above steep Wenaha River canyon "breaks." At the onset of the last Douglas-fir tussock moth outbreak, these stands were composed of mature grand fir and Douglas-fir as well as minor amounts of western larch and ponderosa pine, totaling about 830 trees per hectare and 58 m^2 per hectare of basal area. Ten years after the outbreak, the live residual overstory consisted of about 370 trees per hectare and 23 m^2 per hectare of basal area (Wickman and others 1986). The study area conforms to the grand fir/twinflower plant association as described by Johnson and Clausnitzer (1992).

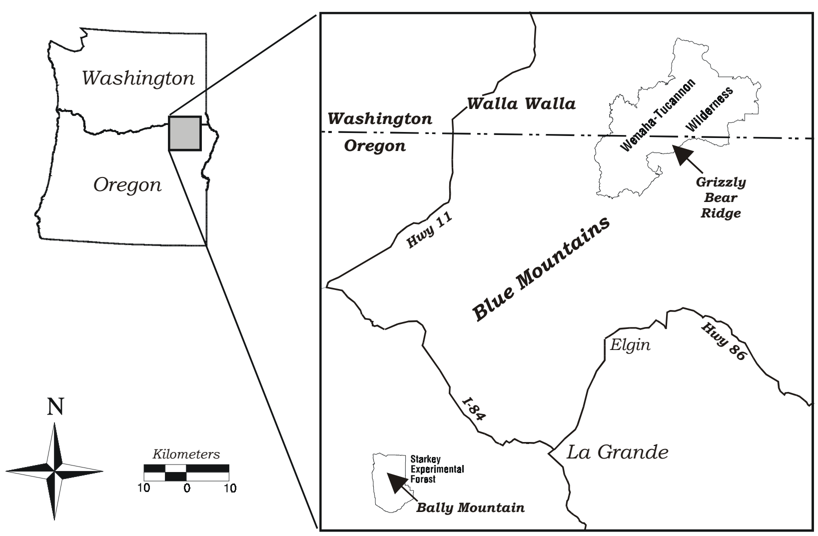

Figure 1—Grizzly Bear Ridge and Bally Mountain study areas for assessing long-term changes in stand structure after severe insect-caused defoliation, northeastern Oregon.

Assessment of stand structure in 1995 was made by using the same sample grid used in 1972 to assess tree mortality and top-kill (Wickman 1978) and later used to document natural regeneration (Wickman and others 1986). Thirty-four circular sample plots, each 81 m^2 (1/50 acre) in size, were systematically located at 30-m intervals along eight transects in two stands. Diameter at breast height (1.37 m high) was measured on all live overstory trees previously tagged, and additional mortality from the assessment in 1986 was noted. All down logs with large-end diameters at least 7.6 cm within the same sample plot were measured for total length to the nearest foot and mid-length diameter to the nearest inch. External and internal wood condition of each log was assessed by using a hatchet to chop into the log at intervals along its length and estimate the percent sound material based on wood hardness, moisture content, and color, and presence of bark (Torgersen and Bull 1995). Heights of all seedlings within a 16-m^2 circular subplot centered on the 81-m^2 circular plot were measured with a height pole to the nearest inch. Total overstory canopy coverage and canopy coverage of all vascular plants by species were ocularly estimated on the same 81-m^2 circular plot.

Stand structure after western spruce budworm defoliation was examined on Bally Mountain in the Starkey Experimental Forest *(fig. 1)*. The study site (latitude 45^{o} 17' 30", longitude 118^{o} 36' 30") is on a gentle east-facing slope at about 1,417 m elevation. At the onset of the western spruce budworm outbreak in 1983, this stand was composed of 77-year-old grand fir, 165-year-old Douglas-fir and 132-year-old western larch, with minor amounts of ponderosa and lodgepole pine *(Pinus contorta* Doug. ex Loud), totaling about 400 trees per hectare and about 27 m^2 per hectare of basal area.[5] Grand fir represented almost 80 percent of the density and basal area. The study area most closely conforms to the grand fir/twinflower plant association as described by Johnson and Clausnitzer (1992).

Stand structure was assessed at Bally Mountain in 1997 with a sample grid similar to that used at Grizzly Bear Ridge. Seventy-five circular sample plots, each 200 m^2 (1/20 acre) in size, were systematically located at about 30-m intervals throughout a single stand. Diameter at breast height was measured on all live overstory trees previously tagged, and additional mortality from the assessment in 1993 was noted. Because mortality at Bally Mountain was more recent than at Grizzly Bear Ridge, and more of the dead stems remained standing, we did not measure logs directly. Instead, we assumed all broken sections of snags in the plot would fall as logs into the plot, and no sections of snags from outside the plot would fall into the plot. Quantity and size of logs on the ground was estimated by calculating the dimensions of tree boles no longer standing. We measured the height at which snags were broken on all snags with breaks above breast height by using a survey laser. All seedlings within the same plot were counted by species. Because the Bally Mountain site was adjacent to open areas that were grazed by cattle and the understory vegetation was frequently disturbed, we opted not to assess species composition of associated vegetation.

We summarized the data by species at both sites to estimate density, basal area, and diameter class distribution of live and dead stems, and density of logs. For Bally Mountain, we calculated total tree height based on diameter at breast height by using the Lundqvest function with specific parameters for each tree species (Moore and others 1996). We then used the USDA Forest Service's (1999) computer program

[5] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

NATVOL to estimate the diameter at the top of broken snags and the length and volume of both the standing and down (log) portions. These estimates were based on measured breast-height diameter and snag height and calculated total tree height, using equations for taper and volume within NATVOL by species derived from more than 14,000 trees. For both sites, we calculated the mass of logs, assuming a constant 0.256 kg per m^3 (20 pounds per $foot^3$). Because the amount of cover provided by logs for small vertebrates is related to size of the logs, we calculated the cover as a percentage of total area based on mid-length diameter and total log length at Grizzly Bear Ridge and large end-diameter and total length at Bally Mountain, and assumed no overlap of pieces. Finally, associated vegetation at Grizzly Bear Ridge was summarized by constancy (the percentage of sample plots containing that species) and the mean cover (average of the observed cover values where present).

Results

Live Tree Structure

Residual live trees with overstory canopies occurred on 74 percent of the plots and provided about 44 percent canopy cover at Grizzly Bear Ridge. Total live tree density was about 2,290 trees per hectare and total basal area was about 30 m^2 per hectare *(table 1).* Most of the live stems and basal area was grand fir. More than 65 percent of the live stems at Grizzly Bear Ridge were grand fir seedlings and saplings that contributed little to the total basal area *(table 2).* Average height of natural regeneration (mean and standard error in cm) was 46.6 ± 12.08 for ponderosa pine, 41.6 ± 12.34 for grand fir, 20.9 ± 6.70 for Douglas-fir, 26.2 ± 144.21 for western larch, and 7.2 ± 25.59 for Engelmann spruce.

Live tree density at Bally Mountain was about 560 trees per hectare, of which almost 50 percent was western larch and 30 percent was grand fir *(table 1).* Total basal area was 2 m^2 per hectare. More than 85 percent of the live trees were seedlings and saplings less than 1.37 m tall *(table 2).* Regenerated species included ponderosa pine, grand fir, Douglas-fir, western larch, and lodgepole pine.

Dead Tree Structure

At Grizzly Bear Ridge, there were 109 stems per hectare standing dead, of which 67 percent was grand fir and 20 percent was western larch *(table 1).* Almost 21 m^2 per hectare in basal area of dead trees remained; about 75 percent of this was dead grand fir *(table 1).* Almost 30 percent of the standing dead was grand fir with breast height diameters greater than 50 cm *(table 2).* The largest standing dead grand fir had a diameter of 87 cm. Although infrequently represented, dead ponderosa pine had diameters greater than 80 cm.

Bally Mountain had the same density of standing dead (109 stems per hectare); almost 90 percent of these were grand fir *(table 1).* Total basal area of dead was almost 8 m^2 per hectare and was dominated by grand fir. Grand fir that were dead had diameters that ranged from 6 to 74 cm; about 13 percent were greater than 50 cm *(table 2).* There were 28 dead stems per hectare with tops broken above breast height; more than 80 percent of these were grand fir. Height of the break ranged from 1.5 to 15.8 m (mean ± standard error = 7.1 ± 0.83) for grand fir, 1.7 to 24.4 m (7.0 ± 3.52) for Douglas-fir, and 5.4 to 24.3 m (14.8 ± 9.45) for western larch.

Table 1—*Average density and basal area of standing live and dead trees (mean and standard error) at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Number of trees[1]		Basal area[2]	
	Mean	**SE**	**Mean**	**SE**
Grizzly Bear Ridge				
Live stems:				
Pipo[3]	152.6	33.01	--[4]	--
Abgr	1780.6	482.28	24.6	5.383
Psme	243.5	74.04	--	--
Laoc	58.1	18.98	4.75	2.051
Pien	58.1	41.15	0.31	0.311
Total	2292.9	506.82	29.6	5.600
Dead stems:				
Pipo	7.3	5.06	4.07	2.839
Abgr	72.7	20.28	15.4	5.126
Laoc	21.8	15.18	0.97	0.615
Hardwood	3.6	3.63	0.04	0.042
Unknown	3.6	3.63	0.26	0.265
Total	109.0	32.48	20.8	7.430
Bally Mountain				
Live stems:				
Pipo	30.7	5.61	0.22	0.149
Abgr	168.7	40.63	0.60	0.361
Psme	90.7	19.63	0.16	0.159
Laoc	266.7	47.33	1.00	0.354
Pico	6.0	2.50	0.01	0.012
Pien	0.7	0.67	0.00	0.000
Total	563.3	74.67	2.00	0.532
Dead stems:				
Abgr	96.0	9.28	6.82	0.851
Psme	10.7	2.73	0.77	0.335
Laoc	2.7	1.31	0.30	0.202
Total	109.3	10.60	7.89	0.930

[1] Stems ha^{-1}
[2] m^2 ha^{-1}
[3] Species codes: Pipo, *Pinus ponderosa*; Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pien, *Picea engelmannii*
[4] – = negligible amount

Table 2—*Cumulative frequency distribution of live and dead stems by diameter class and species at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Pipo[1]	Abgr	Psme	Laoc	Pico	Pien	Other
Grizzly Bear Ridge							
Live:							
< bh[2]	6.7	65.6	10.6	0.9	0	2.4	0
0.0 - 9.9[3]	0	1.9	0	0	0	0	0
10.0 - 19.9	0	3.8	0	0	0	0	0
20.0 - 29.9	0	2.4	0	0.3	0	0	0
30.0 - 39.9	0	1.3	0	0.6	0	0.2	0
40.0 - 49.9	0	0.9	0	0.3	0	0	0
≥ 50	0	1.7	0	0.3	0	0	0
Dead:							
< bh	0	0	0	0	0	0	0
0.0 - 9.9	0	3.3	0	3.3	0	0	0
10.0 - 19.9	0	6.7	0	3.3	0	0	3.3
20.0 - 29.9	0	10.0	0	6.7	0	0	0
30.0 - 39.9	0	16.7	0	6.7	0	0	3.3
40.0 - 49.9	0	0	0	0	0	0	0
≥ 50.0	6.7	29.9	0	0	0	0	0
Bally Mountain							
Live:							
< bh	4.7	27.1	13.6	39.3	0.5	0	0
0.0 - 9.9	0.2	2.4	2.4	6.3	0.5	0	0
10.0 - 19.9	0.1	0	0	0.2	0.1	0	0
20.0 - 29.9	0	0	0	0	0	0	0
30.0 - 39.9	0.1	0	0	0.7	0	0	0
40.0 - 49.9	0.1	0.1	0	0.2	0	0	0
≥ 50	0.1	0.2	0.1	0.6	0	0	0
Dead:							
< bh	0	0	0	0	0	0	0
0.0 - 9.9	0	9.8	1.2	0	0	0	0
10.0 - 19.9	0	28.1	2.4	0	0	1.2	0
20.0 - 29.9	0	0	0	0	0	0	0
30.0 - 39.9	0	26.2	3.7	0	0	0	0
40.0 - 49.9	0	10.4	1.2	0	0	0	0
≥ 50.0	0	13.4	1.2	0	0	1.2	0

[1] Species codes: Pipo, *Pinus ponderosa*; Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pien, *Picea engelmannii*

[2] Breast height (1.37 m tall)

[3] Diameter class in centimeters

Logs

We measured 210 logs at Grizzly Bear Ridge. Logs ranged in length from 0.6 to 10.1 m (mean ± standard error = 5.0 ± 0.20). Density was 763 logs per hectare, of which 55 percent were identified as grand fir, 14 percent were western larch, almost 2 percent were ponderosa pine, and 28 percent could not be identified to species *(table 3)*. These logs totaled approximately 400 m^3 per hectare in volume, 3,800 m per hectare of linear log length, and 128,800 kg per hectare of mass. Slightly more than 11 percent of the ground was covered by logs. Most of the logs exhibited various indicators of advanced decomposition; 70 percent of all the logs were considered 30 percent sound or less and about 14 percent of the logs were considered at least 80 percent sound. Grand fir logs and those unidentified to species generally were less sound, and western larch and ponderosa pine logs were generally more sound.

Table 3—*Stem characteristics (mean and standard error) of logs by species at Grizzly Bear Ridge and Bally Mountain, northeastern Oregon.*

	Number (Stems ha^{-1})		Volume (m^3 ha^{-1})		Length (m ha^{-1})		Mass (kg ha^{-1})		Cover (Percent)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Grizzly Bear Ridge										
Pipo[1]	14.5	8.67	17.4	13.26	64.2	38.97	5582.9	4247.81	0.3	.24
Abgr	425.2	53.50	211.3	49.09	2104.2	325.97	67704.5	15726.72	6.2	1.08
Laoc	105.4	27.67	37.2	14.23	650.9	175.31	11925.1	4558.83	1.4	.40
Unknown	218.0	29.99	136.0	60.61	963.6	153.71	43564.8	19418.96	3.2	.88
Total	763.1	75.13	402.0	76.27	3783.0	404.36	128777.4	22433.49	11.2	1.40
Bally Mountain										
Abgr	51.3	6.64	63.5	27.03	844.1	112.07	20354.6	8659.69	1.3	0.31
Psme	6.7	2.19	2.2	1.09	86.4	30.63	694.9	349.71	0.1	.03
Laoc	1.3	.94	.02	.17	10.8	8.13	67.2	56.04	--[2]	--
Pico	0.7	.67	--	.01	5.3	5.32	--	4.48	--	--
Total	60.0	8.54	65.9	27.02	946.6	128.37	21134.2	8656.87	1.4	.31

[1] Species codes: Abgr, *Abies grandis*; Psme, *Pseudotsuga menziesii*; Laoc, *Larix occidentalis*; Pico, *Pinus contorta*; Pipo, *Pinus ponderosa*
[2] = negligible.

We calculated log characteristics for Bally Mountain based on 48 observed broken snags. Logs were between 4.9 and 50.6 m in length (mean ± standard error = 15.8 ± 0.80). Density was 60 logs per hectare, of which more than 85 percent were grand fir *(table 3)*. Density of Douglas-fir, western larch and lodgepole pine logs was low. Almost all of the log volume (65.9 m^3 per hectare), linear log length (almost 950 m per hectare), and mass (about 21,130 kg per hectare) was from grand fir. Only 1.4 percent of the ground was covered with logs. Large-end diameter of logs at Bally Mountain ranged from 7.1 to 152.4 cm; about 42 percent were less than 15.2 cm (6 inches), 34 percent were between 15.2 and 30.2 cm (6.0 to 11.9 inches), 19 percent were between 30.5 and 50.5 cm (12 and 19.9 inches), and 4 percent were larger than 51 cm (20 inches).

Associated Vegetation

We identified 49 species of shrubs, forbs, and graminoids in the diverse understory at Grizzly Bear Ridge. Common shrubs included *Symphoricarpos albus* (L.) Blake, *Spiraea betulifolia* Pall., *Rosa* species, *Vaccinium membranaceum* Dougl., and *Linnaea borealis* L. *(table 4)*. Common forbs were *Osmorhiza* species, *Galium triflorum* L., *Adenocaulon bicolor* Hook., and the fern *Pteridium aquilinum* (L.) Kuhn. *Calamagrostis rubescens* Buckl. was the most common grass.

Table 4—*Constancy and average cover of important plants at Grizzly Bear Ridge site, northeastern Oregon.*

	Constancy	Mean cover
	Percent	
Shrubs:		
Acer glabrum	26	11
Amelanchier alnifolia	29	8
Berberis repens	12	4
Ceanothus velutinus	9	1
Holodiscus discolor	15	5
Linnaea borealis	44	31
Lonicera ciliosa	9	5
Lonicera utahensis	41	14
Ribes lacustre	21	7
Ribes viscosissimum	38	7
Rosa nutkana/R. woodsii	59	21
Rubus idaeus	3	1
Rubus parviflorus	29	13
Salix scouleriana	9	7
Sambucus cerulea	3	1
Spiraea betulifolia	59	11
Symphoricarpos albus	71	32
Vaccinium membranaceum	53	22
Forbs:		
Achillea millefolium	6	15
Adenocaulon bicolor	32	23
Arnica cordifolia	32	5
Chimaphila umbellata	15	1
Clintonia uniflora	12	9
Disporum trachycarpum	3	1
Galium triflorum	47	14
Goodyera oblongifolia	3	1
Hedysarum boreale	9	10

	Constancy	Mean cover
	Percent	
Hieracium albiflorum	3	1
Mitella pentandra	6	28
Osmorhiza chilensis/O. occidentalis	56	8
Pedicularis racemosa	12	1
Pteridium aquilinum	29	48
Smilacina stellata	26	5
Thalictrum occidentale	15	1
Trifolium longipes	18	20
Valeriana sitchensis	29	15
Graminoids:		
Bromus carinatus	9	12
Calamagrostis rubescens	35	10
Carex geyeri	18	3
Carex rossii	12	3
Elymus glaucus	21	4

Discussion

Although currently dominated by grand fir, Grizzly Bear Ridge and Bally Mountain represent relatively dry, mid-elevation sites throughout the Blue Mountains of northeastern Oregon and southeastern Washington on which mixtures of conifers develop as a result of past disturbances. Under historical fire regimes, these sites were dominated by seral species such as ponderosa pine, western larch, and occasionally Douglas-fir that arose from infrequent stand-replacement fires and were maintained by frequent, low intensity, underburning (Agee 1993, Agee 1994, Hessburg and others 1994). Grand fir rarely dominated in these stands; thin bark and low-growing canopies were easily consumed by frequent wildfires that maintained these sites in open, park-like stands. The presence of wildfire was not uniform across the landscape, however, leading to a wide range in fire return intervals. As ponderosa pine and Douglas-fir matured and perhaps became stressed by climatic conditions, other disturbances such as root diseases, mechanical injuries such as lightning strikes, or insects may have caused mortality (Hessburg and others 1994). Douglas-fir tussock moth and western spruce budworm defoliation occurred in these mixed conifer stands periodically, especially as cohorts of grand fir and Douglas-fir reached into the mid- and upper canopy. Landscape-scale outbreaks probably occurred when less frequent wildfire allowed development of relatively uniform mid-canopy strata composed of grand fir and Douglas-fir. Dendrochronology records indicated outbreak episodes of similar periodicity dating back to the 1700s (Wickman and others 1993). Outbreaks likely were smaller in extent than the most recent outbreaks because the food base (primarily grand fir and Douglas-fir) was discontinuous (Hessburg and others 1994).

With the advent of fire suppression efforts shortly after the turn of the century, sites throughout the Blue Mountains like Grizzly Bear Ridge and Bally Mountain have undergone dramatic shifts in structure and composition. Fire exclusion allowed more shade-tolerant species such as grand fir and Douglas-fir to become established and to develop into dominant positions in the stand canopies. In addition, seral ponderosa pine and western larch were harvested to meet a growing demand for clear lumber for home construction, railroad ties, and shipping boxes for agricultural products (Oliver and others 1994, Wickman 1992). Scattered cut stumps at Bally

Mountain suggest past harvesting of individual stems four to five decades ago. Increased densities of grand fir and Douglas-fir provided a more uniformly distributed food base for insects and led to severe outbreaks of Douglas-fir tussock moth and western spruce budworm. At the onset of the Douglas-fir tussock moth outbreak, stands at Grizzly Bear Ridge probably were composed of multiple cohorts of grand fir and Douglas-fir in the overstory and understory, with remnant ponderosa pine and western larch extending above the upper continuous canopy. Our estimate of pre-outbreak density and basal area (about 830 trees and about 58 m^2 per hectare) suggests that these stands exceeded accepted guidelines of stocking levels for managed stands (Cochran and others 1994). Stocking levels at Bally Mountain were lower, presumably because some harvesting had occurred in prior decades, and only a single cohort of grand fir existed.

Our work at Grizzly Bear Ridge and Bally Mountain suggests that similar patterns of stand dynamics can result from defoliation events that have vastly different durations (2 or 3 years for Douglas-fir tussock moth and 8 to 10 years for western spruce budworm). In these two areas, severe Douglas-fir tussock moth and western spruce budworm defoliation of 40 to 90 percent of the crown weakened trees presumably stressed by competition for growing space and moisture. Fir engraver beetle (*Scolytus ventralis* LeConte) and Douglas-fir beetle (*Dendroctonus pseudotsuga*e Hopkins) and perhaps root diseases then followed at Grizzly Bear Ridge, eventually resulting in up to 75 percent mortality in grand fir and Douglas-fir (Wright and others 1984). We noted little additional mortality in our recent reassessment. In both areas, grand fir mortality exists as both standing dead snags and down logs. Our reassessment of structure at Grizzly Bear Ridge indicated over 70 stems per hectare were dead grand fir that remain standing 23 years after the onset of defoliation and mortality. We have no means of quantifying actual fall rates, but our observations of log wood condition suggest that the dead grand fir that remain standing likely are soft snags that will fall within a decade. Species composition of natural regeneration mirrors the live overstory composition at both locations; ponderosa pine, Douglas-fir, western larch, and Engelmann spruce remain in the overstory and occur as seedlings at Grizzly Bear Ridge, and ponderosa pine, Douglas-fir, western larch, and lodgepole pine remain in the overstory and occur as seedlings at Bally Mountain. We made no attempt to differentiate seedling cohorts by age at Grizzly Bear Ridge, although grand fir seedlings established before the outbreak and grand fir seedlings established immediately after the outbreak existed in about equal numbers 10 years after the outbreak (Wickman and others 1986). Our seedling height measurements indicated relatively rapid growth for the shade-intolerant ponderosa pine, and relatively slow growth for shade-tolerant Douglas-fir, and Engelmann spruce. Mean grand fir seedling height (about 47 cm) probably represents a mixture of two cohorts. Grand fir regeneration was abundant at both Grizzly Bear Ridge and Bally Mountain, setting the stage for the next defoliation event.

Although our description of logs is within normal ranges for similar sites in the Blue Mountains,[6] we urge caution in extrapolation. Our census at Grizzly Bear Ridge was based on relatively small plots and involved counting all logs with large-end diameters at least 7.6 cm. Stand composition at the time of the Douglas-fir tussock moth outbreak suggests that these stands were advanced in age with multiple cohorts of grand fir. Scattered hardwoods presumed to be aspen (*Populus tremuloides*

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[6] Unpublished data on file at the Pacific Northwest Research Station, LaGrande, Oreg.

[Michx.]), ponderosa pine, and western larch previously in the overstory had died. Thus, aspen, ponderosa pine, western larch, and grand fir logs already lay on the forest floor before the outbreak. Our census of logs at Grizzly Bear Ridge represents total accumulation of logs since the last stand-replacement fire. In contrast, our census at Bally Mountain was an indirect estimate of log density, based on estimated volume absent in standing snags. This method accounts only for the volume added to the forest floor since the western spruce budworm outbreak and thus underestimates total log resources. Differences in these two methods also account for differences in average log length. Perhaps the most significant aspect of the log survey was the large number of logs at Grizzly Bear Ridge that exhibited indicators of advanced decomposition. Measured logs were all aboveground, intact, and belonged to log structural class 1 and 2 (Bull and others 1997), yet a majority of the logs were characterized as 30 percent sound or less. This probably represents a high incidence of stem decay after defoliation-caused mortality. Relatively uniform height of broken grand fir snags at Bally Mountain also was a result of stem decay in combination with local storm patterns. Difference between species was expected because of different bole and dead crown architecture. Our sample size, however, prevented a rigorous test of this hypothesis.

Our work suggests that dead wood recruitment after a defoliator outbreak follows a pattern of relatively slow recruitment of snags and logs over a long period of time. This slow recruitment of dead wood probably provides a longer-term and more stable environment for many species of wildlife dependent on dying and dead wood compared to more rapid turnover of snags and logs after stand-replacement wildfire.

We described existing associated vegetation at Grizzly Bear Ridge to help characterize the site and to help identify successional pathways after disturbance. In general, plots at Grizzly Bear Ridge contained numerous species we believe are indicative of past disturbance, especially shade intolerant species such as *Holodiscus discolor* (Pursh) Maxim., *Lonicera utahensis* S. Wats., *Symphoricarpos albus*, *Adenocaulon bicolor*, *Hedysarum boreale* Nutt., *Valeriana sitchensis* Bong., *Bromus carinatus* Hook. and Arn., and *Elymus glaucus* Buckl. Surprisingly, the fern *Pteridium aquilinum* became well established and persistent. Collectively, this species composition describes a lush, early-successional community that might develop after complete overstory removal with little ground disturbance. Few of these plant species would persist after a wildfire. Diversity of shrubs and forbs was greater than would be expected after a stand-replacement fire (Johnson 1998) or in mature stands (Johnson and Clausnitzer 1992).

Our case studies at Grizzly Bear Ridge and Bally Mountain have provided unique opportunities to follow stand dynamics after severe insect defoliation and point to the effect of insect defoliation on long-term maintenance of dead wood resources. Despite annual visits during the first decade and frequent visits through 23 years at Grizzly Bear Ridge, our picture of stand dynamics in mixed conifer ecosystems in the Blue Mountains remains incomplete. A large number of stems remain standing at both sites; these stems will continue to fall as stem decay, wind, and cavity-forming wildlife species function to weaken the boles. Further work is needed to quantify fall rates by species and to quantify log dynamics after similar insect outbreaks. Seedlings will continue to grow, eventually developing a full canopy of susceptible host type. And in the absence of wildfire, both Grizzly Bear

Ridge and Bally Mountain will likely support a major insect outbreak, leading to defoliation and stand mortality.

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