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Natural Tree Regeneration and Coarse Woody Debris Dynamics After a Forest Fire in the Western Cascade Range

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Cover photos

Plot number 16 at 7 and 14 years after fire. At 7 years, there is abundant regeneration of *Pseudotsuga menziesii* under a canopy of snags. At 14 years, the snag canopy is thinning out owing to snag fall and fragmentation; tree, shrub, and herb regeneration mix but trees are the tallest elements.

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Abstract

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We monitored coarse woody debris dynamics and natural tree regeneration over a 14-year period after the 1991 Warner Creek Fire, a 3631-ha (8,972-ac) mixed-severity fire in the western Cascade Range of Oregon. Rates for tree mortality in the fire, postfire mortality, snag fall, and snag fragmentation all showed distinct patterns by tree diameter and species, with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) more likely to survive a fire, and to remain standing as a snag, than other common tree species. Natural seedling regeneration was abundant, rapid, and highly variable in space. Densities of seedlings >10 cm height at 14 years postfire ranged from 1,530 to 392,000 per ha. Seedling establishment was not concentrated in a single year, and did not appear to be limited by the abundant growth of shrubs. The simultaneous processes of mortality, snag fall, and tree regeneration increased the variety of many measures of forest structure. The singular event of the fire has increased the structural diversity of the landscape.

Keywords: Fire severity, monitoring, coarse woody debris, reforestation, snag recruitment, regeneration.

Summary

We monitored natural tree regeneration and coarse woody debris dynamics over 14 years following the 1991 Warner Creek Fire, a 3,631-ha (8,972-ac) mixed-severity fire in the western Cascade Range of Oregon. The results provide a detailed picture of the variety of natural postfire conditions in westside Cascade forests, and demonstrate how a single mixed-severity fire can increase variety in forest structures.

We studied 24 permanent plots representative of the burned area and its mix of fire severities, which ranged from 0.1 to 100 percent of prefire canopy killed. Plots spanned higher elevation forest dominated by *Abies amabilis* (Douglas ex Louden) Douglas ex Forbes and *Tsuga mertensiana* (Bong.) Carrière, and lower elevation forest dominated by *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg. Tree mortality resulting from the fire was strongly related to diameter and species, with larger diameter trees and *P. menziesii* more likely to survive. Tree mortality continued in the years after the fire. Forty-four percent of trees alive at 1 year postfire were dead at 6 to 7 years postfire, and 55 percent at 14 years postfire. This postfire mortality rate was higher in plots with higher initial fire severity. Much of the new snag volume quickly transferred to the ground via snag fall and fragmentation. Small snags, and *A. amabilis* snags, were more likely to fall. Larger snags were more likely to fragment.

Natural seedling regeneration was abundant, and highly variable in space. Densities of seedlings >10 cm height at 14 years postfire ranged from 1,670 to 392,000 per ha in the higher elevation zone, and from 1,530 to 47,500 per ha in the lower zone. New seedlings were observed over all study visits, in patterns demonstrating that establishment was not concentrated in a single year. The growth of shrubs was abundant but did not appear to be limiting tree regeneration.

The mixed-severity fire, followed by variable mortality, snag fall, and tree regeneration, led to an increase in variability, among plots, of several metrics of forest structure. The prominence of *P. menziesii* among both survivors and new seedlings gave some stands a more distinctly two-cohort structure, which may have the potential to develop old-growth features relatively quickly. The fire has increased structural diversity on the landscape, a legacy that should persist as these stands develop.

Introduction

Fire is a defining element in the ecology of moist, productive forests of the Pacific Northwest dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). In these forests, which are common in Oregon and Washington west of the Cascade Crest, and which stretch into portions of British Columbia and California, high-severity fires are a major initiator of new forest stands, while less severe fires contribute to the development of multicohort stands (Agee 1996, Oliver and Larson 1996). Tree mortality caused by fire creates snags, which are crucial as wildlife habitat (Hutto 2006), but are not a permanent fixture of the landscape, because they decay and fall.

One current theme in forest management is emulating the range of historical conditions fostered by natural fire and regeneration (e.g., Halpern et al. 1999). In particular, concepts about the effects of disturbance have played a role in plans to promote the development of "mature" or "old-growth" forest structures (Zenner 2005), for example, with thinning (Comfort et al. 2010). But these efforts, as well as general scientific understanding, have been stymied by a scarcity of clearly quantified, direct field observations of natural forest establishment and of snag creation and decay after fire.

When the Warner Creek Fire burned in the western Cascade Range of Oregon in October 1991, the area became a focal point for debate over forest management in the zone of the northern spotted owl (*Strix occidentalis caurina*). A 1700-ha portion of the burn was set aside as a "natural succession area," to be allowed to develop with little human interference (USDA FS 1993). This report is one outcome of that decision. It documents natural changes at the fire site from 1991 to 2005. The results to date serve as a detailed test case to evaluate several existing notions about forest regeneration and coarse woody debris (CWD) dynamics. They should also provide land managers with an example of the range of forest structures and regeneration trajectories that might be expected in the wake of a large, mixed-severity fire.

In this region, natural regeneration of forests after disturbance has been a subject of debate among foresters and ecologists. Most of the discussion has concerned regeneration after harvest rather than fire. Although it is not clear whether these two processes are identical, discussion of them has occasionally been conflated, so we consider both as background to our study. In the first half of the 20th century, natural regeneration by seed was the standard method of regeneration after harvest (Isaac 1938), but early surveys of harvested land gave the technique a reputation as being unreliable for the purposes of silviculture. Isaac (1938) reported that 20 percent of harvested areas in the Northwest had completely failed to regenerate, while another 50 percent had regenerated inadequately. Planting nursery-grown seedlings became standard practice in harvested areas and is still strongly encouraged by Oregon law, which requires the state forester to approve any plan for natural reforestation (Oregon Revised Statutes 527.745). Since the 1960s, regeneration research in this region has focused on optimizing the survival and growth of planted seedlings, and few quantified descriptions of natural regeneration after harvest have been published. One study showed densities of naturally regenerating *P. menziesii* at >800 trees/ha 40 years after harvest (Miller et al. 1993). In general, natural regeneration after harvest was considered unreliable owing to unpredictable seed source and the presence of competing vegetation (Minore and Laacke 1992, Tappeiner et al. 1997b).

In this region, preconceptions about the speed and density of natural regeneration after fire have not been tested against direct observations.

For some, these expectations extended beyond harvested sites to burned areas. After the Biscuit Fire in southwestern Oregon, Sessions et al. (2004) warned that "without planting and subsequent shrub control… it could take more than 100 years to even establish conifer forests." Some "retrospective studies" have echoed this idea of slow or sparse regeneration after fire. These works examine current-day stands and project their structure backward through time, suggesting that at some sites, establishment of *P. menziesii* can span a century or more (Franklin and Hemstrom 1981, Huff 1995, Tappeiner et al. 1997a), with trees growing in the open at low densities (e.g. about 100 trees/ha, Tappeiner et al. 1997a).

In contrast, direct field observations of natural regeneration after fire show more abundant regeneration. Such studies have been accumulating from all over the region since the 1970s, but to our knowledge have not been synthesized, as we do in figure 1. These studies show *P. menziesii* establishing in considerable densities (often 1,000 to 5,000 trees/ha) in a few decades after disturbance, over a wide range of Pacific Northwest forest types and climate zones. Similar numbers can be found in at least one retrospective study (Winter et al. 2002). It is unclear if the slow, sparse patterns from some retrospective studies are an ecologically distinct mode of regeneration, or an artifact of method, as Tepley (2010) has suggested.

Questions also persist about the mechanics of seedling establishment, in particular its continuity and the importance of fortuitous seed years. In a study at the Warner Creek Fire site unrelated to ours, Larson and Franklin (2005) found abundant regeneration 11 years after the fire, except in low-fire-severity areas, and attribute it to a bountiful seed year and a legacy of viable seeds that survived the fire. This suggests generally that the regeneration occurred in a single pulse. A different postfire study, from northern California, shows steady ongoing establishment over more than a decade (Shatford et al. 2007). Another issue is the role of potentially competing vegetation. Field experiments in harvested areas have suggested that the

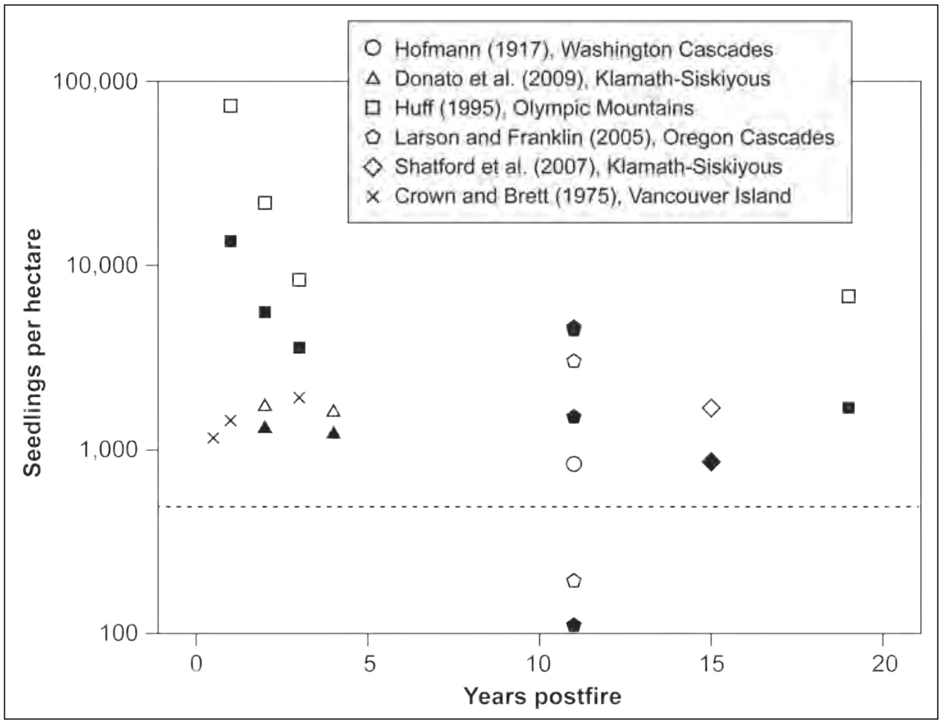

Figure 1—Literature review of direct observations of natural regeneration after fire. Open symbols represent seedlings of any species, while filled symbols represent *Pseudotsuga menziesii* only. The reference line represents a token silvicultural standard for regeneration, 494 seedlings per hectare (Oregon Revised Statutes 527.745).

simultaneous regeneration of shrubs alongside seedlings can hinder survival and growth of planted seedlings (e.g., Stein 1999). However, Shatford et al. (2007) found no interference. It is unclear if these divergent results arise from chance or something substantially different about the postfire and postharvest environments.

Less controversial than natural regeneration, but equally important to forest function, is the fate of coarse woody debris created in the fire. Federal land management agency biologists try to create or maintain natural snag densities using historical guidance provided by information systems such as DecAid (Marcot et al. 2010), and predictive models like the Coarse Wood Dynamics Model (CWDM) (Mellen and Ager 2002). Snag abundance and longevity after fire are influenced by several key factors, including the types of trees most likely to perish and become snags, and the length of time those snags remain standing, without breaking or falling down. Other studies have suggested strong effects of diameter and species; in particular, *P. menziesii* appears to be considerably more resistant to death by fire (Ryan and Reinhardt 1988), and, once converted to a snag, more resistant to falling (Parish et al. 2010). The expectations of managers, and realism of models like CWDM, could be improved with detailed data about tree mortality, snag fall, and snag fragmentation from a postfire landscape.

The Warner Creek area was a promising place to study CWD dynamics and tree regeneration because the fire spanned two major forest elevation zones and involved a range of fire severities. The central region of the western Cascades is characterized as a mixed-severity fire regime, in which a single fire can create a landscape mixture of higher and lower severity patches or stands (Tepley 2010). The Warner Creek Fire clearly illustrated this pattern. Added to this spatial variety in severity was some variety in the prefire age, stature, and composition of the forest stands, and some potential variety in postfire phenomena such as regeneration. These multiplying contingencies might add to the variation in forest structure on the landscape, or alternatively, the main structural effect of the fire might be one of simplification.

Our study asked:

1. What were the rates and patterns of fire-related tree mortality, snag fall, and snag fragmentation?
2. What were the rates and patterns of postfire tree establishment and growth? Was establishment momentary or ongoing? Was tree regeneration negatively affected by competing vegetation?
3. How did the structure of Warner Creek forests change from prefire conditions to 14 years postfire? Are postfire stands more or less variable in structure than prefire ones?

Although basic questions of forest ecology provide the structure of this work, the pragmatic concerns of land managers inform the way the results are reported. Many graphs and tables present results in relatively detailed, unreduced form—more detailed than is strictly necessary for the testing of hypotheses—so that readers can see the true range of natural variation and extract the information most relevant to them.

Methods

Study Area and the Fire Event

The Warner Creek Fire burned 3631 ha of land on October 10–23, 1991, in the Cascade Range near the town of Oakridge, Oregon, approximately 43° 42' N., 122° 12' W. (USDA FS 1993). Elevations in the burned area range from roughly 700 to 1800 m. Physiography is diverse, with broad valley floors; steep, dissected and straight slopes; bowl-shaped headwalls; and broad ridgelines. The climate displays transitions from maritime to Mediterranean and produces wet, mild winters and warm, dry summers. Approximately 90 percent of precipitation (120 to 200 cm/yr) occurs October though March, mostly as rain, with snow accumulating at higher elevations. East winds can occur during the dry months of summer and early fall (Gedalof et al. 2005, Kushla and Ripple 1997).

Forest stands in the burned area can be divided into two zones based on elevation and major tree species. The "western hemlock zone" (<1500 m) is composed mostly of the "western hemlock series" (McCain and Diaz 2002), where *Tsuga heterophylla* (Raf.) Sarg., *Pseudotsuga menziesii*, and *Thuja plicata* Donn ex D. Don dominate the tree layer. Some dryer sites in this zone are of the "Douglas-fir series" (McCain and Diaz 2002), where the tree layer is dominated by *P. menziesii* in association with *Arbutus menziesii* Pursh and *Castanopsis chrysophylla* (Douglas ex Hook) A. DC. The "Pacific silver fir zone" (>1500 m) is composed of forests of the "Pacific silver fir series" and "mountain hemlock series" (McCain and Diaz 2002), where the canopy is dominated by *Abies amabilis* (Douglas ex Loudon) Douglas ex Forbes and *Tsuga mertensiana* (Bong.) Carrière, respectively, in association with *P. menziesii*, *Abies procera* Rehder, and *Chamaecyparis nootkatensis* (D. Don) Spach.

The fire burned in a patchwork of severities ranging from near 0 percent canopy killed to 100 percent crown consumption, according to a map of live cover created from aerial photos in the weeks after the fire (Bailey 1991). About 1700 ha were set aside as a "natural succession area" where postfire processes were to be largely undisturbed by human activity (USDA FS 1993). Our study plots were located in this area. However, several treatments applied from aircraft may have affected our sites. About 750 ha out of the total burn area of 3631 ha were fertilized, and about 1200 ha out of 3631 ha were seeded with the annual grasses *Lolium annuum* (Bernh.) and *Hordeum vulgare* (L.) (USDA FS 1992). *L. annuum* was noted in 5 of our 24 plots at 1 year postfire, but had largely disappeared by 6–7 years postfire.

Our sampling objective was to survey ecological responses across a set of plots representative of the mix of fire severities in the burned area.

Fire Severities and Study Plots

Our sampling objective was to survey ecological responses across a set of plots representative of the mix of fire severities in the burned area. Fire severity is an inconsistently applied but unavoidable concept in fire ecology (Keeley 2009). There is a need to provide an index of significance of a fire, but because actual measurements of energy flux, or "fire intensity," are usually impractical, fire severity describes an observed change in matter—for example, the percentage of canopy scorched or removed, observed via satellite or aerial photo (Odion et al. 2004), the percentage of stems or basal area killed (Larson and Franklin 2005), or the visible effect on soil (Smucker et al. 2005). We chose to use a measure of canopy damage because this could be evaluated both from the air and the ground.

Our initial estimate of fire severity came from a November 1991 map of percentage live tree canopy cover created from post-fire aerial photos (Bailey 1991). In these dense forests, it was reasonable to assume that prefire live canopy cover was near 100 percent, so we subtracted live cover after the fire from 100 percent to calculate a new map of percentage cover killed by the fire. We selected prospective areas for plots based on this map and located plots randomly within those areas. Once plots had been established, we evaluated fire severity within each one by examining the canopies of all trees individually, from the ground, as described in more detail under "Stem Survey in 1992," below.

The distribution of fire severities across the Warner Creek burn and across our study plots are compared in figure 2. There is a general agreement in the "U" shape of the lines. The biggest divergence is among the lowest fire severities, where we surveyed more low-severity (10 to 30 percent canopy killed) plots, and fewer

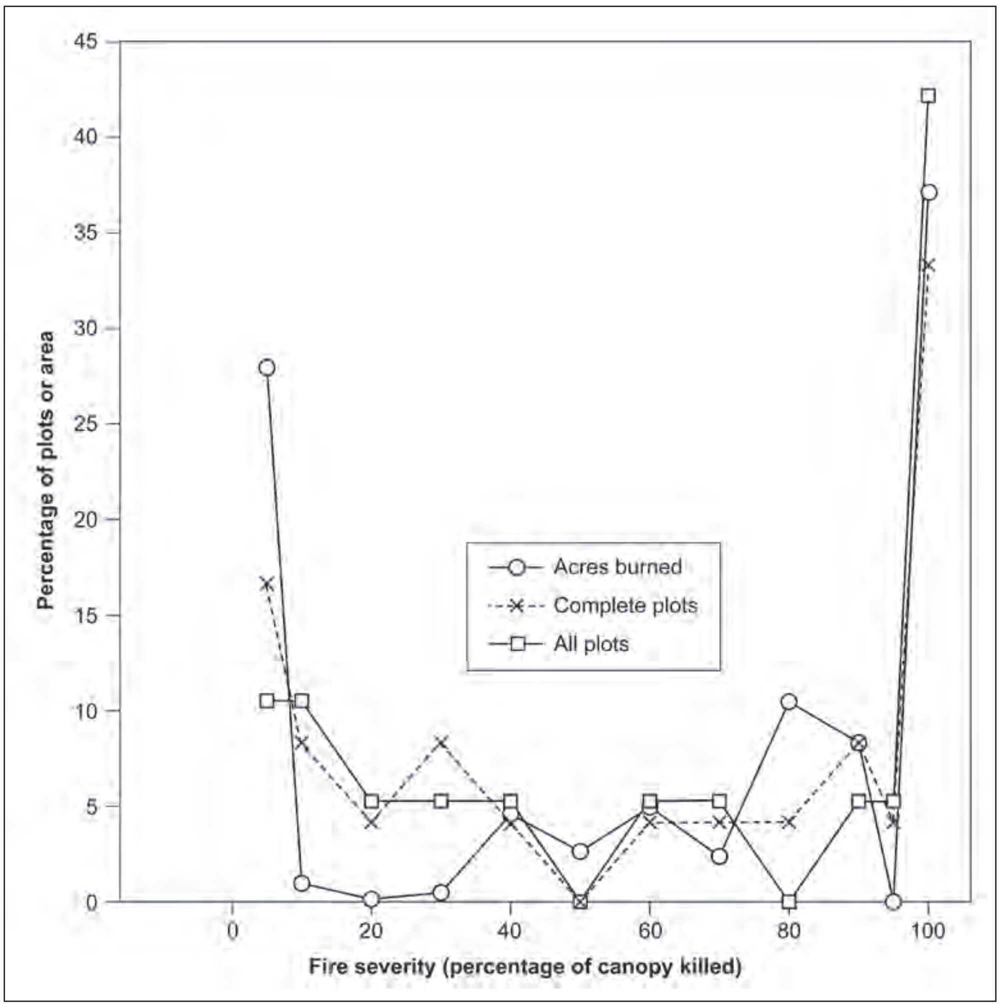

Figure 2—Distribution of fire severity in the burned area and in our samples. "Acres burned" comes from an aerial photo survey completed shortly after the fire (Bailey 1991). "Complete plots" have all survey data for all study years. "All plots" are all plots in table 1, complete or not.

very low severity (<10 percent killed) plots than the aerial photo map displayed. However, estimating very low fire severities using aerial photos is difficult. We conclude our survey is reasonably representative of the entire burned area, and acceptable given the nature of field research and the difficulty of the terrain.

We installed 24 plots: 13 in the Pacific silver fir zone, and 11 in the western hemlock zone (table 1). Each study plot was a rectangle, 30 by 24 m, oriented with the 30-m sides roughly parallel to the slope. This 720-m^2 area was divided into a grid of 80 fixed 3 by 3 m cells. Once established, we visited each study plot three times, first from June through September 1992 (1 year postfire), next from June through September 1997 or 1998 (6 or 7 years postfire), and finally from June

Table 1—Plots studied

Plot no.	Fire severity[a]	Forest series	Prefire age[b]	Elevation	Aspect	Slope	Years trees surveyed	Years seedlings surveyed
	Percent		*Years*	*Meters*	*Degrees*	*Percent*		
Pacific silver fir zone:								
2	0.1	Pacific silver fir	>200	1436	218	55	1992, 1997–1998	1992, 1997–1998
5	35.9	Mountain hemlock	>200	1672	342	26	1992, 1997–1998, 2005	1992, 1997–1998, 2005
6	100	Mountain hemlock	>200	1652	316	33	1992, 1997–1998, 2005	1992, 1997–1998, 2005
7	100	Pacific silver fir	>200	1573	170	66	1992, 1997–1998, 2005	1992, 1997–1998, 2005
9	85.9	Pacific silver fir	100–200	1539	130	35	1992, 1997–1998, 2005	1992, 1997–1998, 2005
10	13.7	Pacific silver fir	>200	1506	24	30	1992, 1997–1998, 2005	1992, 1997–1998, 2005
11	100	Pacific silver fir	100–200	1603	20	55	1992, 1997–1998, 2005	1992, 1997–1998, 2005
12	58.3	Pacific silver fir	>200	1561	76	55	1992, 1997–1998, 2005	1992, 1997–1998, 2005
13	100	Pacific silver fir	100–200	1487	222	70	1992, 1997–1998, 2005	1992, 1997–1998, 2005
14	5.7	Pacific silver fir	100–200	1567	126	65	1992, 1997–1998	1992, 1997–1998
23	77.7	Pacific silver fir	100–200	1686	50	80	1992, 1997–1998, 2005	1997–1998, 2005
24	96.2	Mountain hemlock	50–99	1713	310	42	1992, 1997–1998, 2005	1992, 1997–1998, 2005
25	85.2	Pacific silver fir	>200	1524	340	5	1992, 1997–1998, 2005	1997–1998, 2005
Western hemlock zone:								
1	100	Western hemlock	>200	1329	182	57	1992, 1997–1998, 2005	1992, 1997–1998, 2005
3	10.9	Western hemlock	>200	945	58	78	1992, 1997–1998, 2005	1992, 1997–1998, 2005
4	1.5	Western hemlock	>200	1032	3	65	1992, 1997–1998, 2005	1992, 1997–1998, 2005
15	18.8	Douglas-fir	>200	1219	235	49	1992, 1997–1998, 2005	1992, 1997–1998, 2005
16	100	Western hemlock	>200	1170	240	60	1992, 1997–1998, 2005	1992, 1997–1998, 2005
17	28.6	Douglas-fir	50–99	981	200	63	1992, 1997–1998, 2005	1992, 1997–1998, 2005
18	65.5	Western hemlock	>200	896	210	19	1992, 1997–1998, 2005	1992, 1997–1998, 2005
19	27.9	Western hemlock	>200	829	320	50	1992	1992
20	6.4	Western hemlock	50–99	853	240	53	1992, 1997–1998, 2005	1992, 1997–1998, 2005
21	100	Douglas-fir	100–200	1237	164	53	1992, 1997–1998, 2005	1992, 1997–1998, 2005
22	100	Douglas-fir	100–200	1198	158	30	1992, 1997–1998, 2005	1992, 1997–1998, 2005

[a] Fire severity = the percentage of canopy killed, evaluated from ground observations at 1 year postfire.
[b] Prefire age = the prefire age of dominant trees.

through September 2005 (14 years postfire). A few plots were not resampled in 1997/1998 and 2005 owing to difficult field conditions (see table 1).

Stem Survey in 1992

A survey of all stems (standing trees, live or dead) provided information about tree and snag structure, tree mortality, snag fall, and snag fragmentation. In 1992, we recorded the following information for every stem >2.5 cm diameter at breast height (DBH) in each grid cell in each plot: species, live or dead status, diameter, and by extension, diameter classes frequently used within the Forest Service: saplings and poles combined (diameter 7.7 to 22.8 cm), small (22.9 to 53.2 cm), medium (53.3 to 81.2), large (81.3 to 121.8 cm), and giant (>121.9 cm). We assigned each snag a decay class from 1 to 5, with class 1 being recently dead and class 5 being almost completely decayed (Cline et al. 1980). We assumed that class 1 snags found in 1992 were casualties of the Warner Creek Fire, which allowed us to reconstruct the prefire tree and snag structure of each plot.

Not all trees and snags were evaluated for height during the 1992 visit. We measured the height of the first three trees and snags encountered of each species in each diameter class per plot using a clinometer and distance tape. We estimated the volume of snags by assuming they were shaped as the frustum of a cone, with taper constants for each species taken from a sample of recently fallen snags. We estimated the volumes of snags that were not measured for height using average observed snag heights from each diameter and decay class.

During this visit, we also evaluated canopy condition for every stem that had a canopy (live, or snag decay class 1), by recording the proportions of canopy that were live, scorched (dead, but needles still visible), or consumed (dead, with needles consumed). It was not unusual for a single tree canopy to display more than one condition. We used this survey of canopy condition for individual trees to calculate a measurement of fire severity for each plot, averaging the percentage of dead canopy across all the trees in each plot, and weighting by stem basal area.

Stem Surveys in 1997/1998 and 2005

We repeated this stem survey during a second set of field visits (spread over 1997/1998) and a third (in 2005). On these visits we relocated specific individual stems with the help of the 80-cell grid, diameter measurements, and 1992 field notes. On these second and third visits, we noted any change in the status (live/dead, decay class, height, standing or fallen) of each stem. About 8 percent of 1992's stems (mostly small-diameter snags) could not be relocated in 1997/1998;

in all likelihood they had fallen and become part of small-diameter debris on the forest floor. During the 1997/1998 and 2005 field visits, we measured heights of nearly all standing trees and snags with a laser rangefinder. We ignored height decreases of <10 percent from 1992 to 1997/1998, because they may have resulted from the change in height measurement method. We did not record canopy condition in 1997/1998 or 2005.

Definition of fallen and fragmented snags—

When an entire snag, including its root wad, toppled to the ground between two visits, we characterized the snag as "fallen." When some part of the snag remained standing between two study visits, but decreased in height by ≥10 percent, we characterized the snag as "fragmented."

Coarse woody debris on the ground—

To measure log volume on the ground, we inventoried all logs >7.6 cm diameter in each 3 by 3 m cell in each plot in 1992, 1997/1998, and 2005. This inventory recorded the lengths of logs in five Forest Service diameter classes mentioned earlier. We classified each log by decay class (Sollins 1982), with class 1 being recently dead and class 5 almost completely decayed. Within each plot, cell, diameter class, and decay class group, we calculated the volume of logs by assuming that logs were cylinders and applying the observed length and the quadratic midpoint diameter for the diameter class. Taper was assumed to be negligible as log length was only being measured within the relatively small 3 by 3 m cell. We estimated the prefire (1991) volume of logs as the 1992 log volume, minus the 1992 volume of logs with decay class 1, which we assumed had been killed and felled by the fire.

Regeneration cover survey—

To make an assessment of the abundance of regenerating vegetation, we evaluated cover in eight 3 by 3 m cells in each plot. In 1992 and 1997/1998 we recorded the total cover of shrubs, tree seedlings, and herbs in each cell without reference to species. We use the word "herbs" in a general sense to also include ferns and mosses. In 2005, we recorded those totals, but in addition recorded a cover value for each species in each cell, and a maximum height for the most abundant species of each life form (seedling, herb, or shrub). Later, we summarized these cover values and heights in several ways. We averaged cover values for each life form among cells to create a cover value for each life form in each plot. We calculated the maximum height for each life form in each cell, and then averaged those heights to create a representative height for each life form in each plot.

“Subplot” and “cell” surveys of regeneration density—
To reduce the risk of trampling tiny tree seedlings, we did not initially study tree establishment in the 720-m^2 plot area. Instead, we established eight circular “seedling subplots,” each with a radius of 1 m (area 3.14 m^2), in a standard geometrical pattern just outside the 720-m^2 plot. In 1992, 1997/1998, and 2005, we visited each seedling subplot and counted all seedlings. We tallied seedlings by species in height classes: <1 cm, 1 to 10 cm, 11 to 30 cm, 31 to 100 cm, and 101 to 300 cm. Seedling species were identified using keys in Franklin (1961). *Abies* species are difficult to distinguish when they first germinate, and some error in identifying *Abies* probably occurred.

By 2005, the vigorous growth of individual trees and shrubs was, in places, overwhelming the small 3.14 m^2 seedling subplots. Any future monitoring would require a larger subplot. Also, the vigor of the regrowth suggested that our concerns about trampling had been overblown. Accordingly, in 2005, we also counted seedlings in eight of the “cells” composing the larger tree plot. These were the same 9-m^2 cells where we evaluated shrub and herb cover. This “cell survey” of seedlings uses a total area almost three times as large as the “subplot survey.” However, to keep labor to a manageable level, in the cell survey we only counted seedlings >10 cm in height.

Sample sizes and calculations—
Our primary unit of study is the “plot:” a defined area that is sampled in some detail, mostly for the purpose of creating summary statistics (such as tree density per area, snag volume per area, etc.) that can be compared among plots. Our sample has 24 plots. Because difficult field conditions made some surveys impossible in 1997/1998 and 2005, some surveys were missed (table 1), so effective sample sizes range from 19 to 24 when the vegetation zones are examined together, 9 to 13 for the Pacific silver fir zone, and 10 to 11 for the western hemlock zone.

For some results, our data offers another sampling perspective with larger sample sizes. Because our set of plots is arguably representative of the burned area (fig. 2), the complete collection of live and dead trees that make up those plots should also be representative of the trees in the burned area. We used this sample of >1,500 stems, without reference to plot, to calculate tree mortality proportions, snag fall proportions, and snag fragmentation proportions for species and diameter classes. Confidence limits for these proportions were calculated using the normal approximation of the binomial parameter. We then converted these proportions to annualized mortality, snag fall, and fragmentation rates for easier comparison with the literature. Because the second sample period (1997/1998) spanned 2 years, relevant annualized rate calculations used a midpoint year value of 1997.5.

Results

Overall Trends

Several overarching results apparent in the survey data are illustrated in figure 3. The fire is the immediate cause of widespread, but not complete, mortality among trees > 2.5 cm DBH, visible as a sharp declining line between 0 and 1 years postfire (top row of the figure). This mortality is also reflected in a corresponding increase in snag density (top row) and volume (second row). Between 1 and 6–7 years postfire, there is some additional mortality, visible as a decrease in live tree density, and an increase in snag volume. Despite the increase in snag volume, by 6–7 years postfire, snag density is actually declining, and log volume increasing, as snags created by the fire fall to the ground. This increase in log volume continues through 14 years postfire. Meanwhile, the ground layer is becoming occupied with herbs, shrubs, and thousands of new tree seedlings. Seedlings (bottom row of fig. 3) established and grew in such numbers that by 14 years postfire many have DBH's > 2.5 cm and are showing up as increases in live tree density (in the top row). The abundance of regeneration is also visible in appendix 1, which photographically compares three plots between 6–7 and 14 years postfire.

The clarity of these trends in averages obscures an intriguing variety in the unsummarized plot values for those same variables, notable in figure 4. When the standard deviations of key structural measurements are plotted across time, as in figure 5, it suggests that the Warner landscape at 14 years postfire is not merely different than its prefire state, it is notably more variable. Appendix 2 photographically illustrates an assortment of regeneration and canopy conditions at 14 years postfire.

In the following sections, we explore each of these trends in more detail before returning to investigate the increase in structural variability suggested by figures 4 and 5.

Live Tree Populations and Mortality in the Fire

Live tree densities are listed by time period in table 2. Before the fire, the majority of living stems in Pacific silver fir zone plots were smaller diameter (mean 20.5 cm DBH) *Abies amabilis* or *Tsuga mertensiana* with an occasional *P. menziesii* or *Abies procera* of larger stature (42 to 141 cm DBH). In the western hemlock zone, the majority of stems were larger *P. menziesii* (mean DBH 60.5 cm, range 36 to 157 cm), with some smaller diameter *Thuja plicata* and *Tsuga heterophylla* mixed in.

Only 28 percent of trees >2.5 cm DBH alive before the autumn 1991 fire were still living in autumn 1992. Survival was strongly associated with tree diameter, as figure 6 (top left panel) shows. There was a significant correlation between diameter class midpoint and survival rate (Pearson correlation = 0.83, p = 0.01), with

Table 2—Live trees of sapling size (2.5 cm DBH) or above in the Warner Creek fire area

Species	Years after fire	Density Mean	Density Minimum	Density Maximum	Diameter at breast height Mean	Diameter at breast height Minimum	Diameter at breast height Maximum	Frequency[a]
		- - - Trees/ha - - -			- - - Centimeters - - -			
Pacific silver fir zone (n = 11 plots):								
Abies amabilis	0	474	14	1,514	20.5	8.7	39.1	11
	1	76	0	222	26.0	14.4	55.6	6
	6–7	22	0	125	9.7	4.2	13.7	3
	14	37	0	194	12.8	5.5	19.8	3
Abies procera	0	19	0	56	78.1	42.5	111.8	6
	1	11	0	42	80.1	55.9	111.8	5
	6–7	5	0	28	73.0	69.9	76.2	2
	14	15	0	125	33.4	5.1	72.4	3
Pseudotsuga menziesii	0	35	0	194	99.4	49.2	141.4	4
	1	5	0	42	140.5	139.7	141.4	2
	6–7	5	0	42	140.5	139.7	141.4	2
	14	254	0	1,542	28.3	5.1	141.4	6
Tsuga mertensiana	0	107	0	403	37.7	21.6	68.6	8
	1	37	0	292	44.6	12.1	104.1	5
	6–7	16	0	153	22.2	7.6	36.7	2
	14	15	0	139	23.7	10.2	37.3	2
All species[b]	0	665	208	1,778	30.4	13.7	54.9	11
	1	133	0	431	43.1	26.2	66.0	7
	6–7	49	0	222	62.6	32.3	139.7	4
	14	323	0	1,542	14.9	5.1	42.6	8
Western hemlock zone (n = 10 plots):								
Pseudotsuga menziesii	0	260	28	486	60.5	35.9	157.5	10
	1	124	0	319	71.5	46.8	157.5	7
	6–7	106	0	347	75.1	47.4	157.5	6
	14	813	28	4,458	45.7	5.1	157.5	10
Thuja plicata	0	49	0	222	40.5	19.1	85.9	5
	1	11	0	69	62.5	38.1	85.9	3
	6–7	7	0	42	65.2	38.1	96.5	3
	14	7	0	42	64.9	38.1	95.7	3
Tsuga heterophylla	0	69	0	222	27.4	14.2	53.3	7
	1	6	0	28	44.0	20.3	76.2	3
	6–7	3	0	14	45.7	15.2	76.2	2
	14	4	0	14	31.3	5.1	73.7	3
All species[c]	0	422	125	583	44.1	28.1	94.5	10
	1	151	0	319	59.7	45.0	102.6	7
	6–7	121	0	347	63.7	47.4	113.5	6
	14	829	83	4,472	39.1	5.1	112.6	10

[a] Frequency = the number of plots on which the species was observed.

[b] "All species" for the Pacific silver fir zone include less common species *Abies grandis, Calocedrus decurrens, Chamaecyparis nootkatensis,* and *Pinus monticola*.

[c] "All species" for the western hemlock zone include less common species *Abies grandis, Acer macrophyllum, Calocedrus decurrens, Cornus nuttallii,* and *Taxus brevifolia*.

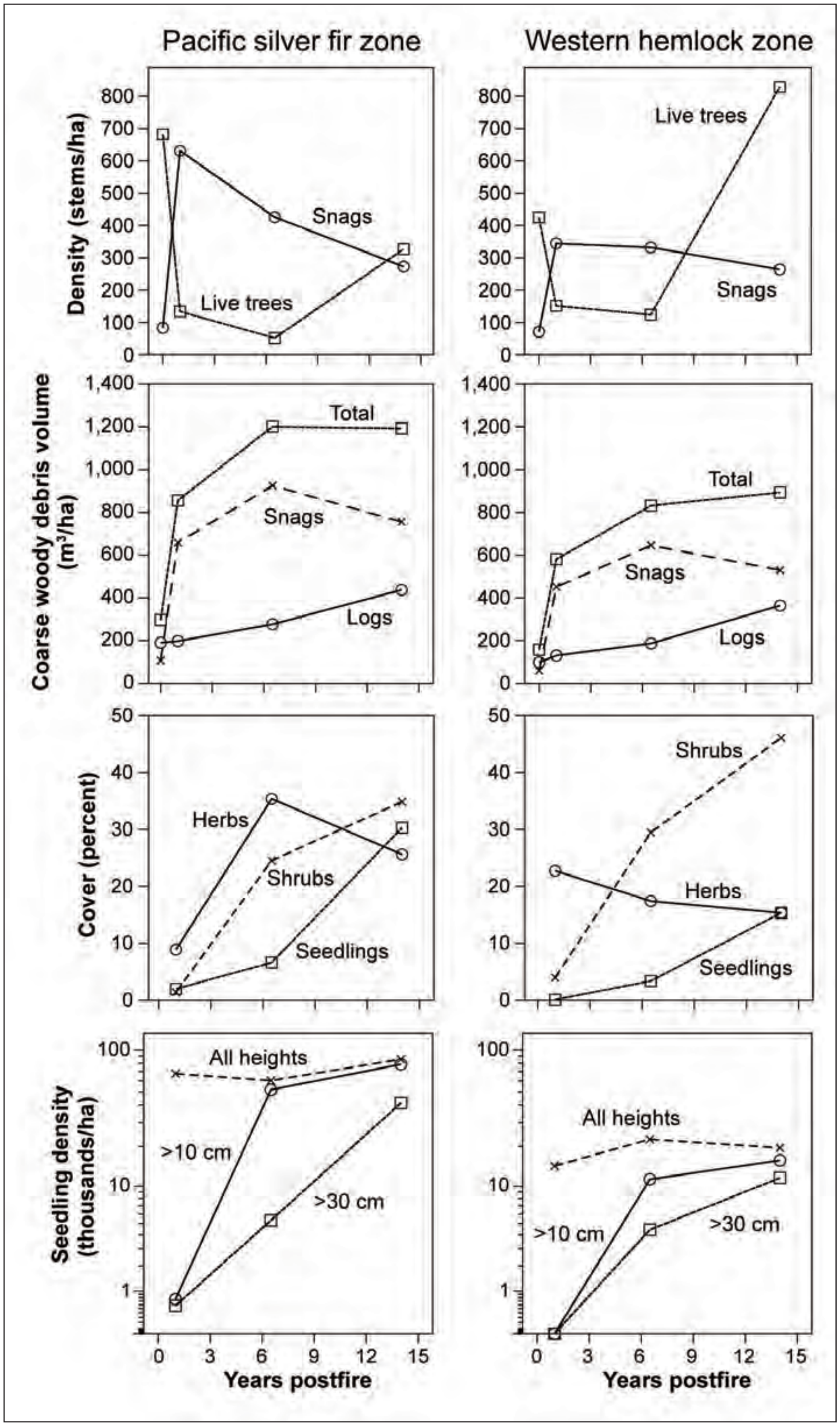

Figure 3—Mean values for key stand metrics compared to time since the fire. Each point represents the mean of plots for that vegetation zone for that study period. Top row: mean live and dead stem densities per plot. Second row: mean snag, log, and total coarse woody debris volume per plot. Third row: mean cover of regenerating herbs, shrubs, and tree seedlings per plot. Fourth row: Mean densities of regenerating tree seedlings per plot, in three height classes: all sizes, >10 cm high, and >30 high. Seedling densities are in **thousands** per hectare. N = 11 plots for Pacific silver fir zone, 10 plots for western hemlock zone; for seedling density panel, N = 9 plots for Pacific silver fir zone, 10 for western hemlock zone.

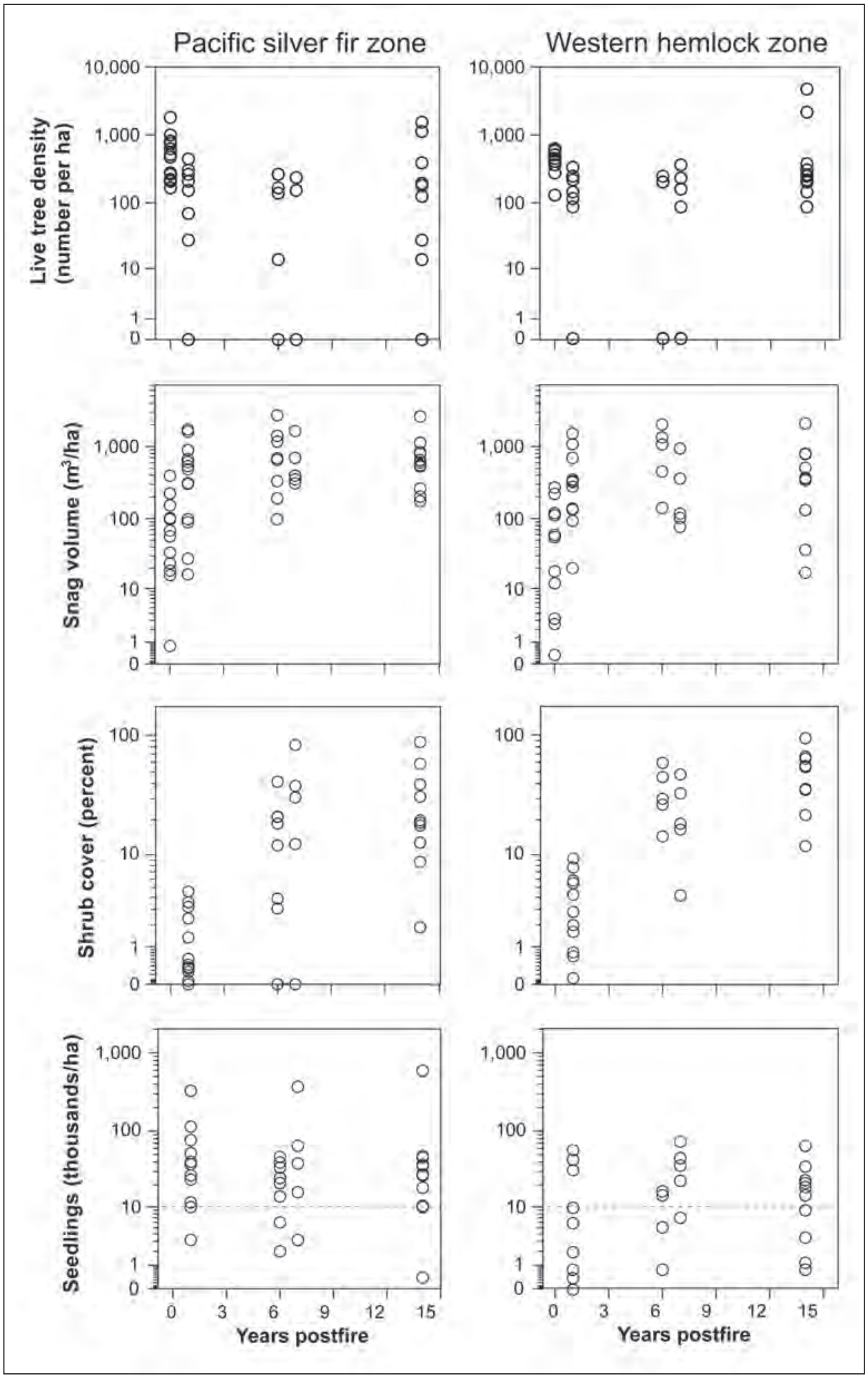

Figure 4—Raw data for four key stand metrics: live tree density (trees >2.5 cm diameter at breast height), snag volume, shrub cover, and seedling density. Each circle represents the observed value for one plot in one study period. All available plots used.

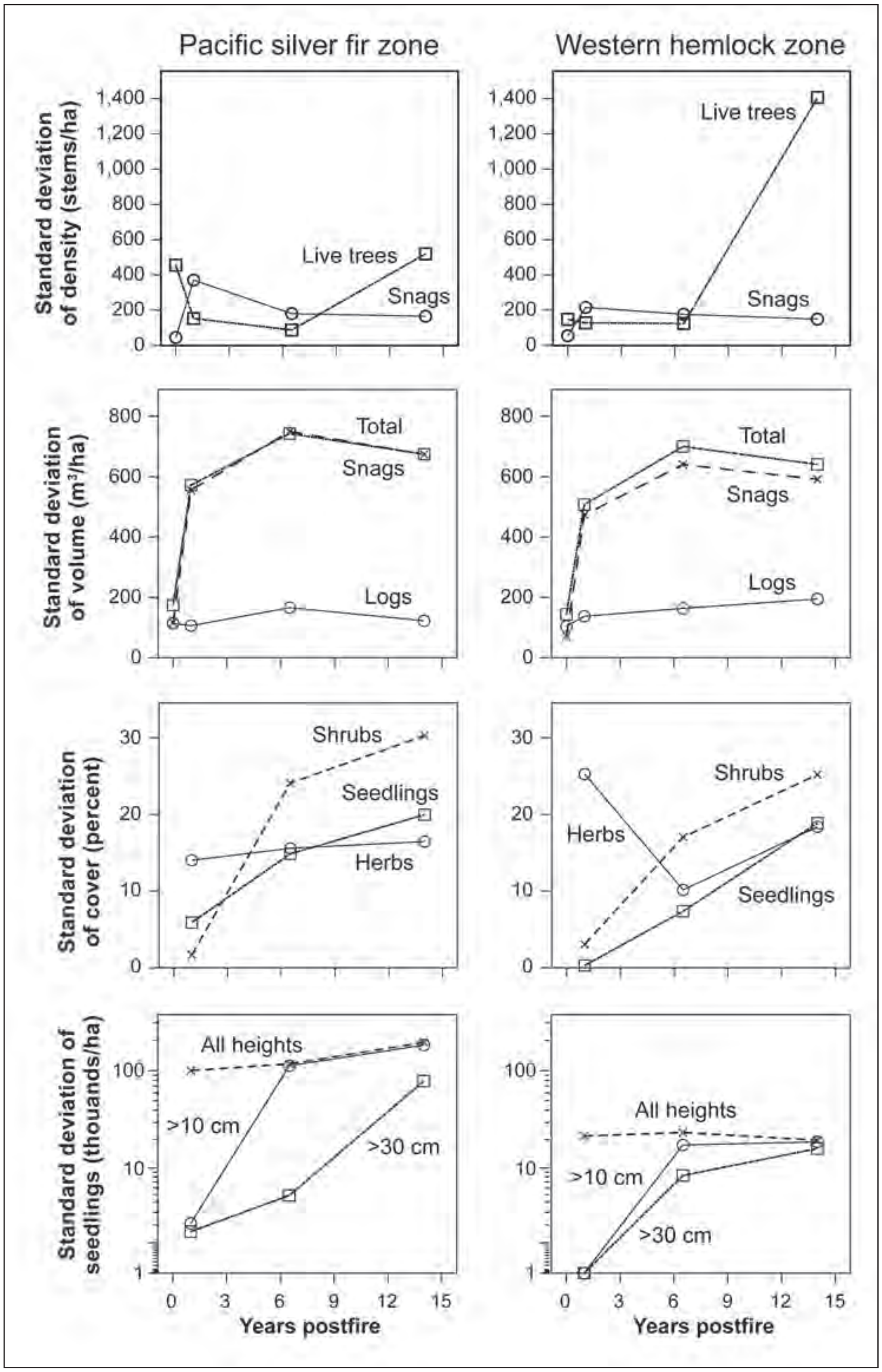

Figure 5—Standard deviation of key stand metrics compared to time since the fire. Identical to figure 3 except that each point represents a standard deviation instead of a mean.

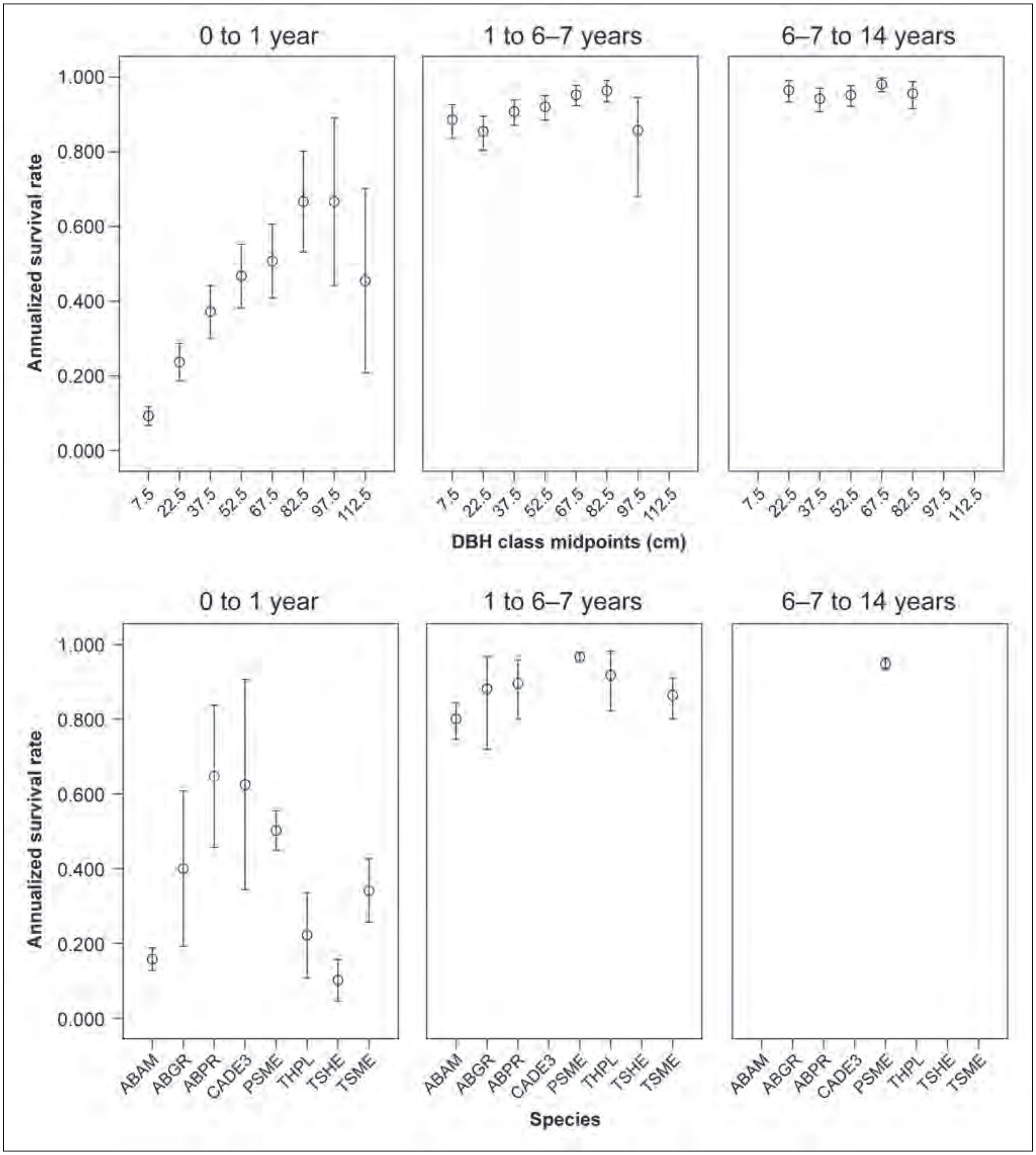

Figure 6—Tree survival rates calculated for several intervals since the fire, with 90 percent confidence limits. All rates expressed in annual (per-year) terms. DBH = diameter at breast height. Top row: survival rates for 15-cm DBH classes centered on 7.5 cm, 22.5 cm, etc., with all species combined. Bottom row: survival rates for species (all DBHs combined), ABAM = *Abies amabilis*; ABGR = *Abies grandis*, ABPR = *Abies procera*, CADE3 = *Calocedrus decurrens*, PSME = *Pseudotsuga menziesii*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*. Rates are not reported for species or DBH groups with ≤5 live trees to start, or for which calculated confidence limits ranged to <0 or >1.

~82.5 cm-DBH trees approximately seven times as likely to survive as 7.5-cm-DBH trees. The very largest diameter trees (>100 cm DBH) appeared to have a lower survival rate (fig. 6, top left panel) during this timespan, though the confidence limits for this result overlap substantially with the next lower size class.

Species showed apparent differences in susceptibility to fire, as shown in figure 6 (bottom left panel). *Pseudotsuga menziesii* and *Abies procera* were significantly more likely to survive than were *Abies amabilis* and *Tsuga heterophylla (*Fisher's exact tests, one-tailed, $p < 0.02$). By 1 year postfire, about 50 percent of the *P. menziesii* had survived, with survival in all diameter classes; while *A. amabilis* and *T. heterophylla* survival rates were below 16 percent. Although part of this distinction between species comes from the typically larger DBH of *P. menziesii*, some differences between species persist when diameter class is held constant. Table 3 has detailed survival rates by species and diameter class.

Delayed Tree Mortality

There was notable mortality of trees during the postfire period (i.e., **after** 1 year postfire). Of the 215 trees alive at 1 year postfire that could be tracked to the end of the study, only 56 percent were alive at 6 to 7 years postfire, and 45 percent alive at 14 years postfire. Such survival rates are easiest to compare with other work when converted to annualized (per-year) terms. The annualized survival rate is defined as the proportion of trees alive at the beginning of the timeframe that are alive at the end, expressed as a per-year probability of surviving. This rate, for all available trees and plots, was 0.915 for the early postfire period (1 to 6–7 years postfire), and 0.960 for the later postfire period (6–7 to 14 years postfire).

Most of the postfire mortality occurred during the early postfire period, 1 to 6–7 years postfire. During this period, survival rates followed a trend with diameter class that was similar to, but less dramatic than, the trend for 0 to 1 years postfire (fig. 6 top row). There was a significant positive correlation between diameter class midpoint and survival rate in this period (Pearson correlation = 0.91, $p= 0.01$), but only when the largest diameter trees, >90 cm DBH, were excluded from the analysis. Some species differed in survival (fig. 6, bottom row, middle panel). *Abies amabilis* survived at a significantly lower annual rate (0.80) than *P. menziesii* (0.97) (Fisher's exact test, $p < 0.001$). Although some of this difference is likely due to the larger diameters of *P. menziesii*, table 3 suggests that this difference persists when

Table 3—Annualized survival rates, by species, diameter class, and postfire timeframe

		Annualized survival rates[a] DBH (cm) midpoint for 15 cm groups[b]								
Time postfire	**Species**	**7.5**	**22.5**	**37.5**	**52.5**	**67.5**	**82.5**	**97.5**	**112.5**	**All sizes**
0 to 1 yr	*Abies amabilis*	0.084	0.286	0.300	0.278	0.300				0.158
	Abies grandis	0								0.400
	Abies procera									0.647
	Calocedrus decurrens									0.625
	Pseudotsuga menziesii		.174	.483	.585	.611	0.684	0.714	0.500	0.502
	Thuja plicata	0		.286						0.222
	Tsuga heterophylla	0		.273						0.101
	Tsuga mertensiana	.333	.438	.278	.308					0.341
	All species	.093	.237	.372	.467	.507	.667	.667	.455	0.280
1 to 6–7 yrs	*Abies amabilis*	.903	.764							0.801
	Abies grandis									0.882
	Abies procera									0.896
	Pseudotsuga menziesii		.941	.951	.962					0.967
	Thuja plicata									0.918
	Tsuga mertensiana	.819	.903							0.864
	All species	.886	.855	.908	.921	.952	.964	.857		0.915
6–7 to 14 yrs	*Pseudotsuga menziesii*			.934	.950	.976	.939			0.949
	All species		.965	.942	.952	.981	.956			0.960

[a] Survival rate = the proportion of trees alive at the beginning of the timeframe that are still alive at the end of the timeframe. Expressed as annualized rates. Rates are not reported for species/DBH groups with ≤5 live trees to start with, or for which calculated 90 percent confidence limits (not shown) spanned to <0 or >1.

[b] DBH = diameter at breast height.

diameter class is held constant. In the later postfire period (6–7 to 14 years postfire), there is no significant correlation based on size, and there were too few surviving trees for statistical comparisons among species.

Postfire mortality also has a relationship to initial fire damage to the stand. Figure 7 considers plots where fire severity (the percentage of canopy dead by 1 year postfire) was less than 100 percent. It shows the proportion of trees dying between 1 and 6–7 years postfire rises significantly with fire severity.

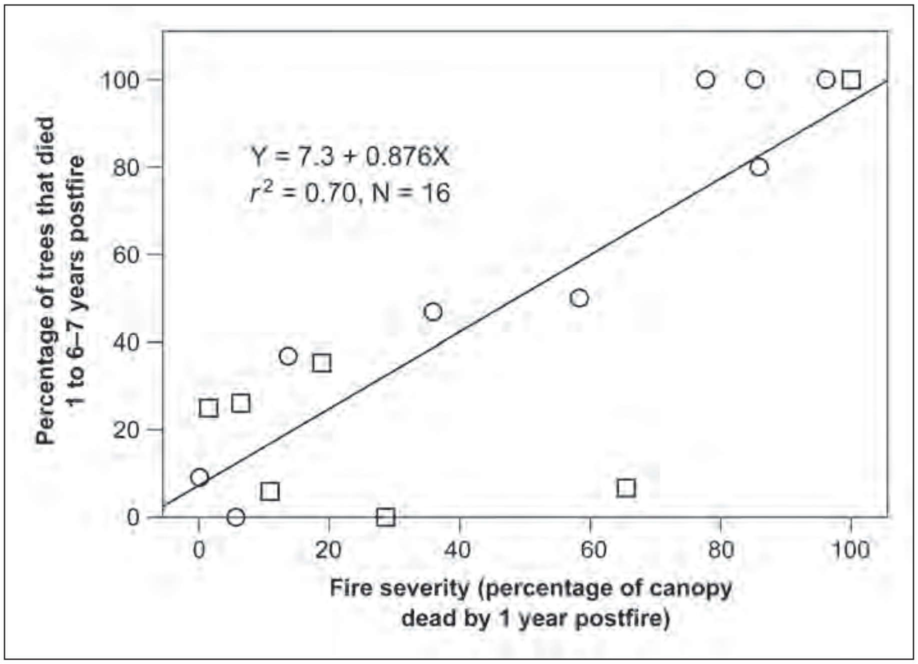

Figure 7—The relationship of mortality in the postfire period (i.e., the percentage of trees dying per plot from 1 to 6–7 years postfire) to fire severity (the percentage of canopy dead in the plot by 1 year postfire). Pacific silver fir zone plots are circles, western hemlock zone plots are squares.

Snag Fall and Fragmentation

Mortality in the postfire period had a relationship to initial fire severity.

As with fire-related mortality, snag fall in the wake of the fire followed strong patterns by diameter class (fig. 8, top row). Smaller diameter snags were more likely to fall. Results are easiest to compare to other work when expressed as annualized snag fall rate—i.e., the proportion of snags standing at the beginning of the timeframe that have fallen by the end of the timeframe, converted to a yearly rate. The annualized snag fall rate for new snags (i.e., snags created by the Warner Creek Fire) of 2.5 to 15 cm DBH was 0.159 between 1 and 14 years postfire, whereas for 45 to 60 cm DBH snags it was 0.007, and for 60+ cm DBH snags, no falling was detected. The great majority of snags that fell between 1 and 6–7 years postfire were <20 cm DBH.

Snag fall may be related to species as well. *Abies amabilis* snags were especially likely to fall (fig. 8, bottom row), with an annual rate of 0.137 from 1 to 6–7 years postfire, compared to 0.005 for *P. menziesii* (Fisher’s exact test, $p < 0.001$). Though much of this difference is due to the predominantly small diameters of *A. amabilis* snags, some differences between species seem to persist even when diameter class is constant; see the detailed rates in table 4.

If a snag did not fall, it was likely to lose some of its height through fragmentation, especially if it stood for more than 7 years. Annualized fragmentation rate is the proportion of snags standing at both the beginning and end of the timeframe

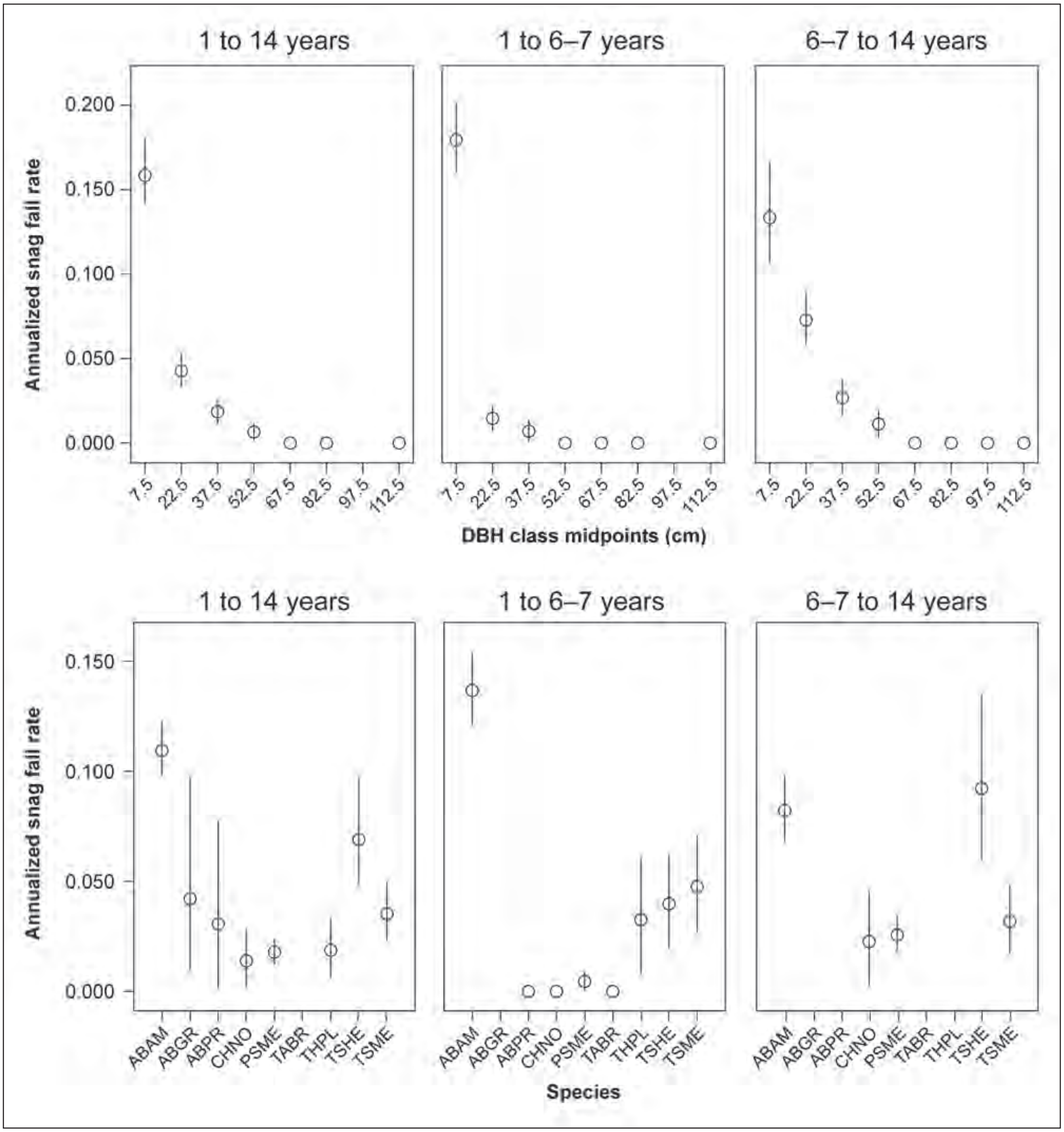

Figure 8—Snag fall rates calculated for several intervals since the fire, with 90 percent confidence limits. Rates are expressed in annual (per-year) terms, and were calculated using only "new" snags, i.e., those killed by the 1991 fire. DBH = diameter at breast height. Top row: survival rates for 15-cm wide DBH classes centered on 7.5 cm, 22.5 cm, etc., with all species combined. Bottom row: survival rates for species, all DBHs combined: ABAM = *Abies amabilis*; ABGR = *Abies grandis*, ABPR = *Abies procera*, CHNO = *Chamaecyparis nootkatensis*, PSME = *Pseudotsuga menziesii*, TABR = *Taxus brevifolia*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*. Rates are not reported for species or DBH groups with ≤5 snags or where confidence limits ranged to <0 or >1. Confidence limits not calculated for snag fall values of 0.

Table 4—Annualized snag fall rates, by species, diameter class, and postfire timeframe

		Annualized snag fall rates[a] DBH (cm) binned into 15 cm groups[b]								
Time postfire	**Species**	**7.5**	**22.5**	**37.5**	**52.5**	**67.5**	**82.5**	**97.5**	**112.5**	**All sizes**
1 to 14 yrs	*Abies amabilis*	0.228	0.062	.017		0				0.109
	Abies grandis									.042
	Abies procera									.031
	Chamaecyparis nootkatensis									.014
	Pseudotsuga menziesii		.037	.016		0	0			.018
	Thuja plicata	.041								.019
	Tsuga heterophylla		.048	.073						.069
	Tsuga mertensiana	1.000				0				.035
	All species	.159	.043	.018	0.007	0	0		0	.059
1 to 6–7 yrs	*Abies amabilis*	.236	.019	0	0	0				.137
	Abies grandis	.059								
	Abies procera									0
	Chamaecyparis nootkatensis									0
	Pseudotsuga menziesii			0	0	0	0			.005
	Taxus brevifolia	0								0
	Thuja plicata	.065								.033
	Tsuga heterophylla	.118								.040
	Tsuga mertensiana	.171			0	0				.048
	All species	.179	.015	.007	0	0	0		0	.071
6–7 to 14 yrs	*Abies amabilis*	.210	.104	.033		0				.082
	Chamaecyparis nootkatensis									.023
	Pseudotsuga menziesii		.060	.023		0	0			.026
	Tsuga heterophylla		.075	.123						.092
	Tsuga mertensiana	1.000	.046	0		0				.032
	All species	.133	.073	.027	0.011	0	0	0	0	.047

[a] Snag fall rate = the proportion of snags standing at the beginning of the timeframe that have fallen by the end of the timeframe. Converted to per-year rates as described in the methods. Rates are not reported for species/DBH groups with ≤5 live trees to start with, or for which calculated 90 percent confidence limits (not shown) spanned to <0 or >1.
[b] DBH = diameter at breast height.

Snags with smaller DBH's were likely to fall, whereas snags with larger DBH's were likely to fragment.

that have lost at least 10 percent of their height, converted to a yearly rate. Between 1 and 6–7 years post fire, 17 percent of the 230 snags that could be followed for breakage lost height, for an overall annualized fragmentation rate of 0.034. But between 6–7 and 14 years, 52 percent of the 223 snags that could be followed lost height, for an annualized fragmentation rate of 0.092. Of the snags that remained standing through all observation periods (1 year, 6–7 years, and 14 years postfire), 49 percent broke once, and 12 percent broke twice.

Snags with larger DBHs were more likely to fragment (fig. 9, top row). The snags in the 7.5-cm DBH group had an annualized fragmentation rate of 0.022 between 1 and 14 years postfire, while those in the 67.5-cm DBH group had a rate of 0.116 (fig. 9 top row). **All** of the snags in the 82.5-cm DBH group that remained standing from 1 to 14 years postfire, and from 6–7 to 14 years postfire, fragmented. This particular result caused us to adjust the calculation of annual snag fragmentation rate for the 82.5-cm group. A raw proportion of 1.0 over any span of years converts to a yearly probability of 1.0, which is deceptive, and also makes the confidence limits we have calculated nonsensical. For the 82.5-cm group we provided no confidence limits, and estimated the raw proportion of 1.0 as 0.99, an estimation that is reflected in the annualized rates.

There may be differences in fragmentation rate between species (fig. 9, bottom row). Between 1 and 6–7 years postfire, *Tsuga mertensiana* was most likely to break, with an annual fragmentation rate of 0.112, higher than *Tsuga heterophylla*, *Abies amabilis*, and *Pseudotsuga menziesii* (Fisher's exact tests, all $p < 0.04$). Between 6–7 and 14 years postfire, the pattern was different: *P. menziesii* was most likely to break, with an annual fragmentation rate of 0.162, higher than *T. mertensiana*, *T. heterophylla*, and *A. amabilis* (Fisher's exact tests, $p <= 0.05$). Though some of these differences are undoubtedly attributable to the effect of diameter, some differences persist when diameter class is held constant (table 5).

The increase in fragmentation rate from the earlier postfire interval (1 to 6–7 years) to the later one (6–7 to 14 years) was common among three major tree species (fig. 9 bottom row). Fragmentation rates of *Abies amabilis* rose from 0.009 to 0.085. *P. menziesii* and *Tsuga heterophylla* also rose dramatically. *Tsuga mertensiana* did not rise, but had relatively high rates in both sampling periods, 0.112 and 0.091.

The broken portions of snags falling to the ground were diverse in size, but included some very large pieces of wood. Between 1 and 6–7 years postfire, the mean absolute height loss (± SD) per broken snag was 13.5 (±8.8) m, with 10 percent of height losses >28 m. Between 6–7 and 14 years postfire, the mean absolute height loss was 12.8 (±10.2) m, with 10 percent of height losses again >28 m. When

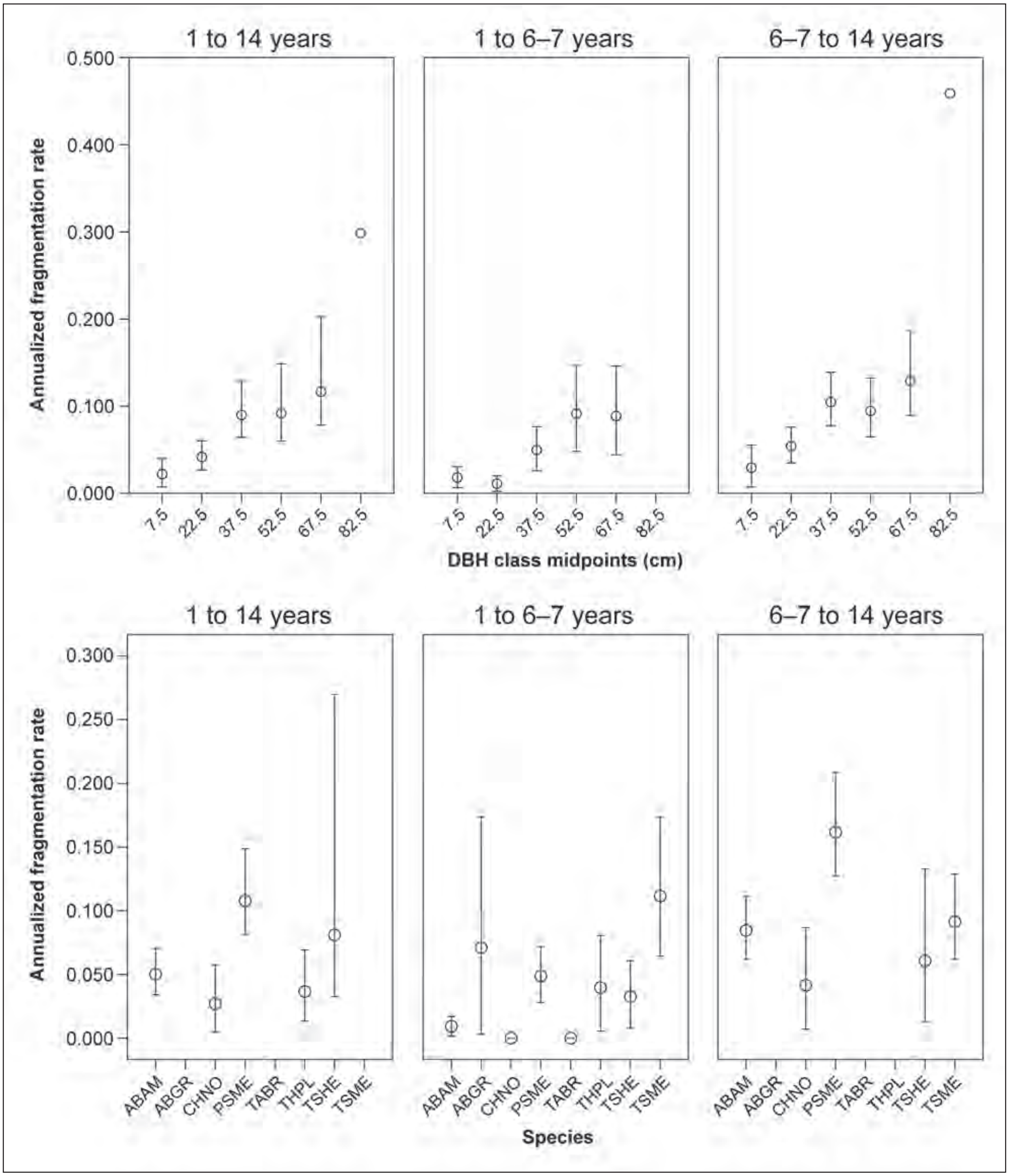

Figure 9—Snag fragmentation rates calculated for several intervals since the fire, with 90 percent confidence limits. Rates are expressed in annual (per-year) terms, and were calculated using only "new" snags, i.e., those killed by the 1991 fire. DBH = diameter at breast height. Top row: fragmentation rates for 15-cm wide DBH classes centered on 7.5 cm, 22.5 cm, etc., with all species combined. Bottom row: fragmentation rates for species, all DBHs combined: ABAM = *Abies amabilis*; ABPR = *Abies procera*, CHNO = *Chamaecyparis nootkatensis*, PSME = *Pseudotsuga menziesii*, TABR = *Taxus brevifolia*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*. Rates are not reported for species or DBH groups with <=5 snags or where confidence limits ranged to <0 or >1. The calculation of annual rates for the 82.5 cm diameter class involved an approximation; see "Results."

Table 5—Annualized snag fragmentation rates by diameter class, species, and postfire timeframe

		Annualized snag fragmentation rate[a] DBH (cm) binned into 15 cm groups[b]						
Time postfire	**Species**	**7.5**	**22.5**	**37.5**	**52.5**	**67.5**	**82.5**	**All sizes**
1 to 14 yrs	*Abies amabilis*		0.020	0.065	0.052			0.050
	Chamaecyparis nootkatensis							.027
	Pseudotsuga menziesii		.052		.298	0.298		.108
	Thuja plicata							.037
	Tsuga heterophylla							.081
	All species	0.022	.042	.090	.092	.116	0.298	.070
1 to 6–7 yrs	*Abies amabilis*		0					.009
	Abies procera							.071
	Chamaecyparis nootkatensis							0
	Pseudotsuga menziesii			.071	.118	.097		.049
	Taxus brevifolia	0						0
	Thuja plicata							.040
	Tsuga heterophylla							.033
	Tsuga mertensiana							.112
	All species	.018	.011	.050	.091	.089		.034
6–7 to 14 yrs	*Abies amabilis*		.033	.095	.088			.085
	Chamaecyparis nootkatensis							.042
	Pseudotsuga menziesii		.079	.186		.459		.162
	Tsuga heterophylla							.061
	Tsuga mertensiana		.088	.098	.042	.154		.091
	All species	.029	.054	.105	.094	.129	.459	.092

[a] Snag fragmentation rate = the proportion of snags that remain standing from the beginning to the end of the timeframe, but lose >10 percent of their height. Converted to per-year rates as described in the methods. Rates are not reported for species/DBH groups with ≤5 snags to examine, or for which calculated confidence limits (not shown) spanned to <0 or >1. Rates for the 82.5-cm DBH class reflect an approximation; see "Results" text.
[b] DBH = diameter at breast height.

expressed as proportions of prior height lost, the proportions were similarly variable: 0.46 ± 0.19 between 1 and 6–7 years postfire, and 0.46 ± 0.25 between 6–7 and 14 years postfire.

Regeneration Species, Cover, and Relative Height

While trees from the prefire stand were dying, falling, and fragmenting, new vegetation was emerging. At 14 years postfire, our regeneration cover survey and cell seedling survey recorded 15 tree species, 35 shrub species, and more than 70 herb species regenerating in plots which, in the immediate aftermath of the fire, had little or no apparent living understory. The complete list of species and cover values is provided in appendix 3. At 14 years postfire, the most abundant shrubs in the Pacific silver fir zone were *Ceanothus velutinus* Douglas ex Hook. (average cover per plot 12 percent), *Rubus lasiococcus* A. Gray (10 percent), and *Rubus parviflorus* Nutt. (5 percent); in the western hemlock zone, they were *Ceanothus velutinus* (15 percent), *Whipplea modesta* Torr. (9 percent), and *Rubus ursinus* Cham. & Schldtl. (8 percent). The most abundant herbs (including ferns and mosses) in the silver fir zone were *Tiarella trifoliata* L. (3 percent), *Anaphalis margaritacea* (L.) Benth. (3 percent), *and Fragaria vesca* L. (1.8 percent); in the western hemlock zone, they were *Lactuca muralis* (L.) Fresen. (7 percent), unidentified mosses (6 percent), and *Polystichum munitum* (Kaulf.) C. Presl (2 percent).

The 15 tree species recorded regenerating at 14 years postfire (app. 3) were nearly identical to the list of tree species alive before the fire (table 2, including footnotes). All species recorded as live trees before the fire, including relatively uncommon species such as *Pinus monticola* Douglas ex D. Don and *Taxus brevifolia* Nutt., were reflected in the regeneration. Two species, *Arbutus menziesii* and *Crataegus douglasii* Lindl., were detected in regeneration but not in prefire stands.

Seedling cover increased in the years after the fire. In the Pacific silver fir zone, mean seedling cover rose from around 2 percent at 1 year postfire to 30 percent at 14 years postfire; in the western hemlock zone, it rose from <1 to 15 percent (fig. 3, third row). Shrubs dominated the understory, reaching mean values of 35 and 46 percent at 14 years postfire (fig. 3, third row). Herb cover (including ferns and mosses) seemed to peak earlier, and at 14 years postfire was equal to or lower than tree and shrub cover in both zones.

Although shrubs were often more abundant than tree seedlings in terms of percentage of cover, tree seedlings were frequently taller.

Although shrubs were often more abundant than tree seedlings in terms of percentage of cover, tree seedlings were frequently taller. Figure 10 compares the mean recorded heights of shrubs and tree seedlings in each plot during the regeneration cover survey. When the cover and height for shrubs and trees are compared with Wilcoxon paired samples tests with both vegetation zones combined, shrubs

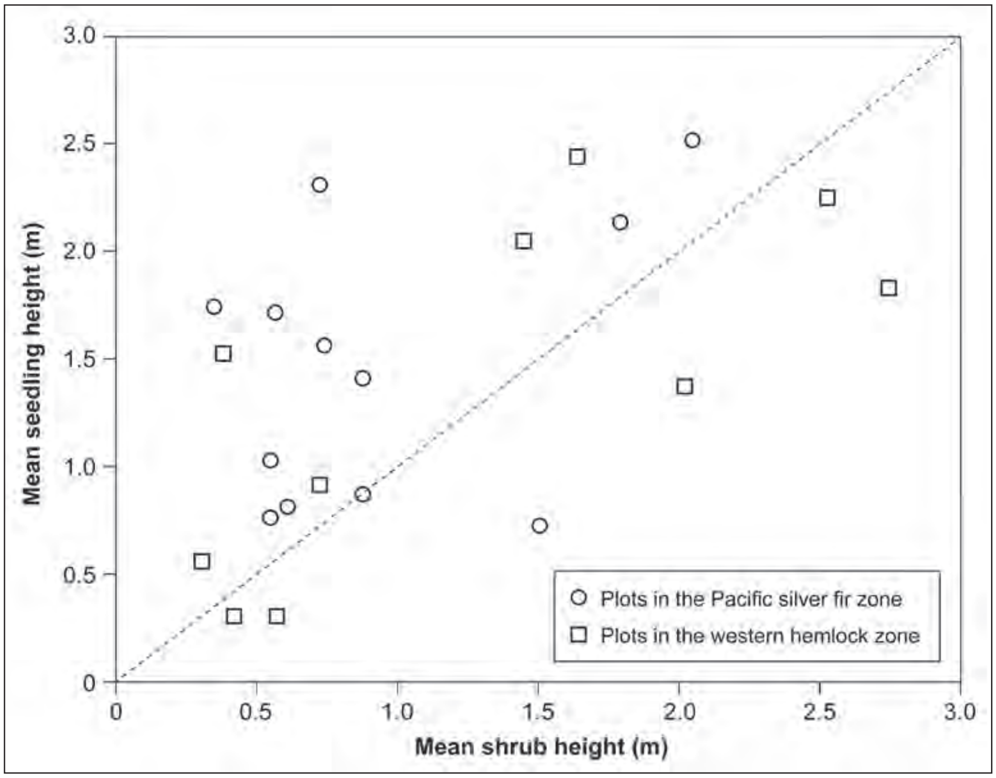

Figure 10—Comparison of shrub and seedling heights observed in study "cells" at 14 years postfire. Eight 3 by 3 m cells were studied per plot. In each cell, the maximum height of each life form (seedlings and shrubs) was recorded. Those eight values were averaged to create a mean representative height per plot for each life form, which is graphed here. The reference line represents equal heights. Circles are plots in the Pacific silver fir zone; squares are plots in the western hemlock zone. In nonparametric paired-samples tests, seedlings are consistently higher than shrubs for both zones combined, and for the silver fir zone individually; for the western hemlock zone there is no significant difference see "Results."

had significantly higher cover than tree seedlings ($p < 0.05$), while seedlings had significantly greater height ($p < 0.03$), with a mean of 1.4 m compared to 1.1 m for shrubs. This height difference is visible in the concentration of points in figure 10, which are above the reference line representing equal heights. If the analysis is split into zones, shrubs did not differ in cover from seedlings in the Pacific silver fir zone ($p > 0.1$), while trees were consistently taller there ($p < 0.01$). In the western hemlock zone, shrubs had greater cover than tree seedlings ($p < 0.001$), but their heights did not differ ($p > 0.5$).

Regeneration Establishment, Density, and Growth

Our seedling subplot survey evaluated the count of seedlings rather than their cover values. In the subplot survey, seedlings were detected on all burned plots in one or more study visits. The consistently small size of seedlings at 1 year postfire (when 100 percent of seedlings in the western hemlock zone, and 99.1 percent of seedlings in the Pacific silver fir zone, were <10 cm tall), in addition to the presence of cotyledons and only one growth whorl, suggested that all of the seedlings we observed established after the fire. Although the subplots contained 16 different species of seedlings, listed in table 6, the great majority of them came from just three species in each elevation zone. In the Pacific silver fir zone, 88 percent of all seedling records over all sampling years were *Tsuga mertensiana*, *Abies amabilis*, and *Pseudotsuga menziesii*; and in the western hemlock zone, 95 percent were *P. menziesii*, *Thuja plicata*, and *Tsuga heterophylla*. Some of the less common species in the seedling subplots, such as *Crataegus douglasii* (see notes to table 6) had not been recorded in the prefire stands.

The total density of seedlings in the subplots was high. In the Pacific silver fir zone, mean density of all seedlings per plot was 67,500/ha at 1 year postfire, 60,200/ha at 6–7 years postfire, and 85,500/ha at 14 years postfire (fig. 3 bottom row; table 6). In the western hemlock zone, these figures were 14,300, 22,600, and 19,500/ha, respectively. Results from the cell survey, available for only 14 years postfire, were slightly lower, perhaps because this survey did not count seedlings ≤ 10 cm height: a mean of 61,400/ha for the Pacific silver fir zone and 11,200 for the western hemlock zone.

A substantial number of the earliest seedlings survived and grew. Figure 11 shows seedling density by height class and time postfire. In general, mean seedling density in the tallest height classes (31 to 100 cm and 1 to 3 m) increased from 1 to 14 years postfire, while densities of the smallest height class (0 to 10 cm) declined from extreme levels. The smallest height classes did not diminish to zero, however. Mean density of seedlings 0 to 10 cm at 14 years postfire was about 6,800/ha in the silver fir zone and about 3,800/ha in the western hemlock zone (fig. 11).

New seedling establishment was not limited to the single large group established by 1 year postfire.

This last detail suggests that new seedling establishment was not limited to the single large group established by 1 year postfire. The ongoing nature of seedling establishment is confirmed by an examination of seedling counts in the individual subplots. In the Pacific silver fir zone between 1 and 6–7 years postfire, seedling counts increased in 36 percent of subplots. Although new seedling establishment could have occurred in any subplot, we could not track seedling death—so it is accurate to say that new establishment occurred in a minimum of 36 percent of subplots. Between 6–7 and 14 years postfire, new seedling establishment occurred in a minimum of 43 percent of Pacific silver fir zone subplots. In the western hemlock zone between 1 and 6–7 years postfire, new seedling establishment occurred in a minimum of 56 percent of subplots; between 6–7 and 14 years, it occurred in a minimum of 35 percent of subplots.

Examining data at the subplot level also demonstrates the extreme nature of spatial variability in natural seedling establishment at this fire site. Whereas

Table 6—Seedling densities by species, from the seedling subplots

		Pacific silver fir zone (n = 9 plots)			Western hemlock zone (n = 10 plots)		
		Years postfire			Years postfire		
		1	6–7	14	1	6–7	14
		Thousands per hectare					
Abies amabilis	Mean	9.8	10.9	11.2	0	0	0
	SD	14.7	18.1	21.5	0	0	0
	Minimum	0	0	0	0	0	0
	Median	2.4	3.2	2.4	0	0	0
	Maximum	45.0	56.9	67.2	0	0	0
Abies grandis	Mean	4.5	0.9	1.7	0	0.1	0
	SD	7.1	1.9	3.3	0	.3	0.1
	Minimum	0	0	0	0	0	0
	Median	2.0	0	0.4	0	0	0
	Maximum	21.9	5.6	9.9	0	.8	0.4
Abies procera	Mean	4.0	1.9	1.8	0	0	0
	SD	9.3	3.6	4.4	0	0	0
	Minimum	0	0	0	0	0	0
	Median	0	0	0	0	0	0
	Maximum	28.3	10.7	13.1	0	0	0
Pseudotsuga menziesii	Mean	12.7	6.3	6.1	11.0	13.3	13.9
	SD	14.7	7.2	7.4	19.3	12.8	13.2
	Minimum	0.4	0	0	0	.8	0.8
	Median	4.0	4.8	2.4	0.8	9.9	11.1
	Maximum	41.0	21.1	18.3	58.1	37.8	40.6
Thuja plicata	Mean	0	0	0	3.0	2.9	3.3
	SD	0	0	0	6.0	7.3	6.2
	Minimum	0	0	0	0	0	0
	Median	0	0	0	0	0	.2
	Maximum	0	0	0	18.7	23.5	19.1
Tsuga heterophylla	Mean	.1	.1	0	.2	3.3	1.9
	SD	.3	.4	.1	.4	5.0	3.2
	Minimum	0	0	0	0	0	0
	Median	0	0	0	0	0.6	0
	Maximum	.8	1.2	.4	1.2	14.7	9.2
Tsuga mertensiana	Mean	35.7	39.7	64.4	0	0	0
	SD	84.2	100.2	172.9	.1	0	0
	Minimum	0	0	0	0	0	0
	Median	3.2	.8	6.0	0	0	0
	Maximum	258.2	305.6	524.8	.4	0	0
All species combined[a]	Mean	67.5	60.2	85.5	14.3	22.6	19.5
	SD	100.3	117.0	191.4	21.8	23.7	19.7
	Minimum	9.9	3.2	.4	0	.8	.8
	Median	37.4	21.1	26.7	1.4	15.7	16.9
	Maximum	329.1	370.0	594.5	58.1	74.8	66.1

[a] "All species combined" includes minor species that were observed in the seedling subplots: *Acer macrophyllum*, *Arbutus menziesii*, *Calocedrus decurrens*, *Chamaecyparis nootkatensis*, *Crataegus douglasii*, *Pinus monticola*, *Prunus* sp., *Salix* sp., and *Taxus brevifolia*.
SD = standard deviation.

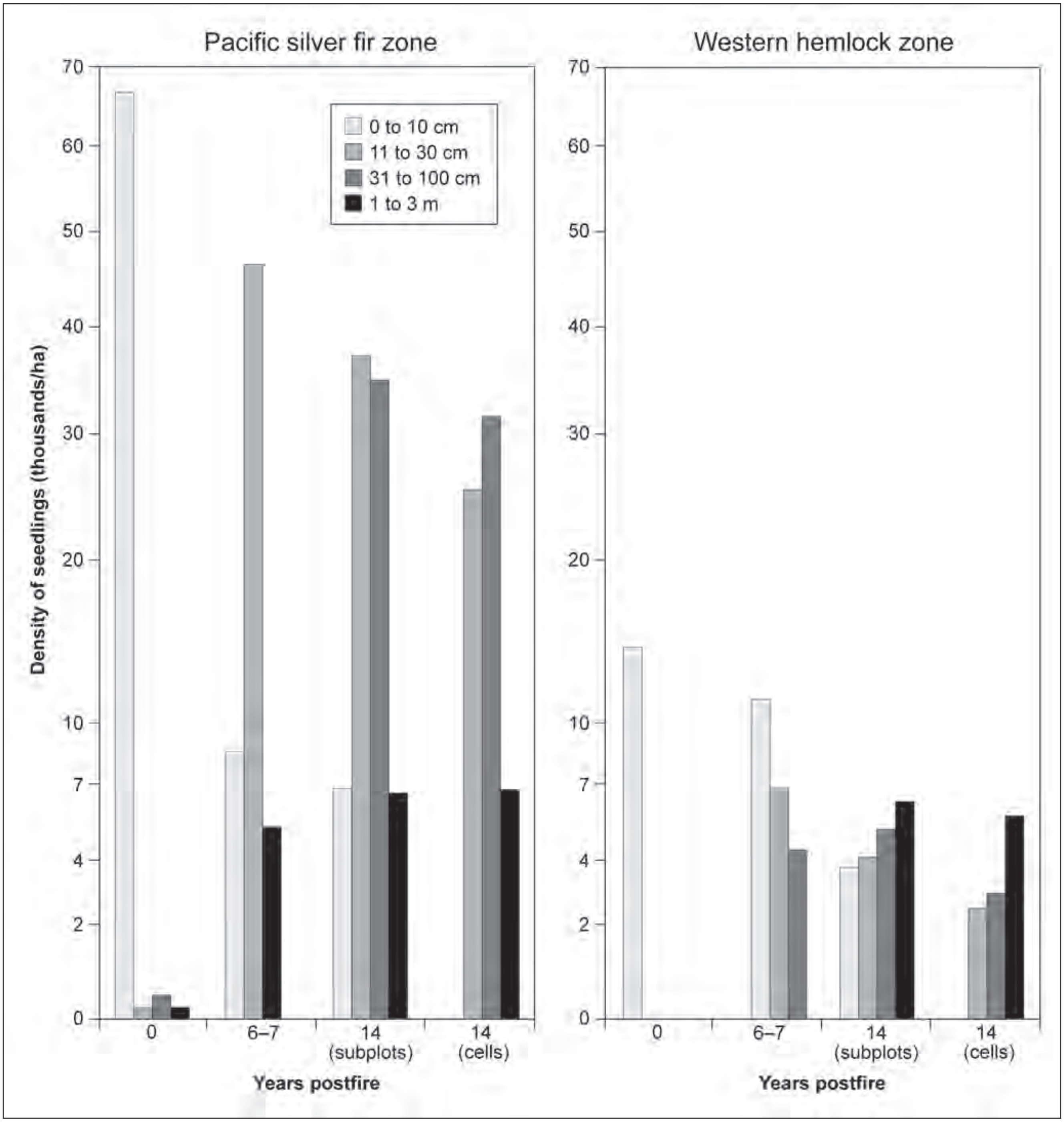

Figure 11—Mean seedling density per plot and time postfire, by seedling height classes. Sample size for each bar is 9 plots for the Pacific silver fir zone and 10 plots for the western hemlock zone. Seedling densities are in thousands per hectare. At 14 years postfire, two data sets are available, "subplots" and "cells" (see "Methods"). Cells are larger but were not surveyed for seedlings 0 to 10 cm in height.

seedling density varied widely among plots, from 400 to 595,000/ha, density in the individual subplots, when expressed in the same units, ranged to more than 1 million. Some 3.14-m^2 subplots had dozens or hundreds of seedlings while neighbors had few or none. Coverage was patchy. Figure 12 compares seedling density per

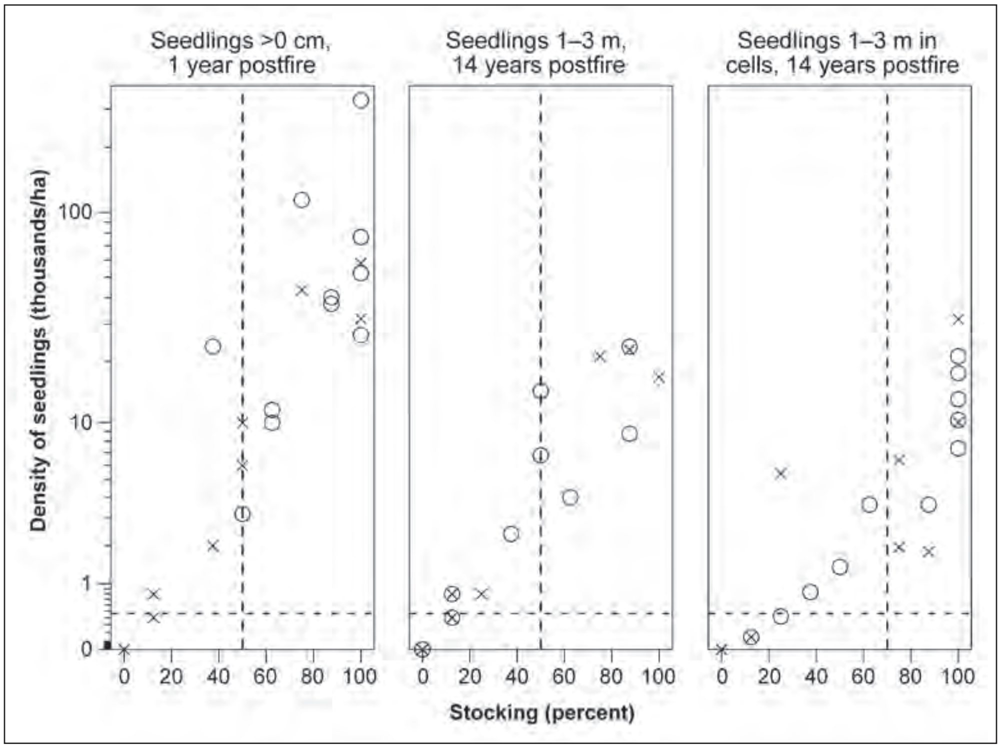

Figure 12—Relation of seedling density to stocking for three combinations of seedling size class and time postfire. Stocking is the percent of subplots or cells occupied by at least one seedling. Seedling density is in thousands per hectare. Each symbol represents one plot: circles for the Pacific silver fir zone, Xs for the western hemlock zone. Reference lines represent token published silvicultural standards for regeneration. On the Y axis: 494 seedlings per hectare (Oregon Revised Statutes 527.745). On the X axis: 50 percent of milacre plots (Stein 1992), comparable in size to our seedling subplots, and 70 percent of 4-milacre plots (Stein 1992), comparable in size to our seedling cells.

plot to a rough estimate of "stocking" (the percentage of subplots or cells occupied by at least one seedling). Stocking of ≤ 50 percent can be associated with mean densities as high as ~25,000/ha.

Seedling density in plots was not strongly correlated with site environment and history variables. Comparing seedling regeneration to aspect was problematic, because Pacific silver fir zone plots frequently had northerly aspects, and western hemlock zone plots southerly ones (table 1). Given that caveat, there was no significant difference in mean density of seedlings at 14 years postfire between northerly and southerly sites (Mann Whitney U-test, $p > 0.2$). There was a weak positive relationship between seedling density and fire severity. The lowest densities were associated with the lowest fire severities. Using the cell survey data, at 14 years postfire seedlings of 30 cm height or greater could be predicted with $Y = 0.468 + 0.0084 * X$ ($r^2 = 0.29$, $p = 0.01$, $n = 21$), where X is fire severity, in terms of percentage of canopy killed by 1 year postfire, and Y is log(seedling density in thousands per hectare, plus 1). In practice this is not a particularly useful predictive relationship because the 90 percent confidence limits are very large, for example at fire severity 100 percent the range of predicted values is 1,000 to 100,000 per hectare.

Structural and Compositional Change and Variation

The fire and its aftereffects changed forest structure in the burned area substantially. Table 7 compares structural metrics between prefire conditions and 14 years postfire. At 14 years postfire, the mean basal area of trees is only 19 percent of its prefire value in the Pacific silver fir zone, 50 percent of its prefire value in the western hemlock zone, and 35 percent of its prefire value overall (Wilcoxon signed ranks tests, $p < 0.05$). The mean live tree density does not change significantly in this interval, in either elevation zone or both zones combined ($p > 0.05$), as regenerating stems replaced killed trees. However, the size distribution of live trees changed (fig. 13, top row). In both vegetation zones, the mean density of the largest trees (≥ 122 cm DBH) declined about 33 percent, to about 5 per hectare. Sapling and pole sized trees (2.5 to 22.9 cm DBH) either suffered a small net reduction in density (as in the Pacific silver fir zone) or increased tremendously (as in the western hemlock zone), owing to regeneration. Meanwhile, trees in intermediate diameter classes ("small," "medium," and "large" trees, between 23 and 121 cm DBH) were decimated, with mean values declining 91, 92, and 94 percent in the Pacific silver fir zone and 83, 43, and 50 percent in the western hemlock zone. Older and younger cohorts became more distinguishable.

Table 7—Summary of structural changes between prefire conditions and 14 years postfire[a]

	Whole burned area		Western hemlock zone		Silver fir zone	
	Magnitude	Variation	Magnitude	Variation	Magnitude	Variation
Live tree basal area	35[b]	113	50[b]	185	19[b]	65
No. live tree species	51[b]	72	56[b]	53	47[b]	99
Mean live tree DBH	77	170[c]	89	181[c]	49	105
Live tree density	101	289	195	947	48	114
Mean snag diameter	132[b]	64	140	70	128	51
Pseudotsuga menziesii as a percentage of basal area	140[b]	79	114[b]	69[c]	178	104
Snag height	194	136	185	151	211	154
Pseudotsuga menziesii as a percentage of density	200[b]	91	144[b]	67[c]	352	140
Log volume	275[b]	138	372[b]	187	230[b]	108
Snag density	347[b]	309[c]	373[b]	269[c]	327[b]	360
Total CWD volume	456[b]	383[c]	569[b]	445[c]	402[b]	386
Snag volume	771[b]	646[c]	895[b]	841[c]	708[b]	582

[a] This table compares the magnitude and variation of forest structural metrics at 0 and 14 years postfire. Magnitude is the mean at 14 years postfire, expressed as a percentage of the prefire mean. Variation is the standard deviation at 14 years postfire, expressed as a percentage of the prefire standard deviation.
[b] Indicates magnitude differs between the two time periods, according to a Wilcoxon signed ranks test ($p < 0.05$).
[c] Indicates variation differs between the two time periods, according to a Levene test for equality of variances ($p < 0.05$).
CWD = coarse woody debris. DBH = diameter at breast height. No trees <2.5 cm DBH are included.

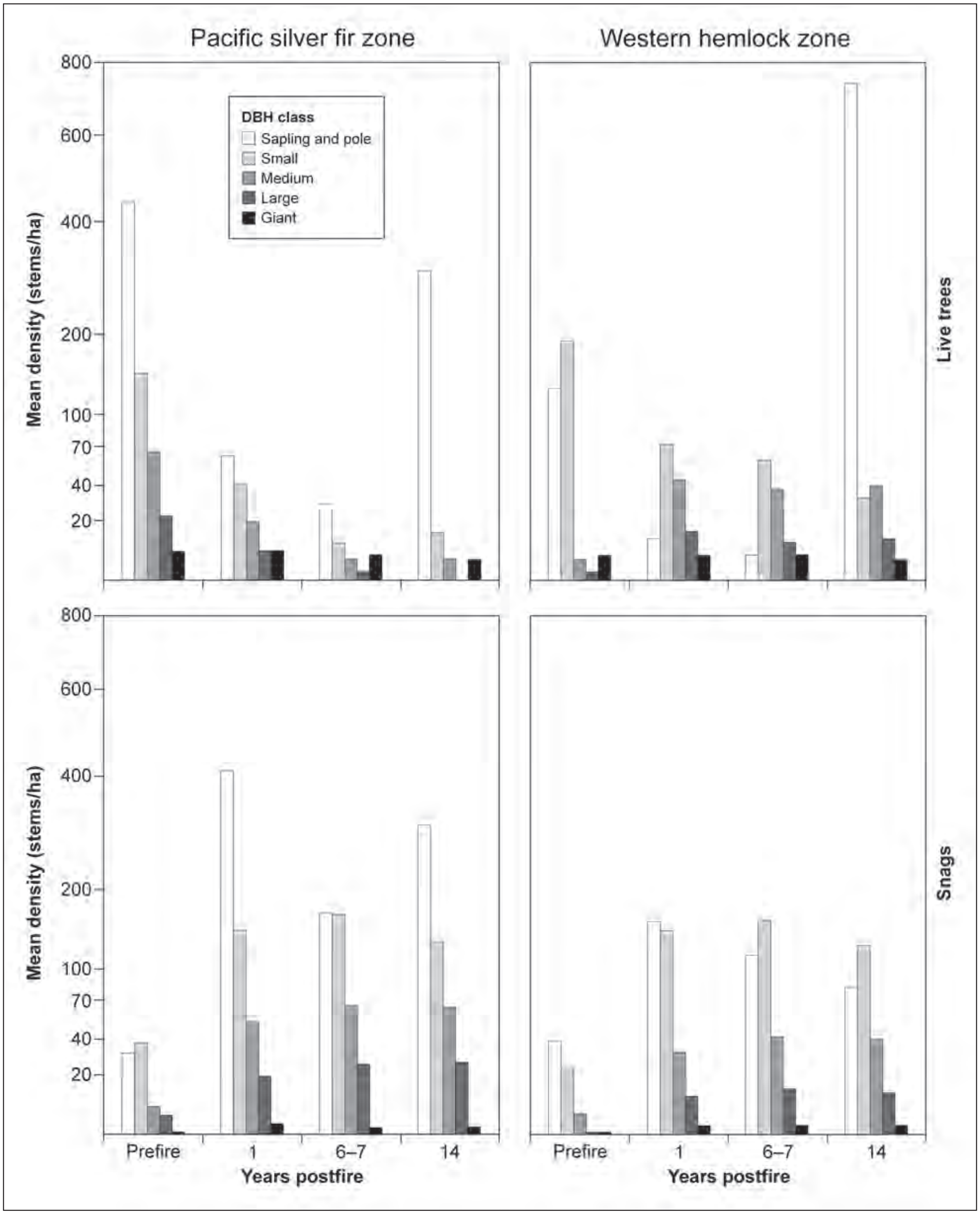

Figure 13—Mean live tree and snag densities per plot and time postfire, by standard Forest Service DBH (diameter at breast height) classes: saplings and poles combined (diameter 2.5 to 22.8 cm), small (22.9 to 53.2 cm), medium (53.3 to 81.2), large (81.3 to 121.8 cm), and giant (>121.9 cm). Sample size for each bar is 11 plots for the Pacific silver fir zone and 10 plots for the western hemlock zone.

Tree species diversity, among live stems >2.5 cm DBH, changed as well, with a reduction in the mean number of tree species recorded per plot, from 3.1 to 1.5 in the Pacific silver fir zone and 3.4 to 1.9 in the western hemlock zone (Wilcoxon signed ranks tests, $p < 0.05$). Because *P. menziesii* was prominent both among survivors of the fire and in new regeneration, its importance in stands increased. Table 7 shows that the proportion of stand basal area represented by *P. menziesii* increased, on average, 78 percent in Pacific silver fir zone plots, 14 percent in western hemlock zone plots, and 40 percent over the whole burned area (increase significant for whole burned area and western hemlock zone, $p < 0.05$, Wilcoxon signed ranks test). The proportion of live tree density >2.5 cm DBH represented by *P. menziesii* rose as well, 251 percent in the Pacific silver fir zone, 44 percent in the western hemlock zone, and 100 percent overall (all $p < 0.05$).

Tree mortality contributed to related changes in the diameter distribution of snags (fig. 13, bottom row). At 14 years postfire, mean snag diameter over both vegetation zones combined is 41.8 cm, 33 percent larger than in prefire conditions (Wilcoxon signed ranks test, $p < 0.05$). Metrics of CWD abundance, including snag volume, snag density, log volume, and total CWD volume increased significantly in both zones (Wilcoxon tests, $p < 0.05$). For example, average log volume in the western hemlock zone at 14 years postfire was 364 m^3/ha, nearly four times the estimated prefire value. The length of logs per hectare increased by similar proportions, rising from 1418 m/ha to 4665 m/ha at 14 years postfire in the western hemlock zone, and from 2399 m/ha to 5044 m/ha in the Pacific silver fir zone. Log volume increases occurred across a range of diameter classes, suggesting that the ground was receiving a steady influx of falling fire-killed wood of various sizes, not just a few immense boles.

While the mean values of these structural metrics were changing, the variation around those means was changing as well. The raw distributions in figure 4, and the standard deviations in figure 5 suggest an increase in variability for many structural variables. Table 7 reports on changes in variability for numerous structural metrics between prefire conditions and 14 years postfire. It compares variability with the Levene test for equality of variances (NIST 2003), because that test is less sensitive than the usual F-test to departures from normality (Zar 1999), which were frequent in our data.

Table 7 suggests that structural changes might be collected into several categories based on relative changes in magnitude and variability. Between 0 and 14 years postfire, several metrics increased in both magnitude and variability: snag density, snag volume, and total CWD volume. Snag height may also fit into this category, although test results for it are not significant. In general, we would expect variability to rise with magnitude. However, one key metric increased in variability, even though its magnitude did not change significantly: mean DBH of live trees ($p < 0.05$ for the western hemlock zone, and the whole burned area). Mean live tree density may also fit into this category, though test results for it are not significant. Meanwhile, in the western hemlock zone, two metrics decreased in variability, even though their mean values increased: the proportions of *P. menziesii* stems in total plot density and total plot basal area ($p \leq 0.05$).

The first 14 years after a forest fire can be a very dynamic time—one that belies the image of forests of the Pacific Northwest as timeless or slowly developing.

Discussion

Our study of the Warner Creek burn shows that the first 14 years after a forest fire can be a very dynamic time—one that belies the image of forests of the Pacific Northwest as timeless or slowly developing. We observed rapid and dramatic changes: dominant organisms died from the stress of a disturbance, biomass in the form of CWD moved quickly from the canopy to the ground, and new individuals of both shade-intolerant and tolerant species established and grew in the tens of thousands per hectare These processes were not uniform across the burned landscape, and only a portion of the natural range of variation we observed resembles the "stand replacement" paradigm of succession.

The Warner Creek Fire and subsequent forest development occurred in a limited area in a specific timeframe, so our work is a detailed case study rather than a systematic review of postfire development. To what extent can our results be generalized? Although specific numbers might be most relevant to mature forests of the central Cascade Range of Oregon, we take some confidence from the way our results correspond with other field reports from the wider region of Pacific Northwest forests dominated by *P. menziesii*. Meanwhile, the ecological mechanisms observed or implied should have even wider relevance.

Tree Mortality and Fire Severity

We found that initial mortality from the fire (i.e., between 0 and 1 years postfire) followed strong patterns by tree diameter and species (figure 6; table 3). Larger diameter trees were less likely to be killed by the fire, perhaps because of the effect of increased bark thickness (Ryan and Reinhardt 1988). *Pseudotsuga menziesii* lived up to its reputation for resistance to fire (Minore 1979; Ryan and Reinhardt 1988). Although *Calocedrus decurrens* (Torr.) Florin and *Abies procera* had higher calculated survival rates than *P. menziesii* (fig. 6), these species were represented in our sample by a low number of high-diameter individuals, so those results are tentative.

These mortality trends continued in the next half decade after the fire (fig. 6). Between 1 and 6–7 years postfire, the annualized survival rate of 0.915 (table 3) is consistent with a population of damaged trees, such as those experimentally topped by Huff and Bailey (2009), whose survival rates after 18 years were equivalent to an annualized rate of 0.917. Moreover, on a plot basis, we found that the magnitude of this "postfire mortality" rose with fire severity (fig. 7). Thus, many trees that survived the fire were injured or weakened by it. Trees injured by fire may be more susceptible to stresses such as drought, fine-root mortality, insect and disease colonization (Agee 2003), and loss of fungal symbionts (Borchers and Perry 1990). Notably, postfire evaluations of the Warner landscape found little evidence of tree mortality related to outbreaks of insects and diseases (USDA FS 1993). Between 6–7 and 14 years postfire, annualized survival at Warner increased to 0.960 (table 3), approaching the >0.99 that might be expected for undisturbed mature forest (Franklin et al. 1987).

While the phenomenon of delayed mortality in fire-damaged trees is common knowledge among forest scientists, it has largely undiscussed ramifications for the widely used, but inconsistently executed, measurement of fire severity (Keeley 2009). When fire severity is measured by tree mortality or visible damage to the canopy, the time of measurement could strongly affect the result. Delayed mortality on the level we report (almost 9 percent per year) could substantially alter estimates of fire severity if the estimates come multiple years postfire. Estimates of fire severity should include an explicit reference to the time of measurement.

Snag fall and fragmentation added so much wood to the ground that it probably constitutes a significant ecological disturbance in itself, a kind of rain of logs.

Snag Fall and Fragmentation

While tree mortality added a huge density and volume of snags to the burned area, that wood quickly began moving to the forest floor. Snag fall and fragmentation added so much wood to the ground—thousands of meters of log length per hectare—that it probably constitutes a significant ecological disturbance in itself, a kind of rain of logs.

This huge transfer of biomass from the canopy to the ground was not the result of extraordinarily high snag fall probabilities, but rather the immense population of snags available to fall. Although several authors (Bagne et al. 2008, Ohmann 2002, Russell et al. 2006) have reported higher snag fall rates in disturbed forests, the probabilities we recorded do not seem unusually high. When species and size classes are matched as closely as feasible, our postfire snag fall rates (table 4) are only slightly higher than those reported by Wilhere (2003) and Mellen and Ager (2002), and similar to those reported by Ohmann (2002), for undisturbed forest. Like Wilhere (2003) and Ohmann (2002), we found an effect of DBH on snag fall rate (fig. 8; table 4). Like Parish et al. (2010) and Mellen and Ager (2002), we found a tendency for low snag fall rates on the part of *P. menziesii* (fig. 8; table 4).

Snag fragmentation has been less discussed in the literature, but our results suggest it plays a major role in delivering wood to the ground. Comparing figures 8 and 9 (or tables 4 and 5) shows that for 6–7 to 14 years postfire, snags were often more likely to remain standing and fragment than fall down. This seems especially true for *P. menziesii*. Like us, Everett et al. (1999) found that *P. menziesii* snags are less likely to fall than other species, but very likely to lose height. Moreover, because larger snags are much more likely to fragment (fig. 9), the volume of wood falling to the ground per snag fragmentation event will likely be larger than the typical snag fall event. Given the massive size of some of these snag fragments (a mean height loss per event 12.8 ±10.2 m, with 10 percent of height losses >28 m), it is clear that a lot of kinetic energy, as well as wood, is being delivered to the forest floor, perhaps destroying some existing regeneration and reexposing mineral soil, as well as increasing fuel loads.

Because of snag fall and fragmentation, the large population of snags at the Warner Creek Fire site is only a temporary phenomenon. If the snag fall rates we observed between 6–7 and 14 years continue, snag density will be back near prefire levels in two more decades, with considerable additional losses in snag volume owing to snag fragmentation.

Natural regeneration and growth of trees was generally abundant and rapid, although extremely variable in space.

Natural Regeneration of Trees

We found that natural regeneration and growth of trees on the Warner Creek Fire site was generally abundant and rapid, although extremely variable in space, both within and among stands. This abundance occurred while other vegetation, notably the shrub *Ceanothus*, was regenerating profusely as well. Regeneration did not seem to be focused in a single pulse of establishment, as numerous new seedlings were observed on all study visits, and individual subplots showed increases between visits. Seedling numbers in the Pacific silver fir zone were particularly large, with mean seedling densities above 60,000 per ha. This is considerably higher than the several thousand per hectare reported by Agee and Smith (1984, p. 813) for a subalpine forest in the Olympic mountains, 3 years after a fire. Beyond this reference there is little in the literature about natural regeneration after fire in the Pacific silver fir zone. Most of our discussion will focus on the western hemlock zone.

The speed of reforestation in our seedling results contrasts with some retrospective studies, which portrayed natural reforestation of *P. menziesii* stands as slow or sparse (Franklin and Hemstrom 1981, Huff 1995, Tappeiner et al. 1997a). However, none of our results are unanticipated when compared to the handful of quantified direct observations of postfire regeneration in the literature graphed in figure 1. For example, our mean abundance of 13,900 *P. menziesii* per ha at 14 years postfire (table 6) fits into the range established by Hofmann's (1917) map, 0 to >37,000 per hectare. Similarly, Shatford et al. (2007) found 83 to 8188 conifers per hectare in regenerating *P. menziesii* stands 18 years postfire. Like us, both of these sources report a wide range in the age of seedlings, from 1 to 11 years in Hofmann (1917), and 1 to 18 years in Shatford et al. (2007). This last finding may be the most interesting one, because it suggests that the natural postfire environment can provide multiple, ongoing opportunities for seedling establishment and growth. Natural reforestation may not be dependent on a single fortuitous season.

Minore and Laacke (1992) list four factors that likely affect the speed and abundance of natural regeneration: seed source, availability of suitable substrate, protection from heat and moisture stress, and the presence of competitive vegetation. It seems unlikely that seed source was limited on the Warner site, given the huge numbers of seedlings. A local silviculturalist characterized seed in the year following the fire as generally sufficient or abundant (Bailey 1992). Larson and Franklin (2005) have suggested that many seeds survived the Warner fire in the canopy. *P. menziesii* that survived the fire were typically larger, older individuals, which tend to produce more seed than younger ones (Hermann and Lavender 1990); such trees may have been littering the ground with seeds even as they took a decade or more to die from the stress of the fire. Even in stands that suffered 100 percent mortality and near-total crown consumption, the patchy nature of the fire may have left seed trees nearby. We did not assess the availability of substrates, but *P. menziesii* is reputed to prefer exposed mineral soil (Minore and Laacke 1992). At the Warner site, high-severity fires exposed some mineral soil, and the steady rain of falling logs (from snag fall and fragmentation) may have exposed more even after revegetation had commenced.

Heat and moisture stress have long been acknowledged as major constraints on tree regeneration in this region (e.g., Isaac 1938). Locations that are dry for physiographic and microclimatic reasons, such as south-facing slopes, are the most likely sites for "regeneration failure" following logging; it can be desirable to leave some shade as protection for the youngest seedlings (Minore and Laacke 1992). At Warner, we found no relation between aspect and regeneration; one south-facing plot had 3,500 seedlings >30 cm tall per ha in the cell survey. The Warner study site, unlike a logged stand, contained an effective source of partial shade: a canopy of dead or dying trees. Though we know of no measurements of the transmittance of light through a snag canopy, it might be approximated with measurements from a deciduous canopy in winter, where average transmittance for visible radiation was about 40 percent of incident values (Brown et al. 1994). In contrast, closed-canopy *P. menziesii* canopies transmit on average only 1 to 2 percent of visible radiation to ground level (Parker et al. 2002). As snag fall and fragmentation bring that canopy to the ground, light and heat to seedlings will be increased, but the newly fallen logs—which at Warner, were in the thousands of meters per ha—may also increase the availability of shaded microsites. Little et al. (1984) proposed that such microsites were important resources in the regeneration of subalpine forests featuring *Abies amabilis* and *Tsuga mertensiana*.

A protective shading effect may explain why we, like Shatford et al. (2007), found no relationship between seedling abundance and shrub cover, despite fears that shrubs may be a major restraint on reforestation in burned areas (Sessions et al. 2004). Whereas experimental work in harvested areas has demonstrated that mechanical removal of shrubs can increase the growth of planted *P. menziesii* seedlings (Stein 1999), in a more natural setting encroaching and even overtopping vegetation may provide a measure of heat and moisture protection for seedlings and saplings (Irvine et al. 2009), allowing them to survive until they overtop the shrub canopy.

Future Development and Management Implications

A decade ago the efficacy of natural regeneration for replacing forest cover in the wake of fire was in doubt (e.g., Sessions 2004). We found that natural regeneration at the Warner fire site often far surpassed some silvicultural standards relevant to planting operations, such as 494 seedlings per hectare (Oregon Revised Statutes 527.745), or >50 percent of milacre plots (Stein 1992). (The Oregon standard also has a more subjective condition, namely, that the seedlings must be “free to grow,” that we did not evaluate.)

There is little doubt that tree cover is returning within one or two decades rather than the centuries that had been feared.

When considered in the light of other direct observations of postfire regeneration collected in figure 1, it seems clear that Douglas-fir forests of the Pacific Northwest are capable of regenerating themselves in a wide range of circumstances. The results in figure 1 span a number of climate zones and topographical conditions, from moist sites in the Olympic Mountains (Huff 1995) to dryer and hotter areas in the Klamath and Siskyou Ranges (Donato et al. 2009, Shatford et al. 2007). Although it is not clear if the resulting forests are optimal for any particular purpose (wood production, habitat for a particular species), there is little doubt that tree cover is returning within one or two decades rather than the centuries that had been feared. The next time a mixed-severity fire burns in this region, it could logically be argued there is no need to plant nursery-grown seedlings.

The regeneration we observed differed from planting schemes in its spatial variability within and among stands. At 14 years postfire, density of large (1 to 3 m tall) seedlings in both elevation zones ranged from near 0 to more than 20,000 per ha (fig. 12, app. 2), with considerable variation within plots. In contrast, planting prescriptions in this area rarely exceed a few thousand per hectare (e.g., 3,000, Scott et al. 1998), and are usually executed in a regular geometric pattern. A prescription written for portions of the Warner burn which were not part of the designated natural succession area ranged from 500 to 1,000 per hectare (Dewitz 1992). If the goal of planting prescriptions in large treated areas is to emulate natural response to fire, their variation should be increased, both within and among stands.

In fact, practically every aspect of the fire event and ecological aftermath showed high variability, from the mixed severity of the fire to the processes of mortality, snag fall and fragmentation, and new vegetation growth. These compounding factors increased the variety of structural conditions on the landscape (table 7), and future conditions should be considerably more variable than they would have been without the fire.

Two kinds of pathways expounded by Zenner (2005) seem apropos. Stands with high mortality and high regeneration fit into the "catastrophic" mode of stand development, where a single cohort of *P. menziesii* dominates the stand; future structural diversity comes from varying growth rates of different tree species and gap formation, a slow process that delays old-growth characteristics for centuries. Meanwhile, stands with moderate severity fit into the partial disturbance model where large remnants and successful regeneration immediately take on a two-cohort structure that may develop old-growth characteristics more quickly.

Areas of high severity and low regeneration might be demonstrating the slow, sparse pattern suggested by retrospective studies like Tappeiner et al. (1997a), where trees establish and grow in low densities, but get big quickly. These low-density stands may look like regeneration failures but appear to be a completely natural feature of response to a mixed-severity fire. They may have interesting attributes for forest health and conservation. Stands with lower initial densities may develop old-growth characteristics more quickly than stands with higher initial densities (Acker et al. 1998, Bailey et al. 1998). And a lower density of trees might allow a lengthy shrub phase of succession, where nitrogen-fixing shrubs like *Ceanothus* enhance soil nutrients. Management plans for large burned or treated areas might consider incorporating such areas in a mix of treatments rather than aiming for the universal return to complete tree cover.

It is common in Oregon and Washington forest management to refer to the landscape as a "mosaic" of mixed forest types and structures. With a variety of fire severities and variety of postfire responses, the Warner Creek Fire area demonstrates how such mosaics are created.

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English Equivalents

When you have:	Multiply	To get:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Cubic meters (m^3)	35.3	Cubic feet

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Appendix 1—Temporal Changes in Three Plots Between 6–7 and 14 Years Postfire

Appendix 2—Photos of the Variety of Site Conditions at 14 Years Postfire

Appendix 3

Percent cover of regenerating species at 14 years postfire, from the regeneration cover survey[a]

	Silver fir zone (n = 11 plots)		Western hemlock zone (n = 10 plots)	
	Mean	Standard deviation	Mean	Standard deviation
Trees:				
Abies amabilis	9.2	10.0		
Abies grandis	1.9	2.5	t	t
Abies procera	2.2	4.9		
Acer macrophyllum			0.3	0.8
Arbutus menziesii			t	0.1
Calocedrus decurrens			t	t
Chamaecyparis nootkatensis	2.5	8.3		
Cornus nuttallii			t	t
Crataegus douglasii			t	t
Pinus monticola	t	t		
Pseudotsuga menziesii	8.5	12.5	17.1	22.3
Taxus brevifolia			t	t
Thuja plicata			0.3	0.5
Tsuga heterophylla	0.2	0.5	1.1	1.7
Tsuga mertensiana	7.6	10.7		
All trees	30.3	20.0	15.4	18.9
Shrubs:				
Acer circinatum	0.2	0.8	0.5	1.1
Acer glabrum			0.1	0.1
Amelanchier alnifolia	0.1	0.2		
Arctostaphylos			t	0.1
Arctostaphylos columbiana	0.5	1.6	0.2	0.4
Berberis nervosa	0.4	1.2	6.6	5.5
Ceanothus integerrimus			2.2	6.6
Ceanothus sanguineus			5.3	12.7
Ceanothus velutinus	11.9	26.4	15.5	21.7
Chimaphila umbellata	t	t	t	0.1
Garrya fremontii	0.3	0.8		
Gaultheria shallon			0.9	1.8
Holodiscus discolor	0.1	0.2	0.3	0.6
Pachistima myrsinites	0.3	1.1	t	0.2
Prunus emarginata	0.6	1.1		
Rhododendron macrophyllum	0.4	0.9	0.7	1.5
Ribes cereum	0.1	0.2		
Ribes lacustre	0.9	1.2		
Ribes sanguineum	0.2	0.5	t	t
Ribes viscosissimum	2.5	3.0		
Rosa gymnocarpa	0.3	0.5	0.6	0.9
Rubus lasiococcus	10.4	14.9		
Rubus nivalis			0.1	0.3
Rubus parviflorus	4.9	12.8	0.5	0.9
Rubus spectabilis	0.1	0.2		

	Silver fir zone (n = 11 plots)		Western hemlock zone (n = 10 plots)	
	Mean	Standard deviation	Mean	Standard deviation
Rubus ursinus	0.7	1.3	7.6	12.2
Salix sp.	0.1	0.2	0.1	0.1
Sambucus racemosa	t	0.1		
Sorbus scopulina	t	0.1		
Sorbus sitchensis	t	t		
Symphoricarpos mollis	2.1	6.2	0.5	0.9
Vaccinium membranaceum	4.8	7.1	0.2	0.7
Vaccinium parvifolium			t	0.1
Whipplea modesta	t	0.1	9.4	11.6
All shrubs	34.9	30.3	29.5	46.1
Herbs, ferns, and mosses:				
Achlys triphylla	0.7	1.1	1.9	3.8
Adenocaulon bicolor	0.2	0.3	t	0.1
Anaphalis margaritacea	3.0	2.8	0.5	0.7
Anemone deltoidea	0.1	0.2	0.2	0.3
Angelica genuflexa	t	t		
Aquilegia formosa	0.1	0.5		
Asarum caudatum	0.7	1.9		
Aster foliaceus	t	t		
Aster occidentalis	t	0.1		
Bromus vulgaris	0.9	1.2		
Calamagrostis canadensis	0.3	0.8		
Campanula scouleri	0.8	1.7	0.2	0.4
Carex sp.	t	0.2		
Carex inops	0.1	0.2		
Carex kelloggii	t	0.1		
Carex luzulina	0.1	0.2		
Carex mertensii	0.1	0.2		
Carex rossii	0.3	1.0		
Cirsium callilepis	t	0.1		
Cirsium vulgare			t	0.1
Claytonia sibirica	t	0.1		
Clintonia uniflora	1.2	1.7		
Cystopteris fragilis	0.1	0.2		
Dactylis glomerata	t	t	0.8	1.8
Dicentra formosa	t	0.2		
Disporum hookeri	0.2	0.6	0.1	0.1
Elymus glaucus	1.1	2.2		
Epilobium angustifolium	1.4	1.7	1.1	1.6
Epilobium minutum	0.1	0.2		
Festuca rubra	t	0.1		
Fragaria vesca	1.8	3.9	0.3	0.4
Galium oreganum	0.4	1.0		
Galium triflorum	0.3	0.3	0.5	0.6
Glyceria elata	0.7	2.2		
Heracleum lanatum	0.2	0.4		

	Silver fir zone (n = 11 plots)		Western hemlock zone (n = 10 plots)	
	Mean	Standard deviation	Mean	Standard deviation
Hieracium albiflorum	1.0	0.7	0.4	0.3
Hypericum perforatum	0.1	0.2	t	0.1
Lactuca muralis	0.8	1.5	6.9	16.7
Lactuca pulchella	t	t		
Lathyrus polyphyllus	t	t	0.6	1.8
Linnaea borealis			t	0.1
Listera borealis			1.0	3.0
Lupinus polyphyllus	0.8	1.1		
Madia sativa			t	t
Mertensia paniculata	0.1	0.2		
Mitella sp.	t	0.1		
Mitella breweri	0.2	0.6		
Osmorhiza chilensis	t	0.1	0.1	0.1
Pedicularis racemosa	t	0.1		
Penstemon sp.	0.1	0.4		
Penstemon cardwellii	0.1	0.2		
Phacelia hastata	0.1	0.4		
Poa canbyi	t	0.1		
Polystichum munitum	0.1	0.2	2.2	3.9
Pteridium aquilinum	1.1	2.7	1.1	2.2
Pyrola secunda	0.5	0.7		
Rudbeckia occidentalis	0.1	0.3		
Senecio triangularis	0.1	0.2		
Smilacina racemosa	t	0.1		
Smilacina stellata	1.5	4.0	0.1	0.2
Stellaria calycantha	t	t		
Tiarella trifoliata	3.2	6.9	0.3	0.9
Trientalis latifolia	0.1	0.4	0.5	0.7
Trifolium latifolium			t	0.1
Trillium ovatum	t	0.1		
Trisetum canescens	0.2	0.8		
Trisetum cernuum	0.7	1.4		
Valeriana sitchensis	0.4	1.2		
Vancouveria hexandra			0.1	0.2
Vicia americana	0.1	0.4		
Vicia oregana	0.1	0.2		
Vicia sativa	t	0.1	0.5	1.4
Viola sp.	0.2	0.8	0.4	1.3
Viola canadensis	t	0.1		
Viola sempervirens	0.9	1.9	0.3	0.9
Xerophyllum tenax	1.0	1.4		
All herbs, ferns, and mosses	25.6	16.5	15.4	18.4

[a] t = trace (<0.1 percent).

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