Fire-related landform associations of remnant old-growth trees in the southern Washington Cascade Range

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Abstract: The spatial distribution of biological legacies left by natural disturbances is an important source of variability in forest development. We investigated one type of biological legacy: remnant old-growth trees persisting in mature Douglas-fir forests. We hypothesized that persistence varies with topographic heterogeneity influencing fire behavior. Our two study areas are located in the southern Washington Cascade Range, USA. They have an unfragmented, mature forest cover that regenerated following wildfire. We mapped all remnant old-growth trees (live and dead) within 4.2–6.4 km long belt transects. Digital elevation models were used to generate convergent and divergent landform classes. Frequency analysis was used to test for landform associations. Live remnant western hemlock and western redcedar were strongly associated with convergent landforms and aspects that had greater availability of soil moisture. Live remnant Douglas-fir were most abundant, but were not correlated with convergence or divergence, although certain landforms had higher concentrations. Remnant snags were abundant across convergent and divergent landforms. We conclude that species with low fire resistance survive most frequently on landforms that have a dampening effect on fire intensity. Topographic variability may indirectly influence ecological functions associated with biological legacies by affecting the spatial distributions of remnant old-growth trees.

Résumé : La distribution spatiale des legs biologiques laissés par les perturbations naturelles est une importante source de variabilité dans le développement de la forêt. Les auteurs ont étudié un type de legs biologique : les vieux arbres rémanents qui persistent dans les forêts matures de douglas. Ils ont fait l'hypothèse que la persistance varie avec l'hétérogénéité topographique qui influence le comportement du feu. Leurs deux zones d'étude sont situées dans la partie sud de la chaîne des Cascades dans l'État de Washington, aux États-Unis. On y retrouve un couvert de forêt mature non fragmentée qui origine d'un feu. Ils ont cartographié tous les vieux arbres rémanents (morts et vivants) le long de transects en bandes de 4,2 à 6,4 km. Des modèles numériques d'altitude ont été utilizés pour générer des classes de modelés convergents et divergents. L'analyse de fréquence a été utilizée pour tester les relations avec les modelés. Les tiges rémanentes encore vivantes de pruche de l'Ouest et de thuya géant sont fortement associées à des modelés convergents et à des orientations qui correspondent à une plus grande disponibilité de l'humidité dans le sol. Les tiges rémanentes encore vivantes de douglas sont très abondantes mais leur présence n'est pas corrélée avec la convergence ou la divergence bien que de plus fortes concentrations soient associées à certains modelés. Les chicots rémanents sont abondants dans les modelés convergents ou divergents. Les auteurs concluons que les espèces qui ont une faible résistance au feu survivent plus fréquemment dans les modelés qui ont pour effet de tempérer l'intensité du feu. La variabilité topographique peut indirectement influencer les fonctions écologiques associées aux legs biologiques en ayant un effet sur la distribution spatiale des vieux arbres rémanents.

[Traduit par la Rédaction]

Introduction

The density, type, and spatial distribution of biological legacies left by natural disturbances are an important source of variability in rates and pathways of natural forest development. Biological legacies have been defined as "the organisms, organic materials, and organically-generated patterns that persist through a disturbance and are incorporated into the recovering ecosystem" (Franklin et al. 2000, p. 11). It has been proposed that biological legacies affecting successional dynamics, such as remnant seed trees (Keeton 2000) or surviving propagules (Halpern 1989; Franklin 1990), may influence the spatial dynamics of landscapes recovering from large, high-intensity natural disturbances (Turner et al. 1998; Keeton and Franklin 2005). Recovery and subsequent successional development occur faster where these types of biological legacies persist in the post-disturbance environment, thereby forming nuclei from which accelerated recovery propagates.

In landscapes disturbed by high-intensity fires, this recovery dynamic is determined by spatial variability in fire effects and the resulting pattern of variable biological legacy density. To predict where recovery processes associated with

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remnant trees are most likely to occur, we must also predict where those trees are likely to have survived. Similarly, we must predict where persistence through secondary succession is likely if we are interested in the spatial dynamics of legacy influences on long-term forest development (Acker et al. 1998; Zenner et al. 2000; Keeton 2000). We investigated these questions for one type of biological legacy: remnant old-growth trees persisting in mature *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) forests in the US Pacific Northwest. The hypothesis tested was that remnant tree persistence varies spatially as a function of topographic heterogeneity that influences the behavior of stand-replacing wildfire.

High-intensity fire effects vary depending on climate, soils, forest structure and composition, and topography (Swanson et al. 1988; Agee 1993). Topography is one of the "boundary conditions" controlling the spatial pattern of disturbance effects (Swanson et al. 1988), because it is associated with variability in hydrology and soil moisture, temperature, wind movement, and physical barriers and corridors. These variables influence the type, frequency, and intensity of disturbances as well as their propagation or spread (Romme 1982; Swanson et al. 1988; Turner et al. 1989; Taylor and Skinner 2003). Some landforms and topographic positions are less likely to experience disturbances (or experience them less intensively), while other landforms are more prone to high-intensity disturbance (Hemstrom and Franklin 1982; Swanson et al. 1988; Turner et al. 1989; Morrison and Swanson 1990; Beaty and Taylor 2001). Protected topographic positions can shelter organisms and forest structures not found in the surrounding forest matrix (Hemstrom and Franklin 1982; Camp et al. 1997).

In temperate coniferous forests of the Pacific Northwest, wildfires often leave variable densities of live and dead remnant trees, depending on fire intensity and the age and structure of the stand at the time of disturbance (Cline et al. 1980; Spies and Franklin 1991). Remnant live conifers, composed of species such as *P. menziesii*, *Tsuga heterophylla*, and *Thuja plicata*, can persist for centuries through postdisturbance stand development. Consequently, remnant old-growth (>200 years old) trees are common in fire-originated mature stands (i.e., 80–200 years old) within the temperate Pacific Northwest (Spies and Franklin 1991). Associations between protected topographic positions and late-successional refugia (late-successional stands persisting within a seral matrix originated from a stand-replacing burn) have been widely reported, for example, for interior forests in eastern Washington (Camp et al. 1997) and south-central Wyoming (Romme and Knight 1981). However, potential associations between dispersed remnant trees and specific landform types are not well documented for *Pseudotsuga* forests of the Western Cascades.

Our research goal is to provide a basis for predicting spatial variability in remnant tree distributions and their influences on habitat and processes of stand development. To achieve this goal, the relationship between topographic variability and remnant tree persistence is investigated. A specific objective is to determine whether there are protected topographic positions that have higher probabilities of sheltering remnant old-growth trees within mature *P. menziesii* stands in the southwestern Washington Cascades. In this paper, we hypothesize that concave or riparian-influenced landforms have a higher probability of having remnant old-growth trees than convex (and thus drier) upslope landforms. We also hypothesize that associations between landforms and remnant tree densities vary by species as a function of species-specific fire resistances, such that species with low fire resistance are more likely to occur on protected landforms.

Materials and methods

Study areas

We selected two study areas that are representative of mature, fire-originated, naturally regenerated forests dominated by *P. menziesii*. They are located on the Gifford Pinchot National Forest in the southwestern Washington Cascade Range and range in elevation from approximately 300 to 1300 m above sea level. The first, the Trapper Creek Wilderness Area and adjoining roadless areas, incorporates portions of a 350- to 500-year-old forest as well as smaller patches originating from 1845, 1890, and 1902 wildfires. However, the majority of the study area (approx. 2000 ha) consists of a single stand that is approximately 135 years old. The second study area is the Siouxon Roadless Area. It consists largely of a single dominant cohort established following a 16 000 ha wildfire in 1902. Peripheral areas include younger or multiaged stands that originated following multiple reburns between 1902 and 1931 (Gray and Franklin 1997).

Plant associations at low to mid-elevations in the study areas are characteristic of the *Tsuga heterophyla* zone described in Franklin and Dyrness (1988). Within this zone, *P. menziesii* is the primary seral species, although *Tsuga heterophyla* is codominant or dominant on some sites. *Thuja plicata*, while abundant within remnant old-growth stands at low to mid-elevations, is a minor component of the mature cohorts. *Acer macrophyllum* (Pursh) Poir. (bigleaf maple) and *Alnus rubra* Bong. (red alder) are abundant on lower gradient floodplains, but are a minor component along first-order streams.

The study areas have a maritime-influenced climate that is moist temperate, characterized by mild, wet winters and warm, dry summers. The topography is moderate to very steeply sloped along generally accordant ridges, with intervening moderate to deeply dissected valleys. Soils are developed from volcanic tuffs and breccias and igneous (andesite and basalt) parent materials and commonly incorporate layers of tephra from Quaternary volcanic activity. They are predominately poorly developed Incepticols or well-developed Haplohumults where tephra is not a primary parent material. The fire regime consists of relatively infrequent (ca. >200-year fire-return interval), high-intensity wildfires of large spatial extent (e.g., 1000 – 10 000 ha) (Hemstrom and Franklin 1982).

Data collection

Selection and design of surveying transects

We used a ground-based survey to map remnant old-growth trees because their locations could not be reliably determined from aerial photographs or 1-m resolution digital orthophotos. We mapped the locations of all remnant old-growth trees, live and dead, along long belt transects. Two transects were established: 6.40 km long in the Trapper Creek Study Area and 4.21 km (live trees) long, with a nested 3.34 km (dead trees) long transect in the Siouxon Creek Study Area. The transects were curvilinear, because they followed continuous trail segments. The beginning and end points for transects were established at trail intersections. Trail segments were selected based on four criteria: (1) location on southwestern-facing aspects for consistency between study areas; (2) located entirely within mature (80–150 years old) forest; (3) located within the central portion of a burn area; and (4) a nearly constant grade, so as to be unbiased with respect to routing across slopes. The fourth selection criterion ensured that the trail segments had been built with no deliberate attention to scenery, such as remnant trees. This assumption was supported by extensive ground truthing: remnant trees were abundant and well distributed both within and outside the range (e.g., above and below slope) of survey transects.

Transect width (66 m) was established following field trials to determine effective upslope and downslope surveying distances using a laser rangefinder. The resulting transects were 42.25 ha (Trapper Creek), 27.78 ha (Siouxon Creek, live trees), and 22.06 ha (Siouxon Creek, dead trees). The Siouxon Creek transect was located on lower to mid-slope positions, while the Trapper Creek transect ranged from lower to upper slope and ridgeline positions. Elevation of the Trapper Creek and Siouxon Creek transects ranged from 395 to 1087 m and from 472 to 650 m above sea level, respectively.

GPS survey of remnant tree positions

Remnant trees were mapped with a surveying system consisting of a Trimble Pro XRS global positioning system, a Trimble Asset Surveyor data logger, an Impulse 200 laser rangefinder, and a MapStar precision electronic compass. Georeferenced positions were determined for live remnant trees >200 years old and remnant snags greater than 50 cm diameter at breast height and 10 m height. Live *Tsuga heterophylla*, *Thuja plicata*, and *Abies grandis* were cored with an increment borer to confirm age. Old-growth *P. menziesii* were easily recognizable from size and morphology, with most belonging to locally common ca. 300- and ca. 500-year-old age-classes.

Global positioning system data were differentially corrected in real time (via a radio receiver) and through post-processing using base-station data downloaded from the National Geodetic Survey. Estimated 80% confidence horizontal precisions were calculated in Trimble Pathfinder Office software. They ranged from 0.10 to 5 m, with 40% of positions achieving 1- to 2-m horizontal precision and 50% of positions achieving <1-m horizontal precision. Corrected tree positions were converted to UTM (NAD 1927 survey) coordinates.

Field description of landforms

Landform classes were assigned in the field to each remnant tree surveyed. Landform classes were based on slope curvature at a scale of approximately 100 m parallel to slope contour. Classes for concave landforms, in order of decreasing dissection depth, were floodplain terrace, ravine, shallow draw, and depression or seep. Classes for upslope (convex and planar) landforms were main slope, mid-slope bench, and narrow spur or ridge line.

Geographic information system database

A geographic information system database was assembled in ESRI ArcInfo. The database consisted of (1) a digital elevation model (DEM) with 10-m resolution covering three adjacent USGS 7.5-min quadrangles; (2) remnant tree positions segregated by species and live versus dead status; (3) survey transects; and (4) study area boundaries.

Data analysis

Curvature analyses

DEMs were used to generate landform classes using a topographic modeling method called curvature analysis. Curvature analysis predicts hydrologic flow lines by smoothing contour lines. This divides land surfaces into elements classified as divergent, convergent, and planar (O'Laughlin 1986; Dietrich et al. 1993). With a DEM of 10-m resolution or better, these land surface elements provide an accurate estimation of slope curvature (Dietrich et al. 1993). Divergent areas tend to be unsaturated during large precipitation events, while convergent areas tend to be saturated; convergent areas are closely associated with hydrologic convergence and thus tend to maintain higher soil moisture (O'Laughlin 1986; Dietrich et al. 1993).

Areas of convergence or divergence were delineated based on calculations of planform curvature on a pixel-by-pixel basis. The ESRI ArcInfo routine calculates a fourth-order polynomial for each pixel of the form:

$$Z = Ax^2y^2 + Bx^2y + Cxy^2 + Dx^2 + Ey^2 + Fxy + Gx + Hy + I$$

Coefficients A through I are generated from a three-dimensional surface (Fig. 1) to which Z values are fit. Figure 1 shows the relationships between coefficients and Z values for each of the nine neighboring values of elevation used to calculate curvature. Curvature output is the second derivative of the surface (i.e., the slope of the slope), such that:

$$\text{Curvature} = -2(D + E) \times 100$$

The curvature analysis resulted in a thematic layer of convergence and divergence at 10-m resolution (Fig. 2).

Frequency analysis

The area of convergent and divergent landforms was calculated within each transect and study area. Transformed into percentages, these represented the sampled or "expected" landform frequencies under a null hypothesis. The number of tree positions on convergent and divergent landforms was calculated for live and dead trees of each species. These values were transformed into frequency values, representing the "observed" landform frequencies. Density values for remnant trees by species, live versus dead status, and landform were calculated by dividing the number of trees observed by the area of convergent or divergent landforms sampled within the corresponding transect. We also calculated the density of remnant trees, by species and live versus dead status, occurring on landform classes assessed in the field. We

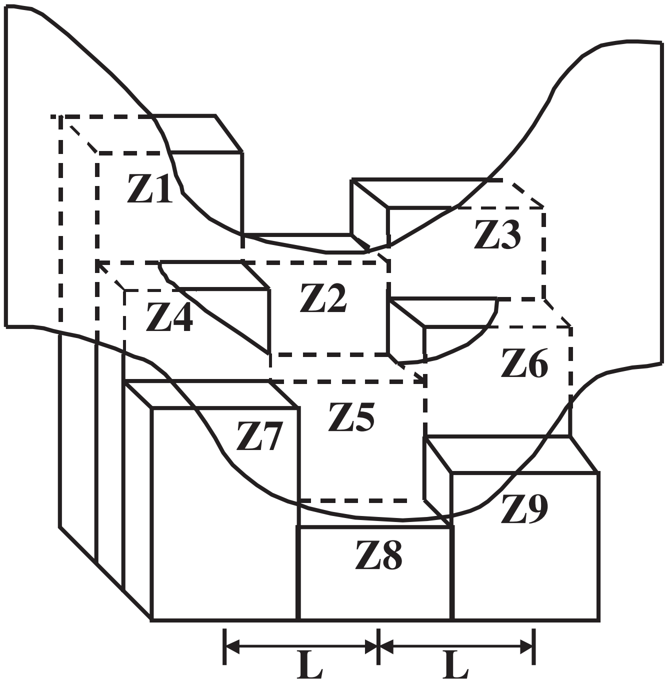


Fig. 1. Calculation of coefficients for curvature analysis. (Figure reprinted and modified with permission from ESRI. © 1998 ESRI. All rights reserved.)

$A = [(Z1 + Z3 + Z7 + Z9)/4 - (Z2 + Z4 + Z6 + Z8)/2 + Z5]/L4$
$B = [(Z1 + Z3 - Z7 - Z9)/4 - (Z2 - Z8)/2]/L3$
$C = [(-Z1 + Z3 - Z7 + Z9)/4 + (Z4 - Z6)]/2]/L3$
$D = [(Z4 + Z6)/2 - Z5]/L2$
$E = [(Z2 + Z8)/2 - Z5]/L2$
$F = (-Z1 + Z3 + Z7 - Z9)/4L2$
$G = (-Z4 + Z6)/2L$
$H = (Z2 - Z8)/2L$
$I = Z5$

normalized these data to the expected distribution of landform classes, which was generated from a supervised classification of the DEMs.

Statistical testing of significant ($\alpha = 0.05$) associations between tree presence and convergent verus divergent landforms and field-assessed landform classes was performed by comparing observed frequencies against expected frequency distributions using a log-likelihood ratio *G* test. The *G* test is a goodness-of-fit test that approximates the χ^2 statistic, but it is more robust than the χ^2 goodness-of-fit test when $|f_i - \hat{f}_i| \geq \hat{f}_i$, where f_i equals the observed distribution and $\hat{f}_i$ equals the expected distribution (Zar 1996), a condition met by these data. Representativeness of survey transects was assessed using the *G* test to compare the frequency of convergent versus divergent landforms sampled within transects against the frequency of those landforms found within the corresponding study area.

Analysis of aspect associations

We generated aspect classes from the DEMs. The classes were northeast (0°–90°), southeast (90.1°–180°), southwest (180.1°–270°), and northwest (270.1°–360°). The expected frequency of aspect classes was calculated within each survey transect. Remnant tree positions were overlaid on aspect classes and observed frequencies calculated by species and live versus dead status. Statistical testing of aspect associations was performed by comparing expected and observed frequencies using the χ^2 goodness-of-fit test. We tested the representativeness of aspect frequencies sampled within transects using the log-likelihood ratio *G* test.

Results

Landform associations

Live remnant old-growth trees

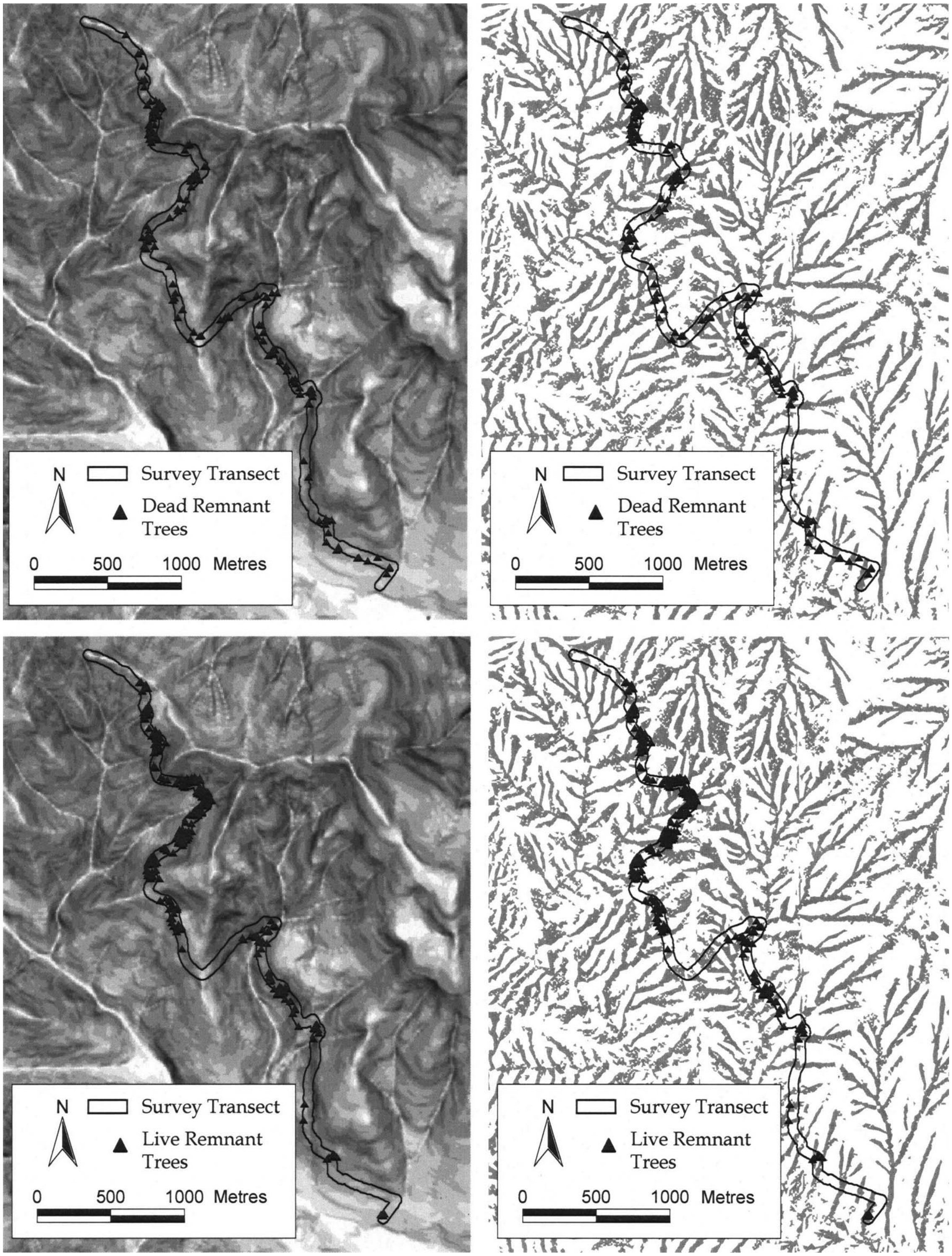
Spatial distributions and densities of live remnant trees differed by species. In the Trapper Creek study area, live remnant *Pseudotsuga* was ubiquitous and abundant (Fig. 3). It occurred at relatively high densities (compared to shade-tolerant species) across all landforms (Table 1) and was well distributed throughout the survey transect. *Pseudotsuga* density was not statistically related to convergent or divergent landform classification in Trapper Creek ($\alpha = 0.05$); it was abundant within both classes (Table 2). In the Siouxon study area, live remnant *Pseudotsuga* occurred at substantially lower density than in Trapper Creek (Fig. 3). The density of *Pseudotsuga* was similar to that of *Tsuga* and only slightly greater than that of *Thuja*. *Pseudotsuga* density was not statistically related to convergent or divergent landform classes in Siouxon Creek (Table 2).

Remnant *Pseudotsuga* density was related to specific types of landforms within convergent and divergent groupings. In Trapper Creek, live remnant *Pseudotsuga* were most strongly associated with draws ($G = 6.72$, $P < 0.05$,) relative to other convergent landform classes (see Table 3 for critical values of the test statistic). In Siouxon Creek, remnant *Pseudotsuga* were also disproportionately abundant on floodplains ($G = 11.77$, $P < 0.01$); a similar association could not be determined for Trapper Creek, because the survey transect did not span low-gradient floodplains there. Within divergent landforms, they occurred in highest densities on spurs and major ridgelines ($G = 42.26$, $P < 0.001$), especially dry, upper slopes with rocky outcrops.

Live remnants composed of shade-tolerant species were at low densities in both study areas (Table 1) but showed strong landform associations (Fig. 3). Densities in Trapper Creek were an order of magnitude or more lower than for *Pseudotsuga*. *Thuja* and *Tsuga* densities were significantly ($P < 0.001$) associated with convergent landforms in both the Trapper Creek and Siouxon Creek study areas (Table 2). *Thuja* was found exclusively on convergent landforms in both study areas. Live remnant *Tsuga* were found exclusively on convergent landforms, except for one individual in the Trapper Creek study area.

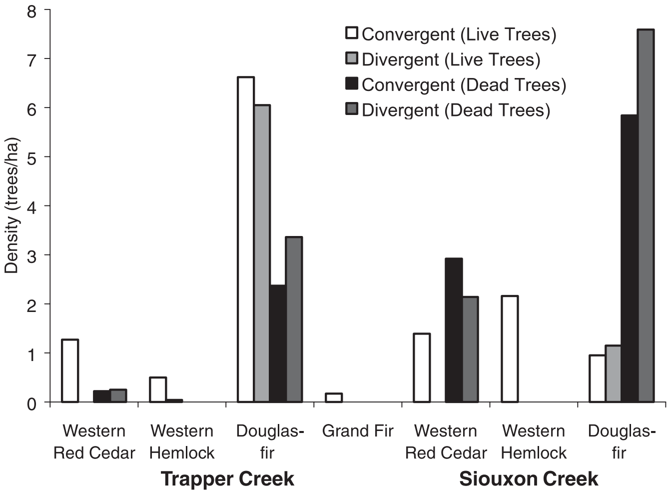
In Trapper Creek, remnant *Tsuga* were relatively evenly distributed across all concave landform classes ($\alpha = 0.05$). These included deeply incised ravines, shallow draws ranging from low to upper slope position, and shallow depressions with ephemeral streams or seeps at mid-slope positions. Remnant *Thuja*, by comparison, were disproportionately clumped in seeps and shallow depressions ($G = 18.16$, $P < 0.001$). In Siouxon Creek, live remnant *Tsuga* and *Thuja* were found primarily on floodplains or within ravines along perennial streams. Compared to Trapper Creek, only a small number of remnant *Tsuga* and *Thuja* were found in shallow

Fig. 2. Remnant old-growth tree positions within the Trapper Creek survey transect are shown as an example. Positions for live (bottom panels) and dead (top panels) remnant trees are shown. Panels on the left show topographic relief (slope steepness). Panels on the right show slope curvature. Note the high resolution of convergent landforms (shaded areas) following main floodplains, finely dendritic perennial and ephemeral draws, and isolated wet depressions. Divergent areas are depicted in white.



draws and none were found in mid-slope depressions or seeps. Thus, they were strongly associated with deeply incised landform classes ($P < 0.001$). Live remnant *Abies grandis* were found, in very low density (Fig. 3), only in the Trapper Creek study area. They were associated ($P < 0.025$) with convergent landforms (Table 2). We found only a few remnant

Fig. 3. Density of live and dead remnant old-growth trees by species, landform, and study area.



Abies. While these were found to be persisting only in shallow draws and depressions at mid-slope, there was no statistical association with landform classes ($G = 4.80$, $P < 0.10$).

Remnant old-growth snags

Remnant old-growth snags were abundant on all landforms in both study areas (Fig. 2). *Pseudotsuga* snags were found in the highest densities, although *Thuja* snags were also abundant. No remnant *Tsuga* or *Abies* snags were found. Both *Pseudotsuga* and *Thuja* snags were found in approximately equal density on convergent versus divergent landforms ($\alpha = 0.05$) (Table 2). Remnant snag densities were substantially higher in the Siouxon Creek study area than in the Trapper Creek study area (Table 1). The density of *Pseudotsuga* snags on all landforms was over twice as high, and that of *Thuja* snags was over 10 times higher in Siouxon Creek than in Trapper Creek.

Associations with aspect

Associations between remnant tree densities and aspect differed by species and study area and between live and dead trees. Live remnant *Pseudotsuga* were significantly associated ($\chi^2 = 20.54$, $P < 0.001$) with northwestern aspects in the Trapper Creek study area, in contrast to the Siouxon Creek study area, where they were not significantly correlated ($\alpha = 0.05$) with aspect (see Table 3 for critical values of the test statistic). Shade-tolerant conifer densities were not associated with aspect in Trapper Creek. However, in Siouxon Creek, live *Tsuga* were significantly ($\chi^2 = 11.61$, $P < 0.01$) associated with northeastern aspects. Live *Thuja* persistence was not correlated with aspect in that study area; the χ^2 test result relative to northwestern aspects was 7.73 ($P < 0.06$). Remnant snags were not statistically associated with aspect in Trapper Creek, but *Pseudotsuga* ($\chi^2 = 48.99$, $P < 0.001$) and *Thuja* snags ($\chi^2 = 14.52$, $P < 0.01$) were statistically related to northeastern and southeastern aspects, respectively, in Siouxon Creek.

Representativeness of results

There was no statistically significant difference between the frequency of convergent or divergent landforms sampled in transects compared with their relative frequency within the study areas (Fig. 4). Landform associations found in survey transects are thus representative of patterns likely to occur throughout the study areas. The survey transects were not, however, representative of aspect frequencies in either the Trapper Creek ($G = 16.27$, $P < 0.001$) or the Siouxon Creek ($G = 80.08$, $P < 0.001$) study areas. This was due to undersampling of northwestern and northeastern aspects. Over two-thirds of the southwestern Washington Cascades physiographic province has geomorphology similar to that of our study areas according to USDA Forest Service classifications.

Discussion

Remnant tree persistence patterns vary with landform setting and by species within a burned area. Remnant live *Pseudotsuga* densities are not correlated with coarse divisions of topography into convergent or divergent classes, being well distributed across both. However, *Pseudotsuga* are patchily distributed and associated with particular landforms, such as dry, rocky outcroppings, ridgelines, floodplains, and draws. The division of land surface into areas of convergence versus divergence does not capture these finer grained landform associations. Spatial variability in the density of surviving shade-tolerant species is statistically related to landform, such that areas with convergent topography are more likely to shelter live remnant shade-tolerant conifers. Topographic classifications are not direct measures of soil moisture gradients. But convergent landforms are correlated with hydrologic convergence (Dietrich et al. 1993) and, consequently, maintain higher soil moisture levels than divergent landforms.

We infer from our results that there is a probable mechanism linking fire behavior with remnant tree persistence in convergent areas. Namely, elevated soil moisture and relative humidity on convergent landforms sustain higher fuel moisture content (Camp et al. 1997; Skinner 2002). This, in turn, reduces surface fireline intensity, flame length, probability of crown fire initiation, and crown fire spread rate (Van Wagner 1977). Consequently, moister landforms are less likely to experience high fire severity (i.e., bole and crown damage) than drier landforms burned in the same fire where fuels are not limiting (Romme and Knight 1981; Camp et al. 1997; Agee 1998) and fires are not channeled upslope through concavities by strong winds or convective processes (Agee 1993; Tollefson 2001). Crown fires do appear to move through moist areas on mid- to upper slope positions, but mortality of shade-tolerant coniferous species is often less severe than on drier, divergent landforms. Riparian areas on valley bottoms and perennial draws at low slope positions can act as fire breaks and can completely escape crown fires (Hemstrom and Franklin 1982).

Species-specific persistence patterns

Patterns of remnant tree persistence reflect the fire-resistance traits of individual species. Fire resistance in conifers is related to bark thickness, rooting depth, height to crown base, bud characteristics, and crown shape (Minore 1979; Peterson and Ryan 1986; Peterson and Arbaugh 1989; Agee 1993). Species with thicker bark and deeper rooting systems at ma-

Table 1. Numbers and densities of remnant trees by species, live versus dead status, and survey transect.

		No. encountered		Density (all landforms) (trees/ha)		Density (convergent landforms) (trees/ha)		Density (divergent landforms) (trees/ha)	
	Species	Trapper Creek	Siouxon Creek	Trapper Creek	Siouxon Creek	Trapper Creek	Siouxon Creek	Trapper Creek	Siouxon Creek
Live	PSME	266	29	6.3	1.04	6.62	0.95	6.05	1.15
	THPL	23	18	0.54	0.65	1.27	1.39	0	0
	TSHE	10	28	0.24	1.01	0.5	2.16	0.04	0
	ABGR	3	0	0.07	0	0.17	0	0	0
	Total	302	75	7.15	2.7	8.55	4.48	6.09	1.15
Dead	PSME	124	138	2.93	6.26	2.37	5.84	3.36	7.59
	THPL	10	52	0.24	2.36	0.22	2.92	0.25	2.14
	Total	134	190	3.17	8.61	2.59	8.76	3.61	9.73

Note: PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*; ABGR, *Abies grandis*.

Table 2. Contingency table and results of goodness-of-fit log-likelihood ratio (*G*) test for remnant tree associations with convergent (conv.) and divergent (div.) landforms.

				Observed		Expected				
Study area	Type	Species	*n*	Conv.	Div.	Conv.	Div.	$\chi^2_{0.05,1}$	*G*	*P* value
Trapper Creek	Live	PSME	266	120	146	114.1	153	3.841	0.53	ns
	Live	THPL	23	23	0	9.86	13.1	3.841	9.86	<0.001
	Live	TSHE	10	9	1	4.29	5.79	3.841	9.86	<0.001
	Live	ABGR	3	3	0	1.29	1.17	3.841	5.08	<0.025
	Dead	PSME	124	43	81	53.18	70.8	3.841	3.49	<0.10ns
	Dead	THPL	10	4	6	4.29	5.71	3.841	0	ns
Siouxon Creek	Live	PSME	29	12	17	13.51	15.5	3.841	0.32	ns
	Live	THPL	18	18	0	8.38	9.62	3.841	42.8	<0.001
	Live	TSHE	28	28	0	13.04	15	3.841	27.5	<0.001
	Dead	PSME	138	60	78	65.83	72.2	3.841	0.99	ns
	Dead	THPL	52	30	22	24.8	27.2	3.841	2.08	ns

Note: PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*; ABGR, *Abies grandis*; ns, not significant.

Table 3. Critical values of the test statistic (α = 0.05) used for goodness-of-fit log-likelihood ratio (*G*) and χ^2 tests.

No. of categorical groups in test	df	Critical values of the test statistic
3	2	5.991
4	3	7.815

turity, such as *Pseudotsuga*, are less susceptible to cambium and root damage (Minore 1977; Peterson and Arbaugh 1989). *Tsuga* and *Thuja* have lower resistance to fire than *Pseudotsuga*, because they have thin bark and shallow root systems (Minore 1977). Thus, *Tsuga* and *Thuja* have a higher probability of surviving in protected topographic locations where fire intensity and (or) frequency are reduced. Resistance to fire-caused crown damage is also influenced by bud morphology and phenology. *Pseudotsuga* has small buds that are unshielded by needles and, consequently, does not have high crown resistance to heat; hence, flame lengths that reach the crown have a high probability of causing mortality (Peterson and Ryan 1986). Another measure of fire resistance is height to crown base (Peterson and Arbaugh 1989; Agee 1996), but for a given tree height, this does not differ significantly between *Pseudotsuga*, *Tsuga*, and *Thuja*. However, the generally faster growth of *Pseudotsuga* and the taller sizes it attains at maturity do give this species a higher mean height to crown base in mixed-species stands. Having greater resistance to fire, *Pseudotsuga* can survive in both protected and unprotected topographic locations.

Long-term persistence of remnant trees may vary between species as a function of resistance to windthrow, which depends on rooting depth and height/diameter ratio. Resistance to windthrow may be particularly important for survival in the exposed, open-canopied conditions encountered after a fire. Susceptibility to windthrow varies with topography (Gratkowski 1957) and by species (Minore 1979). In open, postfire environments, deeply incised landforms provide protection from windthrow. Susceptibility to windthrow can actually increase on wetter soils where rooting zones are restricted (Gratkowski 1957). Hence, convergent landforms may offer protection from wind only where reduced exposure to wind outweighs reduced rooting stability. It is possible that protection from fire and from postfire wind exposure may operate synergistically to create the strong associations of remnant shade-tolerant conifers with concave landforms. It also is possible that postfire insect and pathogen disturbances may have influenced long-term remnant tree survival rates, although we found no direct evidence of this.

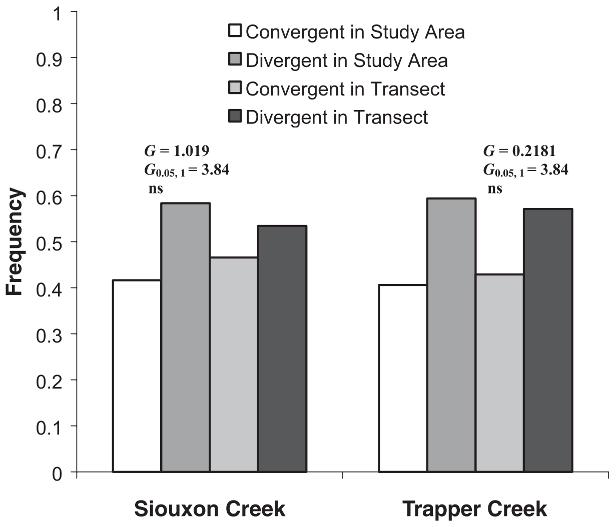


Fig. 4. Representativeness of survey transects relative to landform frequencies as determined by goodness of fit, log-likelihood ratio (G) test. ns, not significant.

Differences in persistence patterns may also be influenced by prefire species distributions. Shade-tolerant mature and old-growth trees can be clumped as a result of spatial variation in regeneration associated with seed rain, remnant tree or canopy structure, gap dynamics, and substrate (Moeur 1997; Goslin 1997). However, the strong landform associations of remnant *Thuja* and *Tsuga* are probably not a legacy of spatial pattern prior to disturbance. We base this conclusion on three arguments. First, remnant *Thuja* snags are not associated with landform type; they are abundant on all landforms, particularly in the Siouxon study area. Second, mature *Thuja* and *Tsuga* are evident in the existing mature cohort on both concave and convex landforms, and their density does not decline with distance from riparian areas (Keeton 2000); they are also extant on both north and south aspects. Third, *Thuja* and *Tsuga* are codominant in the canopies of upper slope (on both north and south aspects) and ridgeline old-growth stands bypassed by fires in both the Siouxon and Trapper Creek study areas. *Thuja* and *Tsuga* were, therefore, significant components of the prefire old-growth canopy in both riparian and upslope areas and on both north and south aspects.

Multiscale patterns of persistence

Remnant shade-tolerant conifers do sometimes occur on upslope, divergent landforms. The few such examples we found in our study areas (primarily outside of survey transects) and nearby burns were all positioned along burn boundaries (Keeton 2000). Upslope examples of remnant *Tsuga* reflect the complex fire history of the southwestern Washington Cascades. At least 14 moderate (e.g., 1000 to 10 000 ha) and large (e.g., >10 000 ha) wildfire events from the 15th to early 20th century have created a mosaic of mature and old-growth age-classes across the Siouxon Creek and Wind River drainage basins (Gray and Franklin 1997). Our determinations of stand ages and boundaries indicate that these age-classes often have highly diffuse or overlapping boundaries. Because of these overlaps, patterns of persistence at a drainage basin or landscape scale may be more complex than those seen within individual burns. For example, at the scale of the Wind River basin as a whole, remnant shade-tolerant conifers may occupy a broader diversity of landform positions because of the persistence of intact remnant stands (unburned fire refugia) and multiaged (partially burned) patches at burn interfaces.

Remnant snags

Remnant snags are abundant and ubiquitous across all landforms in the burns studied. The dominance of remnant *Pseudotsuga* snags is consistent with previous studies (Cline et al. 1980). However, remnant snag and live tree densities do vary between the two study areas. The density of remnant snags in Siouxon Creek is 2.7 times higher than in Trapper Creek. The density of live remnant trees in Trapper Creek is 2.6 times higher than in Siouxon Creek. These results have multiple interpretations. First, fireline intensity may have been greater in Siouxon Creek, reducing remnant live tree densities. Additional indications of a more severe Siouxon burn are the relatively small area of remnant *Tsuga* and *Thuja* in shallow draws and their complete absence in midslope depressions or seeps. The Siouxon fire occurred during a single month, September 1902, in which about 280 000 ha burned in 110 separate fires across western Oregon and Washington. The fires were associated with drought conditions and, possibly, a warm, dry east-wind event (Gray and Franklin 1997). These weather conditions create the potential for fires of high intensity and large extent in maritime- influenced Pacific Northwest forests (Keeton et al. 2005). There are no contemporaneous reports of the Trapper Creek fire, but its extent was about one-third that of the Siouxon fire.

The second possibility is that snag densities are lower in Trapper Creek because the stand originated from an older burn (Cline et al. 1980). In *Pseudotsuga* forests of western Oregon and Washington, the volume and biomass of coarse woody debris carried over from previous stands declines to near zero by age 250; coarse woody debris is least abundant in mature stands (80–200 years old) compared with that in young and old-growth stands (Spies et al. 1998). It might be conjectured that stand age-related losses explain the lower densities found in Trapper Creek, since *Pseudotsuga* snags are known to lose substantial structural integrity after 19–50 years (Cline et al. 1980). However, barring the possibility of a major blowdown, the age difference between the two burns (about 37 years) cannot entirely account for the difference in densities, although it could account for substantial reductions in bole integrity and height.

One or more reburns is a third and probable explanation for reduced snag densities in the Trapper Creek study area. Some areas of the Siouxon burn were reburned (Gray and Franklin 1997), but these were outside the area studied. We found (see Keeton 2000) the dominant mature trees to have a broad age range in Trapper Creek (80–135 years) because of either a protracted establishment period, as occurred in portions of the Siouxon burn (Gray and Franklin 1997), or one or more reburns. Reburns following a stand-replacing burn can substantially reduce coarse woody debris biomass and two or more reburns can essentially eliminate coarse woody debris, including snags (Spies et al. 1988).

The effect of aspect on postfire persistence

There are dramatic differences in thermal conditions on the north and south side of major ridgelines. These differences were not captured by the survey transects, because the transects spanned the southwest side of major ridges. However, the deeply dissected topography sampled within transects provided for a diversity of aspects, including north-facing aspects, at spatial scales smaller than the entire ridge. Aspect variation at this scale will capture environmental variability but perhaps not as dramatically as that encountered on opposing sides of major ridges.

Aspect is an important driver of spatial and temporal variations in fire dynamics across a range of forest types and fire regimes. Aspect correlates with solar flux differences that influence site and fuel moisture status (Taylor and Skinner 2003). Fire frequencies are lower on cool, wet north and east-facing aspects in the central Washington Cascade Range (Hemstrom and Franklin 1982), the eastern Washington Cascade Range (Camp et al. 1997), the California Southern Cascades (Beaty and Taylor 2001), and the Klamath Mountains (Taylor and Skinner 2003). The strong association between remnant live *Pseudotsuga* and northwestern-facing aspects in Trapper Creek suggests a similar relationship. The relationship between remnant *Tsuga* and *Thuja* and northwestern and northeastern aspects, respectively, in Siouxon Creek suggests that cooler aspects reduced fire intensity there as well.

Aspect appears to influence spatial variability in densities of both remnant live and dead trees, although these effects vary between burns. While *Thuja* snag densities were highest on southeastern aspects in Siouxon Creek, the far more abundant *Pseudotsuga* snags were strongly associated with the most thermally isolated aspect (northeast). This is probably due to one or more of the following: (1) initial higher survival followed by mortality due to damage during the fire and subsequent events such as insect outbreaks; (2) reduced combustion during the fire events; or (3) slower decomposition on cooler, moister sites. Aspect may operate synergistically with landform associations, such that survivorship of species with low fire resistance is highest in convergent landforms on north-facing aspects.

Landform influences on tree persistence patterns

Topography affects tree survivorship patterns following high-intensity fire, based on our results and previous research (e.g., Turner et al. 1989, Turner et al. 1995, Taylor and Skinner 2003). However, the specific associations we found between remnant tree persistence and landforms inferred to reduce fire intensity are consistent with some, but not all, previous studies. For instance, in a reconstructed fire history for Mount Rainier National Park, Hemstrom and Franklin (1982) found that protected topographic locations (such as riparian-influenced landforms) sheltered the oldest forest age-classes. Similarly, Morrison and Swanson (1990) found that steep, deeply dissected topography in the Oregon Cascade Range had fires of more moderate severity compared with those on gentler topography. Associations between protected landforms and fire refugia also have been documented for a number of drier, western US forest types, such as the eastern Cascade Range in Washington (Camp et al. 1997), spruce-fir forests in Wyoming's Medicine Bow Mountains (Romme and Knight 1981), and ponderosa pine forests in the Black Hills of South Dakota and Wyoming (Shinneman and Baker 1997). Even narrow, riparian-influenced landforms can act as protected positions in the Klamath Mountains of California (Skinner 2002).

Despite these apparent similarities, it is important to avoid generalizations regarding landform effects on tree persistence patterns, because previous research has reached conflicting conclusions. For instance, Olson (2000) found that riparian-influenced landforms did not have longer fire-return intervals compared with upslope areas in portions of the Blue Mountains of northeastern Oregon. Riparian-influenced landforms in the central Oregon Cascades burned historically with highly variable intensities and frequencies (Cissel et al. 1999). Depending on wind direction and speed, steep, constrained valleys sometimes can amplify, rather than retard, fire effects by channeling fires upward or downward (Agee 1993, 1998; Tollefson 2001). In central Mexican pine forests, valley bottoms and ravines burn more intensively than upland sites, because fuel production is higher and fuels also desiccate during the fire season (Segura and Snook 1992).

In our view, conflicting conclusions reached by previous studies reflect differences in fire regime and fire behavior specific to physiographic region and forest type. They relate also to site-specific differences in stand age, structure, and composition (Agee 1993, Weatherspoon and Skinner 1995) as well as fuel profile (Agee 1991), fuel desiccation rates (Camp et al. 1997), and variables affecting the spread of individual fires, such as wind direction and speed (Agee 1998, Cissel et al. 1999). These differences may explain why our results are consistent with only a subset of previous studies.

Management implications

Landforms are important sources of spatial variation in forest structure and composition within mature *Pseudotsuga* forests, based on our results. By controlling the spatial distribution of remnant trees, landforms have important indirect effects on stand development processes and habitat functions associated with these biological legacies (Franklin et al. 2000, 2002). Understanding the landform associations of remnant trees is useful when designing alternative silvicultural approaches, such as green-tree and snag-retention practices, which are intended to maintain spatial patterns similar to those associated with natural disturbance regimes (Franklin et al. 2002). In addition, using landform classifications to predict variability in remnant tree distributions could help forest managers estimate spatial variability in rates and pathways of stand development (Acker et al. 1998; Keeton and Franklin 2005; Zenner 2000) and other biological functions (Franklin et al. 2002) associated with remnant trees. Both shade-tolerant and shade-intolerant species can survive high-intensity wildfires, but shade- tolerant remnant trees tend to be concentrated in concavities and riparian areas. In silviculturally managed forests, foresters could more closely approximate this pattern by retaining higher densities of shade-tolerant conifers in and near riparian-influenced landforms, while retaining *Pseudotsuga* and snags in similar densities on riparian and upslope landforms. Based on our results, a disturbance-based riparian management approach (Cissel et al. 1999) might include variable levels of biological legacy retention, including ensuring the presence of both live and dead trees.

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