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WINDTHROW DISTURBANCE, FOREST COMPOSITION, AND STRUCTURE IN THE BULL RUN BASIN, OREGON

DIANA S. SINTON,[1,3] JULIA A. JONES,[1] JANET L. OHMANN,[2] AND FREDERICK J. SWANSON[2]

[1]*Department of Geosciences, Oregon State University, Corvallis, Oregon 97331 USA*
[2]*U.S. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon 97331 USA*

Abstract. This study examined relationships among forest landscape dynamics, environmental factors (climate and landforms), and disturbance history in forests dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*) in the Bull Run basin in northwestern Oregon and evaluated the findings in a broader geographic context. Three sets of analyses were conducted: mapping of historical windthrow disturbance patches in the 265-km^2 Bull Run basin over the past century and analysis of their relationships with meteorological conditions, landforms, and vegetation; comparison of forest structure and species composition as a function of mapped windthrow and wildfire disturbance history in 34 1-ha vegetation survey plots in Bull Run; and canonical correspondence analysis of environmental factors and forest overstory species composition in 1637 vegetation plots in the Mount Hood and Willamette National Forests. Nearly 10% of the Bull Run basin has been affected by windthrow since 1890, but only 2% was affected prior to the onset of forest harvest in 1958. Most of the mapped windthrow occurred in areas with 500- to 700-yr-old canopy dominants and no mapped disturbance by fire in the past 500 yr. Most mapped windthrow occurred during three events in 1931, 1973, and 1983 that were characterized by extreme high speed east winds from the Columbia River Gorge. Forest harvest modified the effects of climate, landforms, and vegetation on windthrow disturbance, reducing the importance of topographic exposure to east and northeast winds, and creating a strong influence of recent clearcut edges, which accounted for 80% of windthrow in the 1983 event. Shade-tolerant overstory species (western hemlock and Pacific silver fir) are abundant in present-day forest stands affected by windthrow as well as by fire in the past century. In the western Cascade Range, Douglas-fir and western hemlock decline and Pacific silver fir increases with elevation (summer moisture stress declines but temperature variability increases), but this transition occurs at lower elevations in the Bull Run, perhaps because of the interaction between regional climate processes and disturbance along the Columbia Gorge. Complex landscape dynamics result from these contingent interactions among climate, landform and stand conditions, and disturbance.

Key words: canonical correspondence analysis; clearcut edges; disturbance history; Douglas-fir; forest structure; landscape dynamics; logistic regression; Oregon, northwest; Pacific silver fir; Pseudotsuga menziesii; Tsuga heterophylla; *western hemlock; windthrow disturbance.*

INTRODUCTION

This study examined relationships among forest landscape dynamics, environmental factors (climate and landforms), and disturbance history in forests dominated by Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*) in a 265-km^2 basin in northwestern Oregon, and evaluated the findings in a broader geographic context. Throughout the Pacific Northwest region, forest species composition is associated with climate and its expression along environmental gradients of temperature and moisture (Dyrness et al. 1976, Zobel et al. 1976, Ohmann and Spies 1998). However, the composition and structure of contemporary forests in this region also clearly reflect disturbance history over the past 500+ yr (Morrison and Swanson 1990, Agee 1993, Spies 1997, Weisberg 1998). Inferred relationships between disturbance regime (White 1979, Sousa 1984, Pickett and White 1985) and forest composition and structure (Swanson et al. 1993, Spies and Franklin 1991) have been incorporated in models of forest succession (Dale et al. 1986, Spies 1997) and used as the basis for management of forested landscapes (Cissel et al. 1999, Nowacki and Kramer 1998, Landres et al. 1999). Although many disturbance reconstructions and landscape management plans have focused on wildfire, windthrow also is a major component of forest landscape dynamics in many regions (Canham and Loucks 1984, Franklin and Forman 1987, Foster 1988, Foster and Boose 1992, 1995, Boose et al. 1994, Abrams et al. 1995, Foster et al. 1997, 1998, Rebertus et al. 1997).

Windthrow disturbance appears to be affected by environmental and biotic factors operating from stand to

Manuscript received 24 February 1999; revised 22 September 1999; accepted 23 September 1999.
[3] Present address: Division of Environmental Studies, Alfred University, Alfred, New York 14802 USA.
E-mail: dsinton@alfred.edu

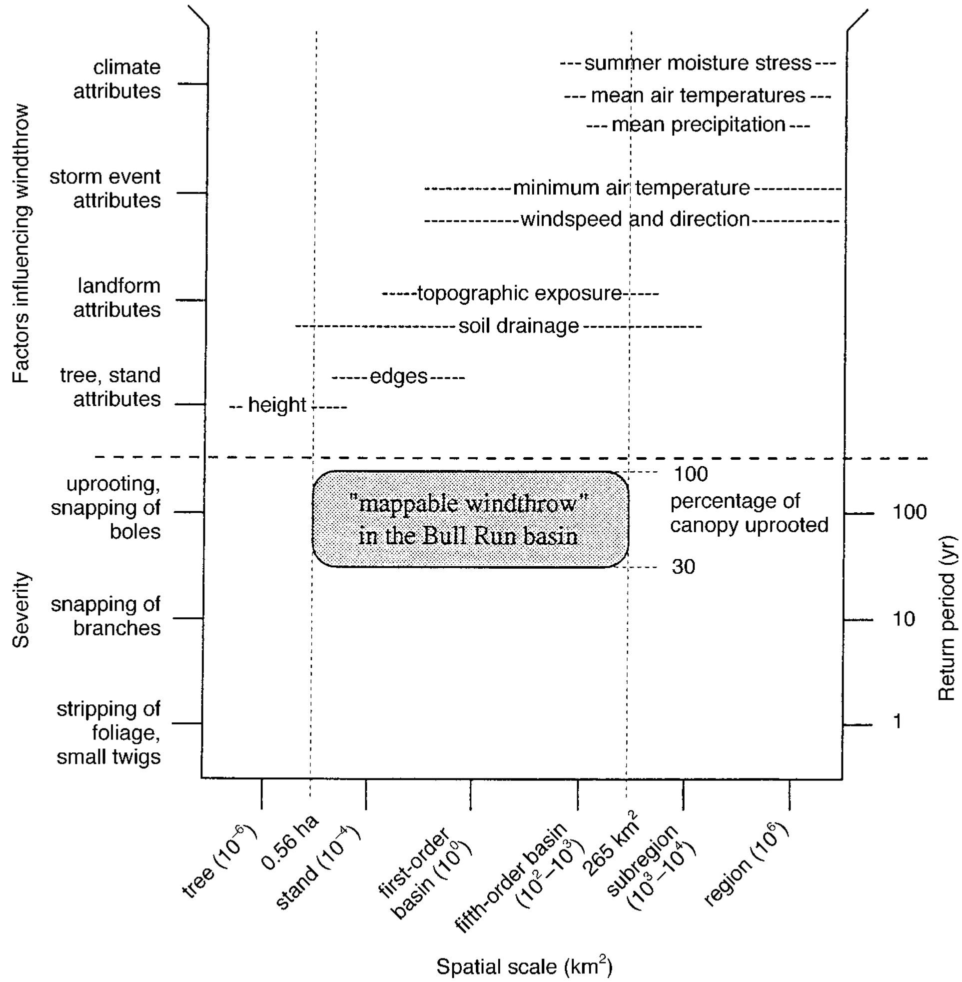

FIG. 1. Spatial scales of hypothetical factors influencing windthrow that were examined in this study, and the spatial grain, extent, and severity of "mappable windthrow" in this study.

landform and regional spatial scales, and over temporal scales ranging from years to centuries (Fig. 1). Severe windthrow events are associated with regional air masses such as hurricanes in the Atlantic (Foster and Boose 1992, Boose et al. 1994, Loope et al. 1994) and severe storms in the northern and southern Pacific regions (Orr 1963, Kramer 1997, Rebertus et al. 1997). Forests in landform positions that are exposed to extreme winds also are particularly susceptible to windthrow (Boose et al. 1994, Kramer 1997, Rebertus et al. 1997). In addition, windthrow may be more likely in forest stands whose biotic structure exposes them to wind because they are very tall (Foster and Boose 1992) or are located along edges of canopy openings, such as meadows or recent forest clearcuts (Franklin and Forman 1987).

Windthrow, wildfire, and individual treefall gaps have distinct effects on the structure and composition of forest stands. By blowing down large, living trees in a stand, with only localized soil disturbances around root wads and boles of downed trees, windthrow increases light availability somewhat and facilitates rapid growth and canopy accession by shade tolerant understory trees (Abrams and Scott 1989), while reducing snags and increasing down wood on the forest floor. In contrast, crown fire dramatically reduces shade, soil surface organic matter, and down wood, which greatly increases light availability and favors succession by invading, shade-intolerant species. In forests of the Pacific Northwest, postwindthrow stands may have advanced regeneration, i.e., understory shade-tolerant species, such as western hemlock and Pacific silver fir, that are released to dominate the new stand, whereas postfire forest stands are typically dominated by the shade-intolerant Douglas-fir (Franklin and Dyrness 1973, Hemstrom and Franklin 1982, Stewart 1988, Spies 1997). In the absence of windthrow or wildfire, forest stand structure and composition evolve through individual tree death and toppling, release of shade-tolerant species in resulting small gaps, and a gradual increase in snags and down wood on the forest floor. In the Pacific Northwest, small-gap processes produce the fine-scale heterogeneity in species composition and structural characteristics of old-growth forest stands (Spies and Franklin 1989, 1991).

General principles of landscape dynamics, including the stability or equilibrium properties of forest landscapes, have been addressed in theoretical and empirical studies. Perceptions of stability and variability are conditioned by temporal and spatial scales of ecosystem processes and how they are sampled (e.g., the grain and extent of the study), and stability can be predicted for landscapes affected by a single disturbance process, with static boundary or forcing conditions (i.e., no climate variability), and homogeneous landforms (i.e., no topo-edaphic variability) (Turner et al. 1993). However, topo-edaphic features (Mladenoff et al. 1993), climate history (Fuller et al. 1998, Long et al. 1998), and the history of human settlement (Frelich and Reich 1995, Impara 1997, Van Norman 1997, Foster et al. 1998, Long et al. 1998, Weisberg 1998) also influence the perceived stability and variability of forest landscape dynamics.

The Bull Run, a 265-km^2 basin located 30 km east of Portland, Oregon, provides the opportunity to examine relationships among forest landscape dynamics, environmental factors, and disturbance history by wildfire and windthrow. Forests in most of the Bull Run basin are dominated by old-growth Douglas-fir regenerated from episodes of severe, widespread wildfire circa 1200 and 1500 (Krusemark et al. 1996). Smaller portions of the basin burned in the 17th to 19th centuries, but little fire has occurred since the early 1900s, when the basin became the primary source of water for the City of Portland and policies of fire suppression and limited public access were enforced (Wilson 1989). Although the basin is part of the Mount Hood National Forest, forest harvest in the basin began in 1958 (Wilson 1989), whereas clearcutting began in the 1930s and 1940s on other nearby national forest lands (Jones and Grant 1996). Episodic, severe windthrow events in the Bull Run in the 1970s and 1980s prompted study of the possible effects of forest harvest on windthrow (Franklin and Forman 1987), and public concern led to litigation that ended commercial timber harvest operations (Wilson 1989) and now strictly limits any other logging operations in the Bull Run watershed.

We used disturbance reconstruction methods in the Bull Run basin and vegetation plot data from a larger surrounding area to examine these questions: (1) What were the spatial and temporal patterns of severe windthrow in the basin, and how were they related to climate, landforms, and stand structure and composition? (2) How do present-day forest structure and composition differ among stands affected dominantly by historical windthrow, wildfire, and individual tree gap processes? (3) What are the implications of these relationships for landscape dynamics and management?

Methods

Approach

Three sets of analyses were conducted of the relationships among forest landscape dynamics, environmental factors (climate and landforms), and disturbance history in and around the Bull Run basin. We used field mapping and other techniques to reconstruct historical windthrow events in the Bull Run basin, and then examined statistical relationships between environmental factors and mapped windthrow patterns for three extensive windthrow events. Based on mapped windthrow and fire history (Krusemark et al. 1996), we compared forest structure and species composition as a function of disturbance history in 34 1-ha vegetation survey plots in the Bull Run. Finally, we conducted a canonical correspondence analysis of environmental factors and forest overstory species composition in 1637 area ecology plots in the Mount Hood and Willamette National Forests in the western Cascades, and we assessed the regional significance of Bull Run by comparing the 80 plots within the Bull Run to those outside.

Study site

The Bull Run is a 265-km^2 basin located in the Mount Hood National Forest, Oregon (Fig. 2). Elevations in the Bull Run range from 225 to >1400 m. The climate of the Bull Run and the surrounding western Cascade Range of Oregon is characterized by warm, dry summers and cool, wet winters. Average annual precipitation in the Bull Run ranges from 2280 mm at the lowest elevations to 4300 mm at the highest elevations (U.S. Forest Service 1987). From 70% (in the Bull Run) to 80% (in the rest of the western Cascades) of precipitation occurs from November to April, falling as rain at low elevations and as snow at higher elevations. Mean monthly air temperatures in Bull Run range from 3°C in December and January to 14°C in July; temperatures in the western Cascades range from 2° to 19°C. Below-freezing temperatures are rare; mean monthly soil temperatures range from 2° to 16°C in the western Cascades and 2–12°C in the Bull Run. Although summer winds are predominantly weak and originate from the west and southwest, extreme winds originate from the east during winter storms (Cameron 1931, Lawrence 1939, U.S. Forest Service 1987). This wind pattern appears to be the result of the convergence of marine and continental air masses above the deep, narrow Columbia River Gorge, the lowest elevation along the north–south trending Cascade Range.

The geology of the Bull Run basin is dominated by basalt and andesite overlain with glacial till (Schulz 1981). The Bull Run and its tributaries have incised steep canyons in wide glacially carved valleys; only 5% of the basin has slopes <5%, and only 12% has slopes >50%. Soils are colluvial and range in depth from <1.25 m (''severe windthrow hazard'') to >2 m

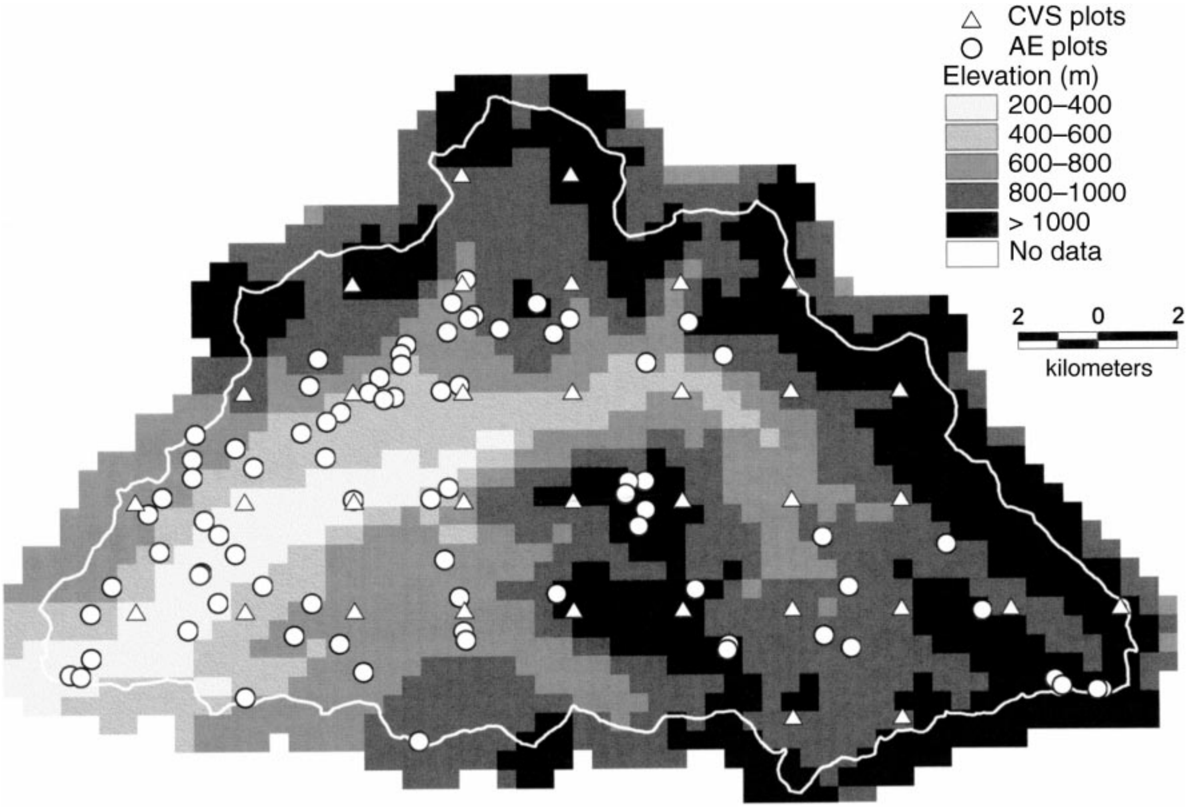

FIG. 2. The Bull Run basin, western Oregon, showing topographic relief and location of 80 Area Ecology plots (AE plots) and 34 Current Vegetation Survey plots (CVS plots) used in the analysis.

(''slight windthrow hazard'') (U.S. Forest Service 1964). Limited areas have experienced landslides and other mass movement events (Schulz 1981), but the basin has been described as ''geologically stable'' (U.S. Forest Service 1979).

Coniferous forest, composed principally of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Pacific silver fir (*Abies amabilis*), and western red cedar (*Thuja plicata*) occupies almost all of the Bull Run basin and the western Cascade Range. Douglas-fir is the canopy dominant, reaching nearly 100-m height in stands affected by infrequent, moderate- and high-severity fire (Agee 1993, Krusemark et al. 1996). Western hemlock (at low elevations) and Pacific silver fir (at high elevations) occur as understory shade-tolerant species and as canopy dominants (Franklin and Dyrness 1973). Deciduous species, notably big leaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*), occur in riparian zones and along the edges of the reservoirs. Meadows and talus slopes occupy 8% of the basin.

Public access to the Bull Run basin has been restricted since 1904 to protect water supplies for the City of Portland, but forest harvest was conducted from 1958 to the early 1990s. By 1973, 2278 ha of forest (9% of the basin) had been harvested in clearcut patches (Jones et al. 1997). Nearly 8% of the remaining forest was affected by windthrow during two east-wind winter storm events in January 1973 and December 1983. Following each of these events, salvage logging was undertaken, creating clearcuts on an additional 2 122 ha (8% of the basin). A lawsuit filed in 1973 ended commercial timber harvest operations (Wilson 1989); today the basin is part of a late successional reserve and all logging, including salvage removal of downed timber, is strictly regulated. Altogether 17% of the basin area has been harvested in distributed patch harvests connected by an extensive road network (Sinton 1996).

Windthrow mapping in the Bull Run basin

''Mappable'' windthrow from storms in 1973 and 1983 was defined as areas having >30% of boles uprooted in patches of forest >0.56 ha (Fig. 1). Individual crowns and boles of standing and down Douglas-fir were visible on the air photos. Windthrow patches from the January 1973 event were identified on air photos (1:7920, true color) taken in February 1973, while the windthrow from the December 1983 event was mapped from air photos (1:12 000, true color) taken in July 1984. Air photos were obtained from the Mount Hood National Forest.

For earlier events (i.e., prior to 1973), windthrow was identified on the July 1984 air photo series (chosen for its extensive, cloud- and snow-free coverage) by locating stands of Pacific silver fir or western hemlock (both shade tolerant species) with fine-grained canopy texture, indicative of a stand created by a single disturbance event within the past century. Each of these 105 sites was field checked and defined as having experienced historical windthrow only if it had ~25 or more uprooted trees per hectare, oriented in the same direction, as well as pit-and-mound topography created by uprooting of trees (Fig. 1).

Years in which field-mapped historical windthrow had occurred were estimated from release dates, supplemented by woody-debris decay stage. Single-date windthrow was defined as sites with downed trees oriented within 90° of one another, in a similar decay stage following Harmon et al. (1986). At each single-date windthrow site, increment cores were taken from five to ten live Pacific silver fir or western hemlock located within 10 m of uprooted trees and of sufficient age to have been growing in the understory at the time of the windthrow event. Each core was assigned a release date, at an abrupt ring width increase of ≥100% that persisted for ≥10 yr (Henry and Swan 1974, Lorimer and Frelich 1989, Frelich and Lorimer 1991, Abrams et al. 1995). Each stand was assigned a single date of windthrow if five or more cored trees in the stand had the same release year. When release dates varied among cored trees, the windthrow date was attributed to the earliest release date, and the range of years was recorded. Although no cross-dating was undertaken, release dates fell within a 3-yr range for each of the mapped windthrow events. Errors were low because cored trees were <200 yr old, release dates were <100 yr ago, and rings were readily distinguished using a hand lens.

All mapped windthrow was digitized and transferred to GIS. Windthrow was digitized by placing a mylar grid over each photo, with grid-cell sizes corresponding to 75 × 75 m (0.56 ha) on the ground, and marking the center point of each cell containing visible windthrow (for the 1973 and 1983 storms) or the windthrow-attributed Pacific silver fir or western hemlock stand (for pre-1973 windthrow). These points were transferred to a second mylar grid overlaid on orthophotoquads (1:12 000, enlarged from 1:40 000) and digitized into a GIS.

Analysis of environmental factors and windthrow patterns

Environmental factors, i.e., elevation, slope, aspect, soils, and vegetation edges (Fig. 1) were identified from a set of GIS data layers obtained in digital format from the Mount Hood National Forest, the U.S. Forest Service Pacific Northwest Forest Research Station, and the U.S. Geological Survey. Spatial data were managed using ArcInfo (Versions 6.0 and 7.01) and Erdas (Version 7.5) (Sinton 1996). Slope, aspect, and elevation data layers were constructed from a 30-m digital elevation model. Soil windthrow-hazard classes (none, slight, moderate, and severe) were digitized from the Mount Hood National Forest soil survey (U.S. Forest Service 1964).

Two types of vegetation edges were documented as GIS layers. ''Artificial'' (i.e., human-created) edges were defined as the boundaries between clearcuts or reservoirs and native forest; clearcutting began in 1958 and so these edges were ≤25 yr old at the time of the 1973 event. Artificial edges were delineated from a digital map of clearcut patches distinguished by harvest date; partial harvests were excluded because of very limited extent. ''Natural'' edges were defined as the forested boundaries of lakes, meadows, and talus slopes, and other nonclearcut forest openings. Roads and streams were not considered because they fell below the minimum mapping resolution of 0.56 ha. Natural edges were distinguished from artificial edges using a classified 1988 Landsat Thematic Mapper (TM) satellite image (Cohen et al. 1995) combined with the forest harvest layer. Mapped windthrow cells falling within a 300-m buffer placed on the forested side of a natural or artificial edge were considered to be associated with that edge type.

Meteorological conditions during windthrow events were defined from data on average daily and maximum wind speeds and direction, temperature, and precipitation. Data covering short periods from the 1970s to 1990s in the Bull Run basin were provided by the City of Portland Water Bureau. Data covering the period from 1948 to 1994 at the nearest long-term station, the Portland Airport, 30 km west of the Bull Run, were obtained from the Oregon Climate Service. Data on meteorological conditions prior to 1948 were obtained from published records (Cameron 1931) and the National Climatic Data Center.

Statistics on windthrow patch sizes were estimated using FRAGSTATS (McGarigal and Marks 1995). Logistic regression (Hosmer and Lemeshow 1989) was used to relate the spatial distribution of windthrow (dependent variable) to landscape features, i.e., aspect, elevation, slope, soil type, and adjacency to natural and artificial edges (independent variables) (Fig. 1). One logistic regression model was constructed for each of the three windthrow events (1931, 1973, and 1983). Spatial autocorrelation was assessed from a two-dimensional semivariogram for each windthrow event. Because autocorrelated distances ranged from 150 m for windthrow to 750 m for vegetation (Sinton 1996), the sample size for each model was a subset of cells with mapped windthrow separated by 750 m, and an equal number of cells without windthrow separated by 750 m. Models were tested sequentially in SAS (Release 6.10) using a stepwise procedure with addition of variables. The final model was accepted based on a drop-in-deviance criterion (Hosmer and Lemeshow 1989). Model results were interpreted based on the odds ratio, a measure of the relative likelihood of the occurrence of windthrow for various classes of independent variables. Odds ratios were calculated among statistically significant variables ($P < 0.05$) following Hosmer and Lemeshow (1989).

Analysis of disturbance type and forest composition and structure

We computed four measures of forest structure and composition: live-tree basal area, standing dead basal area, percentage of basal area in shade-tolerant trees, and down wood, for each of 34 1-ha Current Vegetation Survey (CVS) plots (obtained from the Mount Hood National Forest, Pacific Northwest Region, U.S. Forest Service) on a 2.83-km grid in the Bull Run basin (Fig. 2), and we qualitatively compared these measures among plots coded by disturbance history. Data for individual trees, living and dead (species, diameter at breast height, basal area, and age [for all large trees]) were collected in nested plots within each 1-ha plot (Umatilla National Forest 1996). Down wood estimates were obtained by line-intercept methods along five 15-m transects, three oriented north–south, and two oriented east–west. Trees were cored to determine age, but projections (Krusemark et al. 1996) were used to estimate tree age where cores did not reach the center of very large trees.

For each CVS plot we tabulated living and dead basal area for all trees >20 cm in diameter by dominant species; living and dead basal area were summed for each plot. We calculated ''shade tolerant percentage'' for each CVS plot as the sum of living basal area of *Tsuga heterophylla* and *Abies amabilis* divided by total basal area. Biomass was calculated using a truncated conical volume based on the maximum and minimum diameter and length for each piece >10 cm in diameter, and summed over each CVS plot. Maximum stand age was the highest age of the selected trees aged in each CVS plot. The disturbance history of each plot was determined in ArcInfo using overlays of mapped windthrow (Sinton 1996) and fire (Krusemark et al. 1996).

Analysis of broad-scale environmental factors and forest composition

Field data on forest composition from 1637 Area Ecology (AE) plots on the Mount Hood National Forest and on the Willamette National Forest north of the McKenzie River (Fig. 3), including 80 plots in the Bull Run (Fig. 2), were obtained from the Area Ecology Program, Pacific Northwest Region, U.S. Forest Service. The 500-m fixed-radius AE plots were selected subjectively without preconceived bias (Mueller-Dombois and Ellenberg 1974) from older, natural stands of tree series *Tsuga heterophylla, Abies amabilis,* and *Tsuga mertensiana* (Hemstrom et al. 1982). Crown cover by tree species and canopy layer (overstory or understory) was visually estimated on the plots. Data on the climate, geology, topography, and stand age (time since last major disturbance) of each plot were obtained from

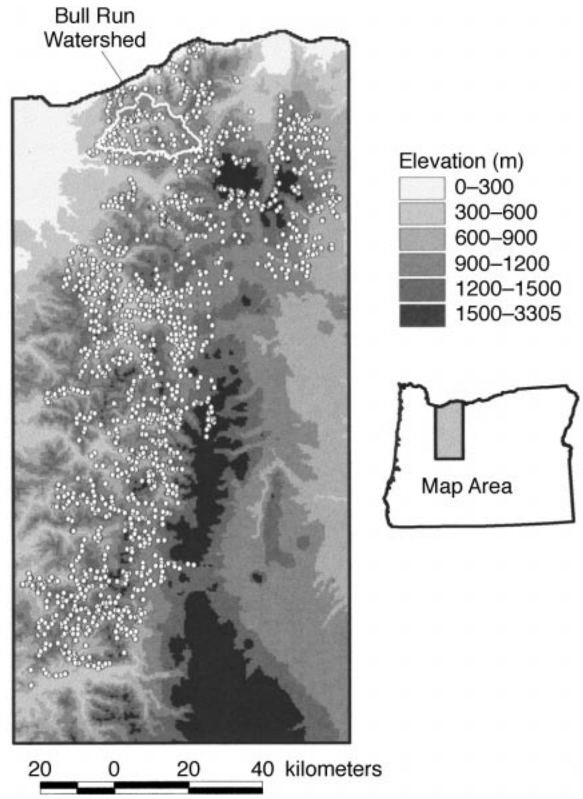

FIG. 3. The western Cascades of Oregon, showing the location of the Bull Run basin, and elevation and locations of 1637 area ecology plots used in the CCA analysis.

field-recorded measures and digital maps. Climate data were derived from map surfaces generated by precipitation (Daly et al. 1994) and temperature (Dodson and Marks 1997) models using methods described in Ohmann and Spies (1998). Potential solar radiation was estimated using the program SOLARPDX (Smith 1993). Geology data were from Walker and MacLeod (1991).

Forest composition data were analyzed by stepwise canonical correspondence analysis (CCA) (ter Braak 1986, 1987*a*, *b*, ter Braak and Prentice 1988), using program CANOCO, version 3.12 (ter Braak 1987*a*). CCA is a method of direct gradient analysis in which sites and species are arranged in a multidimensional space, with the restriction that the ordination axes must be linear combinations of the specified environmental variables. We used log-transformed relative-abundance values for each species; for all other variables CANOCO defaults were used. We added explanatory variables to the stepwise model in the order of greatest additional contribution to explained variation, but only if they were significant ($P < 0.01$) and not strongly multicollinear with other variables. Scores of Axis 1 and Axis 2 were kriged and mapped to show how environmental gradients are distributed in space, following Ohmann and Spies (1998).

TABLE 1. Windthrow-patch data from forest windthrow episodes over the past century in the Bull Run basin, Oregon.

Episode year	Windthrow patch area (ha)	Forest >80-yr-old area (ha)†	Windthrow patch area as percentage of: Forest >80-yr-old area	Basin area	No. windthrow patches	Patch size (ha) Min.	Max.	Mean	Median
1893, 1900, 1910, 1921	156	20 073	0.8	0.6	17	0.56	37	9.1	7.3
1931	463	19 027	2.3	1.7	47	0.56	157	8.6	4.1
1973	552	19 368	2.8	2.0	62	0.56	116	8.3	3.9
1983	1319	18 506	7.1	5.0	209	0.56	104	6.5	2.3
Undated	69	. . .	. . .	0.3	12	0.56	22	5.7	3.3
Total	2559	. . .	13.0	9.6	347	0.56	116	7.2	3.1

† Estimated forest area >80 yr old at the time of each windthrow episode was back-calculated by Sinton (1996) using information on clearcut areas and dates, estimated stand ages in 1988 on the classified satellite image (Cohen et al. 1995), and maps of historical fires (Krusemark et al. 1996).

‡ Patch size statistics were determined using FRAGSTATS (McGarigal and Marks 1995).

RESULTS

Mapping of historical windthrow

Altogether 2611 ha (9.3% of the basin) has been affected by mapped windthrow since 1890, but only 2% was affected prior to the onset of forest harvest in 1958 (Table 1). Altogether the events of 1893, 1900, 1910, and 1921, and those which could not be dated, produced patches occupying <1% of the basin. Windthrow events in 1931, 1973, and 1983 accounted for nine-tenths of mapped windthrow (Table 1, Fig. 4). Windthrow patch sizes for these events ranged from the minimum mappable patch size (0.56 ha) to 157 ha, with a median patch size of 3.1 ha (Table 1). Median patch size decreased from 1931 to 1983 with increases in patches of <4 ha, but the number of patches >10 ha increased from 1931 to 1983 (Table 1, Fig. 5).

Different portions of the basin were affected in each windthrow event (Fig. 4). In April 1931, most windthrow occurred in the southern and central portions of the basin. In December 1973, most windthrow occurred in the eastern portions of the watershed, with small widely scattered patches elsewhere. In December 1983, most windthrow occurred in the central and eastern parts of the basin, commonly in patches adjacent to 1973 windthrow and subsequent salvage logging units.

Factors associated with windthrow patterns

The three major windthrow episodes in 1931, 1973, and 1983 were associated with extreme meteorological conditions. In each of the three storms, winds were from the north or east, and maximum wind speeds exceeded 13 m/s at Portland (Sinton 1996). Events occurred under rather dry conditions: daily precipitation was <5 mm and cumulative precipitation over the previous 14 d was <100 mm, i.e., <5% of winter precipitation. Air temperatures exceeded 13°C throughout the 1931 event, but were below freezing during the events of 1973 and 1983; nevertheless, daily minimum soil temperatures at 50 cm depth at a mid-elevation site remained >0°C during the 1973 and 1983 events (D. Henshaw, *unpublished data*). Windthrown trees in 1973 and 1984 air photos of Bull Run were primarily oriented with boles pointing west and southwest, and this was subsequently confirmed in the field by locating unsalvaged boles. Field-mapped windthrown trees from the 1931 and earlier events (i.e., trees downed for >60 yr) were on average oriented 220° (southwest).

Exposed topographic positions, deep and shallow soils, and clearcut edges were significantly associated with mapped windthrow, but the relationships varied somewhat among the three events (Sinton 1996). Windthrow predominantly affected old-growth Douglas-fir trees in stands unaffected by fire for ~500 yr. In all windthrow episodes, downed trees visible in air photos or counted in field surveys were very large Douglas-fir individuals, and windthrow patches had no evidence of historical fire (Sinton 1996, Krusemark et al. 1996). In 1931, windthrow was significantly concentrated (i.e., odds ratio >1, see Table 2) on northeast- and southeast-facing aspects ($P < 0.002$), and on soils with severe windthrow-hazard ratings (<1.25 m deep, $P < 0.0001$). In 1973, windthrow was significantly concentrated on southwest- as well as northeast-facing aspects ($P < 0.0038$) and on soils with severe windthrow-hazard ratings, but only if they fell within 300 m of a clearcut edge ($P < 0.006$). In 1983, windthrow was significantly concentrated on soils with severe windthrow hazard ratings ($P < 0.0006$) and within 300 m of a clearcut edge ($P < 0.001$). Nearly 80% of the mapped windthrow in 1983 occurred in patches within 300 m of the downwind edge of a clearcut. Windthrow not associated with clearcut edges tended to follow a pattern determined by topographic exposure on windward slope aspects. Soil depth was not a consistent predictor of windthrow since both shallow and deep soils were affected (Table 2). Thus, forest harvest modified the effects of climate, landforms, and vegetation on windthrow disturbance, reducing the importance of topographic exposure to east and northeast winds, and creating a strong influence of recent clearcut edges.

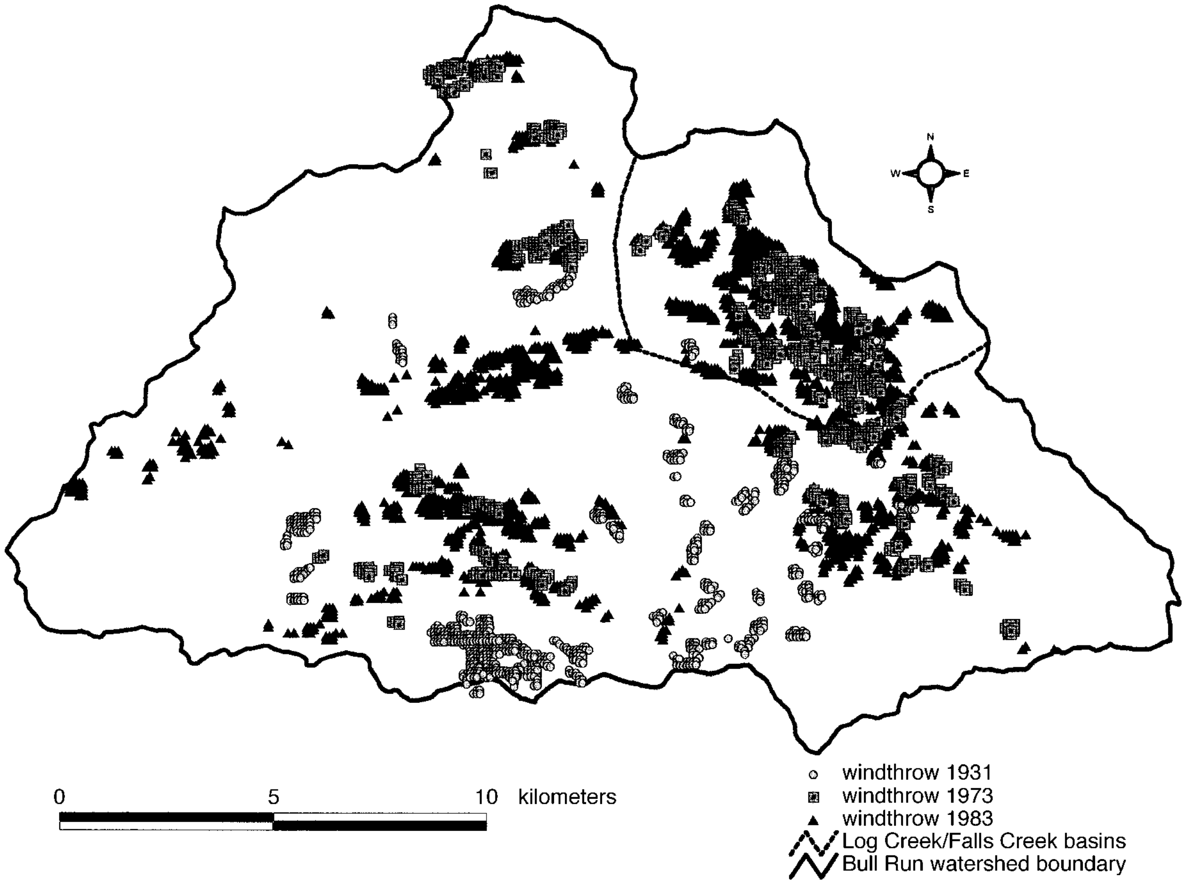

FIG. 4. Mapped windthrow for the 1931, 1973, and 1983 storm events. Each symbol represents the center of a 0.56-ha area on the ground that experienced windthrow. The dashed line shows the general location of the Log Creek/Falls Creek subbasins.

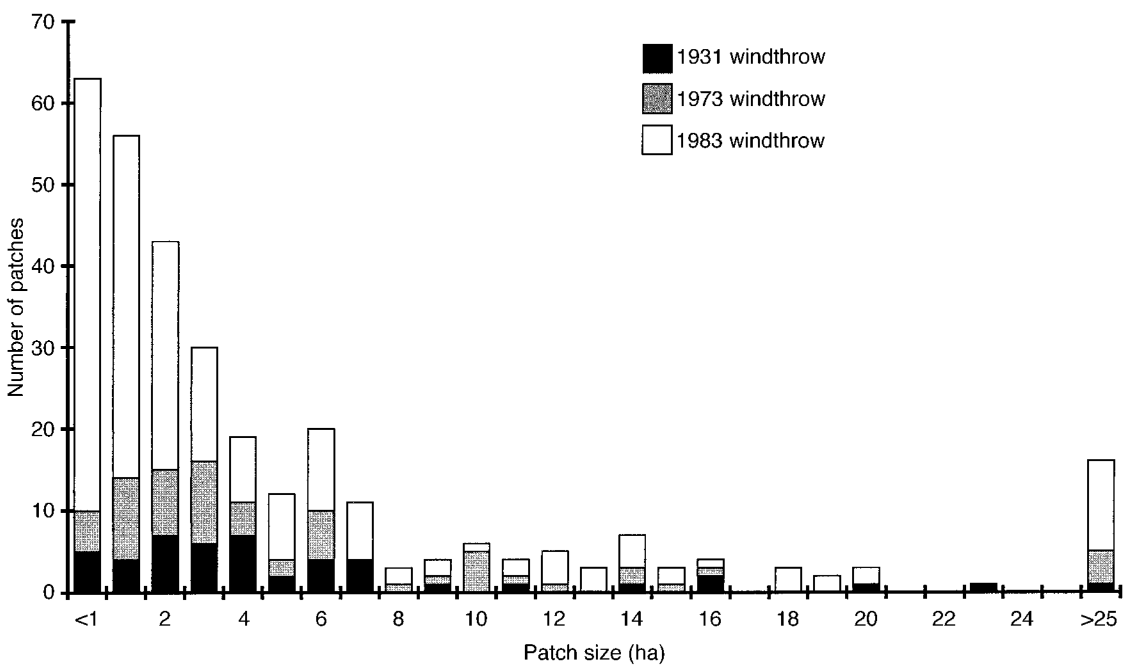

FIG. 5. Patch size distribution for the 1931, 1973, and 1983 storm events.

TABLE 2. Odds ratios from logistic regression models relating forest windthrow to landscape features for the three largest windthrow-producing events in the Bull Run basin, Oregon, during the 1900s.

Variable/class	1931					1973					1983				
	Yes†	No†	β	SE	e^{β}	Yes†	No†	β	SE	e^{β}	Yes†	No†	β	SE	e^{β}
Aspect															
Northeast	35	18	1.04	0.46	**2.8**	31	16	1.07	0.48	**2.9**					
Southeast	17	15	0.45	0.51	**1.6**	10	19	0.19	0.53	0.8					
Southwest	14	29	−0.67	0.47	0.5	42	30	0.56	0.43	**1.8**					
Northwest	21	25	0.0		1.0	19	22	0.0		1.0					
Soil windthrow hazard rating															
None	3	14	−2.15	0.70	0.1						5	13	−0.77	0.57	0.5
Slight	60	47	0.0		1.0						59	63	0.0		1.0
Moderate	5	18	−1.74	0.57	0.2						13	24	−0.37	0.40	0.7
Severe	19	8	0.51	0.49	**1.7**						38	15	1.15	0.37	**3.2**
Edges															
Artificial											87	64	0.96	0.31	**2.6**
Natural											28	51	0.0		1.0
											115	115			
Edges × Soil windthrow hazard rating															
Artificial															
Slight						30	31	0.0	⋯	1.0					
Moderate						4	5	−0.34	2.62	0.7					
Severe						20	3	2.31	1.52	**10.1**					
Natural															
Slight						32	25	0.0	⋯	1.0					
Moderate						5	12	−1.29	0.95	0.3					
Severe						11	11	−0.37	0.85	0.7					

Notes: Statistically significant odds ratios ($P < 0.05$) are shown in boldface type; β is the parameter estimate for each class in column 1; SE is the standard error of the estimate; and e^{β} is the odds ratio, a measure of the likelihood of windthrow in that class relative to the class with e^{β} set to 1 (Hosmer and Lemeshow 1989).

† The numbers of cells with windthrow (Yes) vs. without windthrow (No) were used to calculate regression parameters. Sample sizes were 87 cells each with and without windthrow in 1931, 115 cells each in 1983, and 102 cells with and 87 cells without windthrow in 1973.

‡ Areas mapped as having no soil hazard for windthrow were excluded from the model in 1973 because of inadequate sample size.

Most edge-related windthrow occurred along recently created clearcut edges, and the susceptibility of clearcut edges appeared to decrease as edges became older (Table 3). However, this trend was confounded by the fact that most recently created edges occurred in areas of the basin with old forest on shallow soils in exposed topographic positions. The Log Creek/Falls Creek subbasins (Fig. 4, Fig. 6) contained high densities of clearcut edges affected by windthrow: 90% of the 1- to 5-yr-old edges in 1973 and >50% of the 6- to 10-yr-old edges in 1983, which received higher than average amounts of windthrow (Table 3), were located in these subbasins. This area may be inherently susceptible to windthrow along cut edges because of its shallow soils and lee (southwest-facing) slope, and the shape of the ridge above might funnel winds through natural openings (Fig. 6). Forest cover is naturally sparse on the upper slope, but prior to harvest, forests on lower slopes were dense and old, with little or no fire in recent centuries (Krusemark et al. 1996), and little or no windthrow in 1931 (Fig. 4). Much of the edge-related windthrow in 1973, 90% of which was within 300 m of recent clearcut edges (Table 3), occurred in this area. These clearcut openings were enlarged by additional clearcuts to salvage wind-toppled trees in the subsequent years, and in 1983, 40% of edge-related windthrow occurred along the edges of these recent salvage clearcuts (Table 3), sometimes to the point that small patches coalesced (Fig. 4, Fig. 6). Clearcut edge susceptibility and coalescing patches contributed to an increase in numbers of >10 ha windthrow patches over time (Fig. 5).

Disturbance type and forest structure and composition in the Bull Run

Maximum ages of trees in 34 CVS plots in the Bull Run ranged from 33 to 900 yr, with clusters of younger ages corresponding to two episodes of stand-replacement fire mapped by Krusemark et al. (1996) and older ages from areas unaffected by fire. A set of fires 65–120 yr ago burned low elevation sites in the western portion of the basin and along the northern and southern basin boundaries (represented by 10 plots), and a fire 330 yr ago burned along the eastern and northeastern basin boundaries (represented by 5 to 9 plots). Forest stands in the broad central portion of the basin have not burned for 500 to >700 years (Krusemark et al. 1996); these stands are represented by 15 plots. One

TABLE 3. Total length and windthrown length of edges, by five-year age classes, for windthrow events in 1973 and 1983 in the Bull Run basin.

Date edge was created	Edge age (yr)	Edge length† (km)	Edge length† (Percentage of total)	Windthrown edge‡ (km)	Windthrown edge‡ (Percentage of total)	Windthrow (Percentage of edge)
1973 event						
Natural edges		302.1	100	2.5	100	0.8
Artificial edges						
1958–1962	11–15	75.1	28	2.2	14	2.9
1963–1967	6–10	124.4	46	7.4	46	5.9
1968–1972	1–5	68.5	26	6.6	41	9.6
Total artificial		268.0	100	16.0	100	6.0
1983 event						
Natural edges		304.2	100	12.9	100	4.2
Artificial edges						
1958–1962	21–25	69.1	17	2.5	5	3.6
1963–1967	16–20	117.0	29	5.8	10	5.0
1968–1972	11–15	63.0	16	5.1	9	8.1
1973–1977; nonsalvage	6–10	68.8	15	9.9	19	14.4
1973–1977; salvage	6–10	71.9	16	28.3	52	39.4
1978–1983	1–5	28.9	7	2.5	5	8.7
Total artificial		418.7	100	54.1	100	12.9

† Total edge lengths were calculated from a GIS layer of polygons representing natural and clearcut openings digitized from aerial photographs.

‡ Windthrown edge lengths were determined from the GIS by overlaying the edge layer on the mapped windthrow layers and calculating the lengths of subsections of these edges that overlapped mapped windthrow cells (Sinton 1996).

of these latter plots falls within a forest patch created by the 1931 windthrow event, which affected 2% of the basin.

Generally the ages from current vegetation survey plots agree quite well with independently mapped disturbance types and dates, but some errors are apparent (Fig. 7). Maximum tree ages >750 yr are somewhat suspect, as they were based on projections which are prone to errors (Krusemark et al. 1996), and very few trees exceeding 550 yr have been found in the western Cascades (Morrison and Swanson 1990). Three or four high-elevation plots with maximum ages in the vicinity of 300 yr were probably affected by fire 330 yr ago, but if so these fire-affected patches fell below the spatial resolution of the fire mapping (Krusemark et al. 1996). Also, plots with no mapped disturbance may have been affected by windthrow that did not meet our mapping criteria (Fig. 1).

Living basal area was not related to maximum age of CVS plots; high values of live basal area are attained

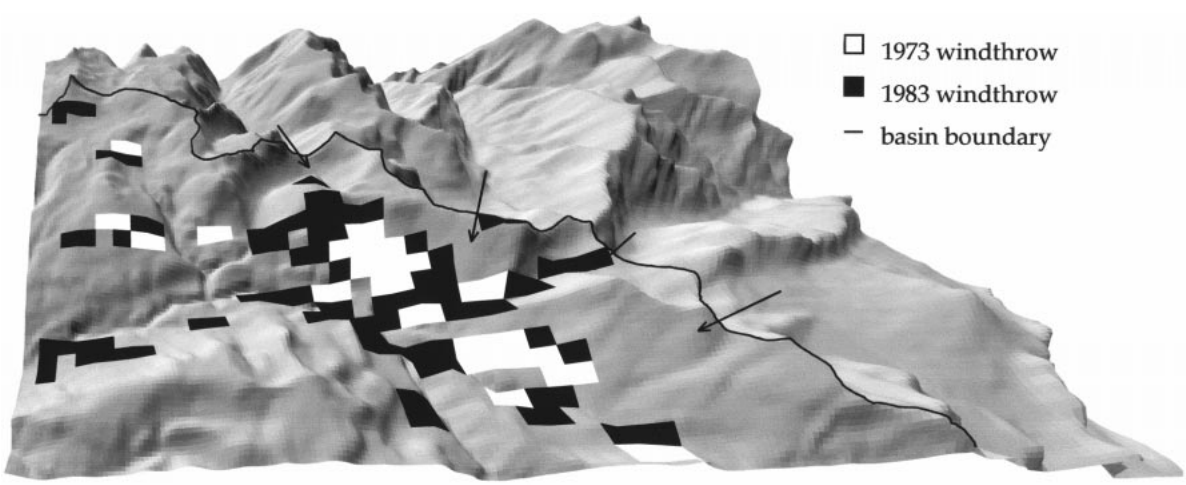

FIG. 6. Spatial patterns of windthrow in the 1973 and 1983 events in the Log Creek/Otter Creek subbasins of the Bull Run, shown in landscape view looking toward the northeast. This ridge, which separates the Bull Run basin from the Columbia River Gorge beyond it, has several saddles (shown with arrows) through which winds appear to have been funneled, contributing to the patterns of windthrow.

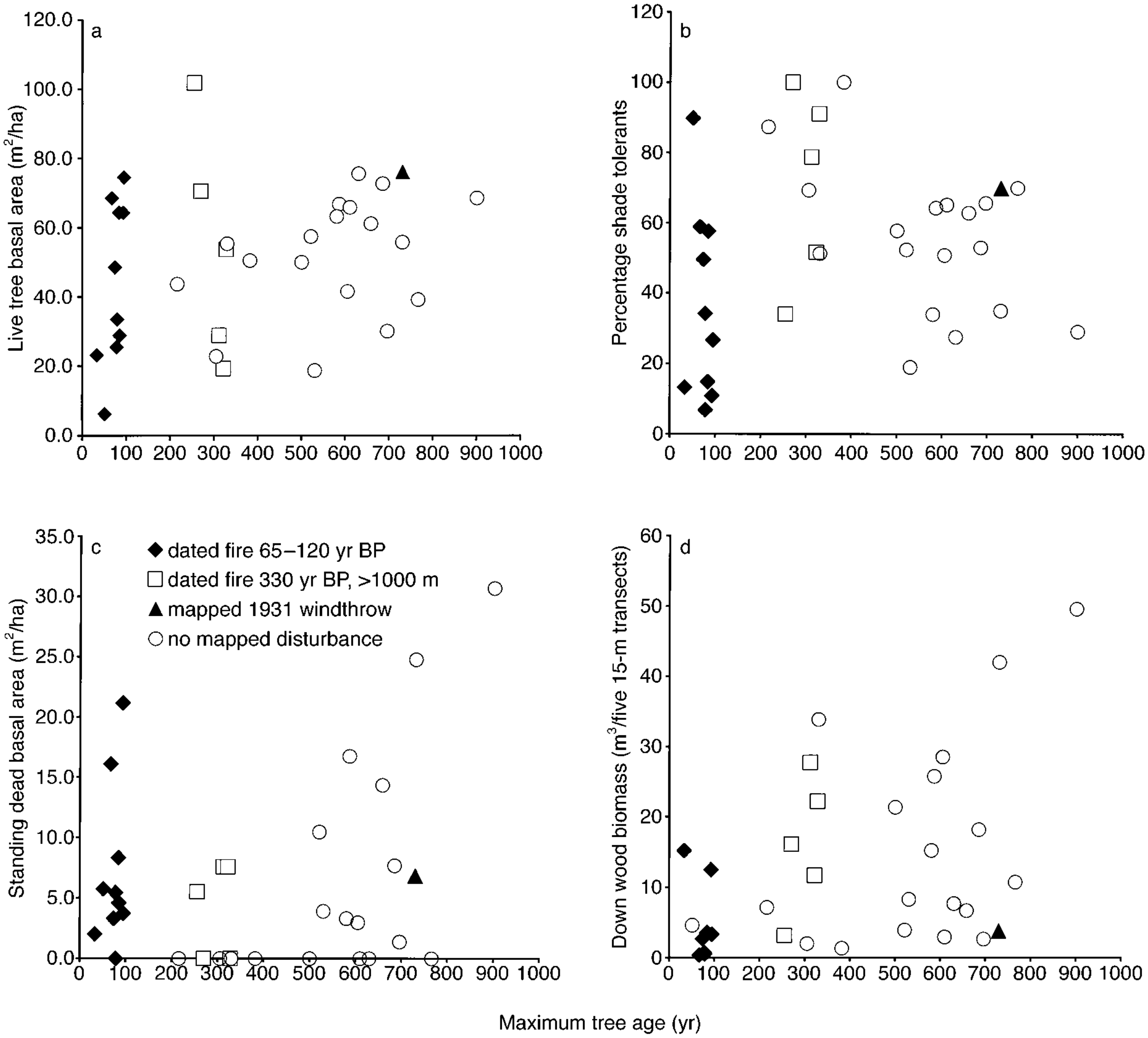

FIG. 7. Forest structure and composition as a function of maximum tree age in 34 1-ha CVS plots in the Bull Run basin coded according to their correspondence with mapped windthrow patches (Sinton 1996) or dated historical fires (Krusemark et al. 1996): (a) living basal area, (b) percentage shade tolerants ([*Tsuga heterophylla* + *Abies amabilis* basal area]/total basal area), (c) standing dead basal area, and (d) down-wood biomass.

in early postfire plots, older high-elevation postfire plots, and plots with no mapped disturbance since ~1500, as well as in plots affected by mapped windthrow 60–100 yr ago (Fig. 7a). Live basal area ranged from 5 to 70 m²/ha in plots affected by fire since 1900, 20–100 m²/ha in high-elevation plots regenerated by fire 330 yr ago, and 20–80 m²/ha in plots with no mapped disturbance since ~1500. The plot falling within the mapped 1931 windthrow event had the greatest observed living basal area (80 m²/ha) of the CVS plots with maximum age >400 yr.

Shade tolerant tree species made up 5–90% of total basal area in CVS plots at low elevations affected by fire since 1900, 30–100% in high-elevation plots affected by fire 330 yr ago, and 15–70% in plots with no mapped disturbance since ~1500 (Fig. 7b). The plot falling within the 1931 windthrow event had the greatest observed shade tolerant basal area percentage (70%) of CVS plots with maximum age >400 yr. Shade tolerant basal area percentage was highest in plots affected by fire 300 yr ago. Forests in these wildfire-affected, high-elevation, eastern plots in the Bull Run are dominated by shade-tolerant species; relative canopy cover by Pacific silver fir is 38% from 900- to 1200-m elevation, and 60% from 1200 to 1500 m.

The plot with mapped windthrow had relatively low standing dead basal area (of trees >10 cm in diameter) compared to plots with other disturbance origins (Fig. 7c). Standing dead basal area ranged from 0–22 m²/ha in plots affected by fire since 1900, 0–8 m²/ha in high-elevation plots affected by fire 330 yr ago, and 0–30 m²/ha in plots with no mapped disturbance since

TABLE 4. Correlations between explanatory variables and axes 1 (69% of variation) and 2 (8% of variation) from canonical correspondence analysis (CCA), and scores of four dominant species on CCA axes 1 and 2, from stepwise CCA of 1637 area ecology (AE) plots in the western Cascades of Oregon.

Variable/species	Correlations		CCA scores	
	Axis 1	Axis 2	Axis 1	Axis 2
Elevation (m)	96.0			
Moisture stress during the growing season: mean temperature in May–September/mean precipitation in May–September (natural log, mm)	−88.9			
Coefficient of variation of mean monthly temperature of the coldest and warmest months, e.g., January, August	64.0			
Crown cover of all overstory trees (%)	−54.1	−31.8		
Stand age (yr)		−44.3		
Mean annual precipitation (natural log, mm)		−37.2		
Percentage of mean annual precipitation, June–August		−35.6		
Total potential solar radiation (10^8 J/m^2)		30.9		
Igneous: mafic rocks (basalt, basaltic andesite, andesite, gabbro), Pliocene and younger	35.0			
Thuja plicata (western red cedar)			−0.4860	−0.2027
Pseudotsuga menziesii (Douglas-fir)			−0.2622	0.0736
Tsuga heterophylla (western hemlock)			−0.2127	−0.1500
Abies procera (noble fir)			0.7980	−0.0770
Abies amabilis (Pacific silver fir)			0.8952	−0.1504

Notes: Only correlations >0.30 and <−0.30 are shown. Equations for correlations and scores are in Ohmann and Spies (1998).

~1500. The plot falling within the 1931 windthrow event had an intermediate amount of standing dead basal area among plots with maximum age >400 yr.

Maximum down wood biomass values per CVS plot increased with maximum stand age, but low amounts occurred in plots of all ages (Fig. 7d). Down wood biomass ranged from 0–15 m^3/transect in recent post-fire plots, 2–35 m^3/transect in high-elevation plots regenerated by fire 330 yr ago, and 3–50 m^3/transect in plots with no mapped disturbance. The plot falling within 1931 windthrow had almost the lowest down wood biomass of plots with maximum age >400 yr. This low level of down wood contradicts field observations of historic windthrow (Sinton 1996); the short (15-m), north–south and east–west transects may have undersampled large, widely spaced, southwest-oriented windthrown trees.

Environmental factors and forest composition in the western Cascades

Tree species composition in area ecology plots in the western Cascades is related to climate and geographical factors, but not to stand age, and forest composition in the Bull Run is distinct from the rest of the western Cascades. Canonical correspondence analysis of 1637 area ecology plots explained 14% of the variation in the data (Table 4). This high level of unexplained variation is typical of vegetation gradient analyses and is attributable to (unknown) factors not included in the analysis, as well as to the tendency for CCA to explain less variation with increasingly large numbers of plots and species (Ohmann and Spies 1998).

The predominant gradient in species composition revealed by CCA in the western Cascade Range was associated with elevation, moisture stress during the growing season, temperature variation, canopy cover, and more recent volcanic rock substrates (Table 4). This environmental gradient is also a spatial gradient, since Douglas-fir declines and western hemlock and Pacific silver fir increase with elevation (Fig. 8 top). Elevation, summer moisture stress, and stand age accounted for 65%, 55%, and 5%, respectively, of total explained variation when added first to the stepwise model. While the secondary gradient accounted for much less explained variation, it indicated a tendency for younger stands to occur in drier, hotter places, and to have more Douglas-fir but less red cedar, Pacific silver fir, and western hemlock (Table 4, Fig. 8 bottom).

Relative cover by shade-tolerant species (western hemlock and Pacific silver fir) is greater, that of shade-intolerant species (Douglas-fir) is less, and species maximum cover values occur at lower elevations, in the Bull Run compared to the rest of the western Cascades. In the western Cascade Range as a whole, maximum relative cover percentages occur at <600 m for Douglas-fir (62% of cover), 600–1200 m for western hemlock (33% of cover), and 1200–1500 m for Pacific silver fir (28% of cover). However, within the Bull Run, species cover maxima occur at lower elevations. Douglas-fir reaches its maximum relative canopy cover (46%) below 600 m, and at 900 and 1200 m Douglas-fir canopy cover is <17% in the Bull Run compared to 42% for the rest of the western Cascades. Western hemlock reaches its maximum relative canopy cover (59%) at 600–900 m in the Bull Run, and at 1200 and 1500 m western hemlock canopy cover is 0%, com-

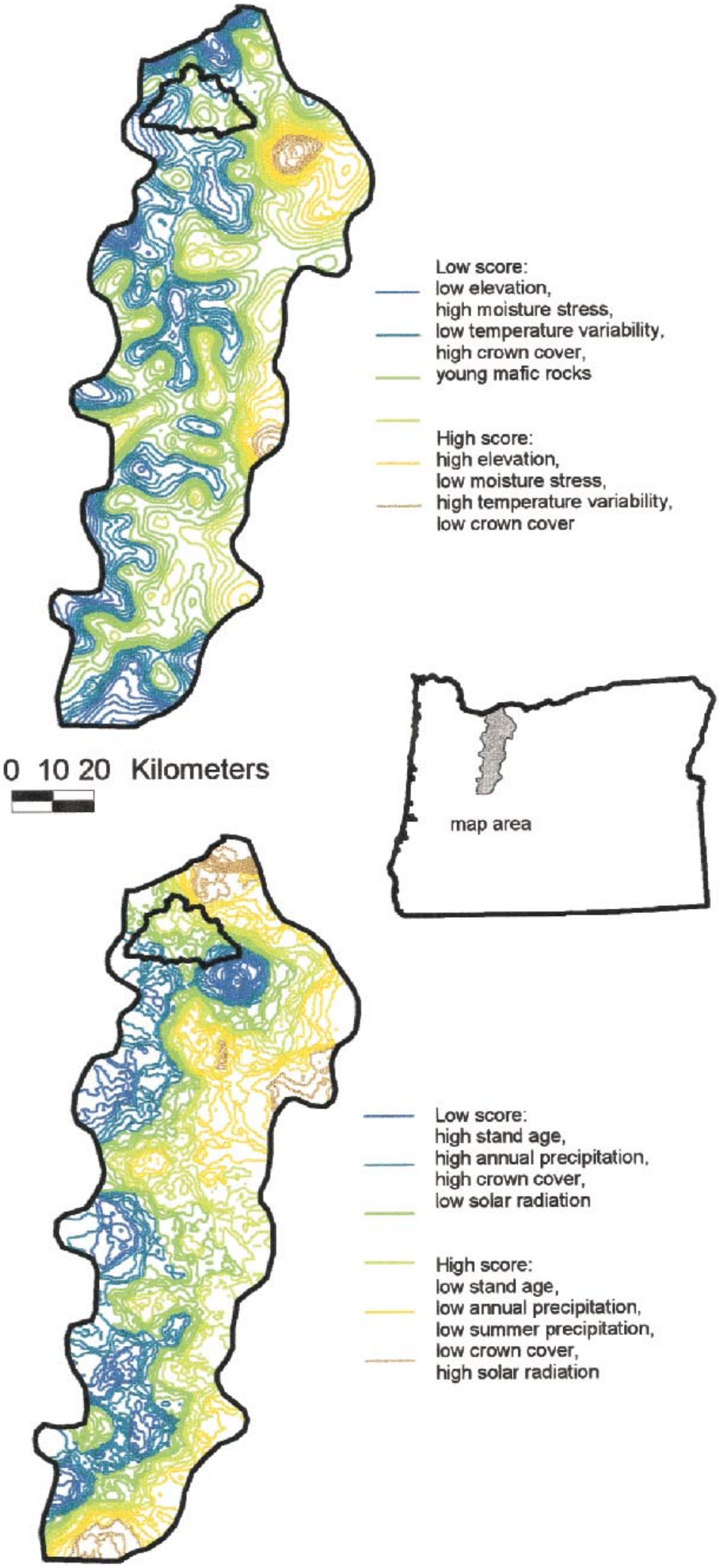

FIG. 8. The western Cascades of Oregon, showing (top) the plot of CCA axis-1 scores, and (bottom) the plot of CCA axis-2 scores.

pared to 13% for the rest of the western Cascades. Pacific silver fir reaches maximum relative canopy cover of 38% at 900–1200 m and 60% at 1200–1500 m in the Bull Run, compared to 9% at 28% at corresponding elevations in the rest of the western Cascades.

Discussion

Climate and landform controls

Windthrow patterns in the Bull Run were associated with geophysical factors, especially climate and landforms. Along the east and west coasts of North and South America severe windthrow is associated with landfall of cyclonic marine air masses (Orr 1963, Foster and Boose 1992, Boose et al. 1994, Loope et al. 1994, Kramer 1997, Rebertus et al. 1997). In contrast, in the Bull Run basin windthrow occurs when marine low pressure air masses west of the Cascade Range interact through the Columbia Gorge (the only major river valley cutting across the Cascades) with continental high pressure air masses to the east, producing extreme east winds that are funneled into the basin from the northeast. As in other high-relief forest landscapes (Boose et al. 1994, Kramer 1997, Rebertus et al. 1997), windthrow in Bull Run was most likely to occur in landform positions that were exposed to extreme winds (i.e., north- and east-facing slopes and the upper portions of leeward, southwest-facing slopes). Forests on comparatively shallow soils ($<$1.25 m deep) also were particularly likely to experience windthrow. Many windthrow-affected areas on shallow soils in Bull Run also are in topographically exposed landform positions, especially those on upper portions of SW-facing slopes in the lee of NE-facing slopes in the NE corner of the basin (Fig. 6).

Biotic controls

Windthrow patterns in the Bull Run also were influenced by biotic conditions, i.e., stand structure and composition, and edges created by natural and human disturbances. Windthrow meeting the mapping criteria (Fig. 1) was most likely to affect old-growth, fire-initiated stands dominated by Douglas-fir located in the central portions of the basin, and was least likely or absent in stands initiated by fires within the past century or two, which tended to be located in the low-elevation western and high-elevation eastern portions of the basin (Fig. 4). Windthrown trees that had been downed for 10, 20, 60, and 80–100 yr (corresponding to mapped windthrow events in 1983, 1973, 1931, and the 1890s) were dominantly old-growth Douglas-fir, identifiable by their distinctive bark, bole size and shape, and decomposition class (Harmon et al. 1986). Windthrow-affected stands may have been similar to present-day adjacent undisturbed stands, which are dominated by old-growth Douglas-fir and have varying amounts of basal area, some western hemlock and Pacific silver fir in the canopy, and a wide range of amounts of standing dead and down wood (Fig. 7).

Forests adjacent to clearcut edges, especially those on shallow soils, also were much more likely than forests in other locations to have experienced severe windthrow in 1973 and 1983 (Table 2). Many of the largest patches of severe windthrow occurred along the northeast- and southwest-facing edges of clearcuts created within 10 yr prior to the windthrow event (Fig. 4, Table 3). The most dramatic examples of edge-related windthrow occurred around clearcuts in the northeastern portion of the basin (Fig. 6). In this area, most windthrow occurred along clearcut edges in 1973 ($>$40% of edges $<$10 yr old experienced windthrow, Table 3), then clearcuts were enlarged by windthrow salvage logging, and most windthrow in 1983 occurred along the newly created clearcut edges ($>$50% of edges of salvage clearcuts $<$5 yr old experienced windthrow, Table 3). Extensive old-growth Douglas-fir and lack of historical windthrow or wildfire (Krusemark et al. 1996) in these areas suggests that patch clearcutting may have destabilized natural disturbance patterns.

Climate–disturbance interactions

Present-day species composition and structure differs among stands in long-term forest plots in the Bull Run according to combined, interacting effects of climate with disturbance history. Three different combinations of disturbance history and climate in three different parts of the Bull Run appear to have contributed to abundance of shade-tolerant overstory species (western hemlock and Pacific silver fir) in present-day forest stands. First, at mid-elevations in the central portion of Bull Run, historical windthrow is associated with abundant western hemlock and Pacific silver fir in present-day stands; these stands lack evidence of historical fire since ~1500, but many of these portions of the basin appear to be exposed to windthrow-producing extreme east winds. Second, western hemlock is quite abundant in some stands at low elevations affected by fires within the past century (Fig. 7b); in these stands fire history and postfire succession appear to have interacted with regional climate. In the Coast Range of Oregon, which was affected by widespread and repeated burns in the 1800s (Impara 1998), presence of western hemlock is associated with availability of a nearby seed source (Schrader 1998, Wimberly 1999), consistent with the hypothesis that hemlock has been removed from some areas by repeated burns. In the Bull Run, where fires in the 1800s were less extensive than in the Coast Range (Krusemark et al. 1996), hemlock seed sources may have been preserved. This factor, combined with relatively moist conditions year-round, leads us to expect hemlock to be more abundant in young postfire stands in the Bull Run compared to other parts of western Oregon. Third, at elevations above ~1000 m, fire in the mid 1600s led to canopy dominance by Pacific silver fir in present-day stands (Fig. 7b), also apparently as a result of climate interactions with fire history. At these elevations, both

Douglas-fir and western hemlock are almost absent, presumably because of elevation-related temperature and moisture controls (Ohmann and Spies 1998). The transition from Douglas-fir and western hemlock to Pacific silver fir appears to occur at a lower elevation in the Bull Run compared to the rest of the western Cascades because of the Bull Run's exposure to cool continental winter air through the Columbia Gorge to the east, and maritime summer fog through the Columbia Gorge to the west.

Windthrow and wildfire disturbance processes have distinctive responses to climate, landforms, stand structure, and species composition in the Bull Run, producing dynamic changes in forest structure and composition. Fire created larger disturbance patches than windthrow (or clearcuts) and was less sensitive to landforms. Perhaps more importantly, these two processes appear to push forest succession, hence landscape-scale forest composition, in different directions: wildfire favors succession by shade-intolerant species whereas windthrow favors shade tolerant species. There has been a very wide range of natural variability over the >500 year disturbance history of the Bull Run. Widespread wildfires ~1500 appear to have favored a forest landscape dominated by Douglas-fir, while shade-tolerant species may have gradually accumulated during several subsequent centuries of relatively low fire frequency and severity, and through treefall gap processes. Disturbance history in the Bull Run is consistent with a regional synthesis of fire history (Weisberg 1998) and paleoecological studies of fire history (Long et al. 1998) that suggest no tendency toward disturbance ''equilibrium'' in these forested landscapes.

Management interactions

Forest management (fire suppression and patch clearcutting) clearly modified the disturbance regimes of windthrow and wildfire, and hence forest structure and composition in the Bull Run. Between 1958 and 1973 the dominance of shade-intolerant Douglas-fir was favored by clearcutting and replanting with Douglas-fir in 9% of basin area. Throughout the 20th century, the combined effects of fire suppression, episodic severe windthrow, and the apparent augmentation of windthrow by forest harvest would have pushed the remaining natural forest stands toward dominance by shade-tolerant species, except that most of the forest affected by severe windthrow in 1973 and 1983 (10% of natural forest area) was salvage logged and replanted with Douglas-fir. The periods of clearcutting and fire suppression affected small areas and short time periods relative to basin size, forest age, and fire disturbance interval. The net effect of clearcutting over 30 yr has been to convert roughly 20% of the landscape into distinctive postclearcut stands dominated by Douglas-fir, with increases in shade-tolerants in unsalvaged, edge-related windthrow-affected stands that probably occupy less than a few percent of the basin. It is difficult to evaluate the effects of fire suppression over ~90 yr because this period is short relative to the fire return period (Krusemark et al. 1996).

In the Bull Run late successional reserve, wildfire will continue to be suppressed, but future windthrow seems inevitable. As recently created clearcut edges age, edge-related windthrow susceptibility is likely to decrease, but landform influences on windthrow susceptibility and resulting forest patches will persist. Douglas-fir plantations and young stands initiated by fire in the 20th century are unlikely to become susceptible to severe windthrow for perhaps several centuries (Sinton 1996), and are unlikely to develop old-growth characteristics of naturally regenerated, post-wildfire stands (sensu Spies and Franklin 1991).

Landscape dynamics

Simplifying assumptions about landscape dynamics do not hold in the Bull Run; as a result, the causes and consequences of disturbance have varied greatly in time and space. Both wildfire and windthrow have affected forests over the past few centuries, but fire suppression and clearcutting in the 20th century augmented the expression of windthrow. Also, both wildfire and windthrow have been tied to climate variation, but to different aspects of climate, over the historical record. Topoedaphic features in the Bull Run produce natural vegetation edges (i.e., meadows, talus slopes), which are more susceptible to windthrow than interior forest, and clearcut edges in certain topoedaphic positions are much more susceptible to windthrow. Moreover, disturbance susceptibility by, and effects of, windthrow vs. wildfire are tied to different stand characteristics; windthrow has tended to eliminate old-growth Douglas-fir along edges and foster dominance by shade-tolerant species, whereas wildfire in general reduced shade-tolerant species and fostered shade-intolerant species.

Aspects of the Bull Run case study provide a framework for addressing landscape dynamics generally. Certain aspects of the history and current conditions of a landscape may push the system toward or away from stability and variability. A tendency toward stability is fostered by several landscape attributes. Homogeneity of climate (Frelich and Lorimer 1991), the existence of topoedaphic controls on presence, composition, and structure of vegetation (Mladenoff et al. 1993), and strong coupling between topoedaphic features and disturbance susceptibility (as in the Bull Run), all provide stability in landscape dynamics. Also, the existence of a single dominant disturbance/recovery cycle, in which the probability of the disturbance is tightly coupled to successional stage (e.g., wildfire in chaparral or ponderosa pine forests), and tight coupling between the disturbance and particular climate conditions, foster a tendency toward stability. However, these tendencies toward stability are counteracted by several other attributes of the history and current conditions of a landscape. Climate variability and settlement by Europeans, with attendant human effects on vegetation species and structure as well as on disturbance processes (noted in the Bull Run; and by Frelich and Reich [1995], Foster et al. [1998], Fuller et al. [1998], Impara [1998], Long et al. [1998], Weisberg [1998], and Van Norman [1999]) foster tendencies away from stability, or even irreversible changes in landscape dynamics. In addition, a loose coupling between disturbance and recovery, in which the probability of a disturbance is not tightly related to successional stage, or the existence of more than one disturbance/recovery relationship (such as wildfire and windthrow in the Bull Run) contribute to instability and variability in landscape dynamics. Consideration of these inherent and historically acquired landscape attributes can condition our expectations and expand our understanding of forest landscape dynamics.

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