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The influence of fire and windthrow dynamics on a coastal spruce–hemlock forest in Oregon, USA, based on aerial photographs spanning 40 years

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Abstract

To gain understanding of patterns in forest structure and their causes, we mapped the distribution of three canopy cover classes and measured change in one of them over 40 years using aerial photographs for the 500 ha Neskowin Crest Research Natural Area (Lincoln and Tillamook Counties, Oregon). One class (fine texture, trees of uniform crown diameter and height) covered about half the area; it was identified as second growth originating after a large regional fire in 1845. The other major class (coarse texture, trees of variable crown diameter and height), occupying about 35% of the area, was unburned or partially burned in 1845. The third class (openings with down stems visible on the ground) was blowdown patches. The blowdown patches were very small in 1953; they grew incrementally, and by 1994 had coalesced into a large patch occupying about 15% of the area. A long-term windstorm susceptibility model developed for southeast Alaska identified the region where the blowdown patch occurred as being very susceptible to maritime windstorm disturbance. This correspondence between predicted susceptibility to damage and actual blowdown supports the hypothesis that windstorm effects may be strongly constrained by topography. The results also suggest that blowdown in storm-susceptible topographic settings can be the result of multiple windstorm events over time, rather than a single event. The resulting forest is a mosaic of large multi-aged chronic-disturbance patches embedded in a matrix structured by fine-scale patch processes. A consequence of a constraint on blowdown is that at the scale of hundreds of hectares biomass may not fluctuate strongly over time unless stand-destroying fires occur.

Keywords: Blowdown; Stand-structure; Stand development; Disturbance

1. Introduction

The coastal margin of northwestern North America is an area in which intense maritime windstorms are common (Schumacher and Wilson, 1986; Harris,

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1989; Taylor and Hatton, 1999). Such storms can cause extensive loss of timber (Greeley et al., 1953; Orr, 1963) and substantial areas of blown-down timber (Kramer et al., 2001). Discrete blowdown patches have been identified on the coastal margin of northwestern America by finely-textured forest patches on aerial photos (e.g., Henderson et al., 1989; Kramer et al., 2001). However, many studies have characterized the disturbance regime in terms of fine-scale gap processes (e.g., Harcombe, 1986; Taylor, 1990; Greene et al., 1992; Lertzman et al., 1996; Veblen and Alaback, 1996; Wells et al., 1998; Acker et al., 2000; Hennon and McClellan, 2003). In one study, ground-plot data suggested a diffuse blowdown pattern, but field observations suggested that there were discrete patches in a pattern not captured by plot data (Greene et al., 1992). Neither the relative importance of fine-scale versus coarse-scale blowdown, nor the role of multiple versus single windstorm events in shaping the age and structure of individual patches are known.

Fire can also be an important force in the disturbance dynamics in coastal forests (Agee and Flewelling, 1983; Teensma et al., 1991; Long et al., 1998; Wimberly et al., 2000; Gavin et al., 2003a,b). One important fire was the catastrophic Nestucca Burn of 1845, a fire that spread west from the Willamette Valley of Oregon to the coast, covering more than 120,000 ha (Morris, 1934; Munger, 1944; Teensma et al., 1991). Earlier studies had reported rapid, uniform restocking following the fire (Ruth, 1951; Harcombe, 1986), leading to the assumption that the fire burned uniformly through the area (Greene et al., 1992; Acker et al., 2000). This assumption is contradicted by some studies reporting strong topographic constraints (e.g., Romme and Knight, 1981; Kushla and Ripple, 1997; Heyerdahl et al., 2001, 2002), but is supported by other studies suggesting there may be limited topographic variability when fire intensities are extreme (e.g., Turner and Romme, 1994; Lertzman and Fall, 1998; Heyerdahl et al., 2001; Wimberly and Spies, 2001; Gavin et al., 2003a).

The study reported here uses a time series of aerial photos and maps to more fully characterize stand dynamics at a coastal site within the perimeter of the Nestucca Burn. The goal is to contribute to our understanding of the dynamics of disturbance patches through space and time for North American coastal temperate forests, and particularly to test the hypothesis that topography constrains disturbance.

This study also addresses how wind disturbance influences temporal variation in stand biomass. A system dominated by small, frequent gaps, would show low, relatively high-frequency variation in stand biomass, whereas a system with larger, less-frequent gaps, would show trends indicative of larger, slower variations (Peet, 1992; Turner et al., 1993), especially if recruitment lags were involved (Peet, 1992). In coastal spruce–hemlock forests, the regime of small, frequent gaps should lead to relatively constant biomass. However, at this site, recent measurements (Harcombe et al., 1990; Greene et al., 1992) and models (Acker et al., 2000) show declines in biomass over many years. We undertook this analysis at a broader spatial and temporal scale to investigate whether better characterization of the disturbance regime could resolve the apparent conflict between theory and observation regarding biomass dynamics.

2. Methods

Neskowin Crest Research Natural Area in the Cascade Head Experimental Forest is located along the central coast of Oregon, USA, in the *Picea sitchensis*–*Tsuga heterophylla* (Sitka spruce–western hemlock) zone of Franklin and Dyrness (1988). The prevailing climate is cool and wet with annual precipitation of 2500 mm, falling mostly between late fall and spring. Mean annual temperature is 10.3 °C for nearby Otis, OR (Franklin and Dyrness, 1988). The Research Natural Area is situated on highly dissected terrain, with moderate to steep slopes (Fig. 1). Soils have developed primarily from tuffaceous siltstones. Basalt bedrock can cause significant local modifications of the soil profile, and is often seen at the surface in ravines.

To gain insight into topographic constraints on wind and fire, we used maps derived from an aerial photograph time series, along with data from a permanent-plot study (Harcombe, 1986; Harcombe et al., 1990; Greene et al., 1992; Acker et al., 2000). Aerial photos for 1993, 1984, 1979, 1969, 1961 and 1953 were obtained from a variety of US Government sources. All were approximately 1:12,000 scale.

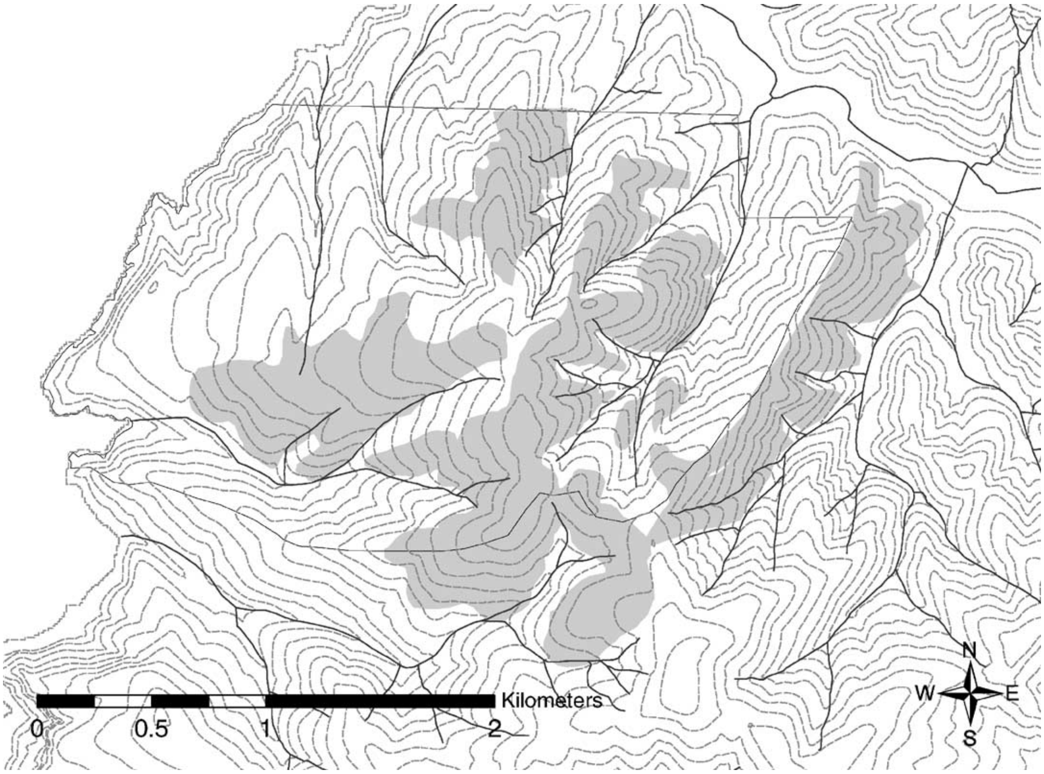

Fig. 1. Map of Neskowin Crest Research Natural Area showing location of fine-texture cover type (gray shading) in 1994 relative to 20 m contours and streams.

Stereo pairs were inspected, and then structural classes were mapped by delineating homogeneous polygons on acetate overlays. Three main classes were identified: fine-textured canopy composed of trees of relatively uniform height and crown diameter; coarse-textured canopy composed of trees of variable height and crown diameter; and broken, open canopy with large blown-down stems often visible on the ground. Gaps smaller than 0.5 ha were not mapped because they could not be delineated with confidence, given the resolution of the photos and the steep terrain.

The acetate overlay maps were digitized and spatially corrected using a PC-based digital terrain model (Carson, 1987) and a 10 m digital elevation model. The spatially-corrected map files were imported to Arc/Info, corrected for polygon closure errors, and converted to themes. The oldest photos known (1953) could not be spatially corrected because not enough control points could be identified; nevertheless, they proved useful for qualitative comparisons.

The six spatially-corrected cover map themes were superimposed over a 1993 digital orthoquad image in ArcView, and differences in polygon boundaries were inspected. The principal causes of the differences were errors in spatial correction (especially in older photos) or in photointerpretation. The differences were reconciled visually on the screen, and a new synthetic map of the main structural pattern elements in 1953 was screen-digitized. It was subsequently converted into a theme in Arc/Info.

To investigate possible causes of the pattern, an additional map layer was created depicting vegetation structure in 1934; it was based on a hand-drawn timber survey map for Cascade Head Experimental Forest (Archives, Forestry Sciences Laboratory, USDA-Forest Service, PNW Research Station, Corvallis, OR). Ten mapping units were represented on the map; they consisted of various combinations of spruce and hemlock, in ‘‘old-growth’’, ‘‘second-growth’’, or mixed stands. We condensed these classes to three (old growth; mixed old growth/second growth; second growth) and traced the resulting polygons on acetate, along with streams and the coastline which served as geographic reference points. Because of the approximate nature of this map, it was not digitized directly; instead it was screen-digitized freehand using the geographic reference points.

To characterize wind effects, a synthetic map depicting blowdown history was screen-digitized by comparing and adjusting blowdown patches on the map layers from 1993, 1984, 1979, 1969, and 1961.

To investigate whether blowdown location corresponded with exposure to winter maritime windstorms, we ran a maritime windstorm susceptibility model developed in southeast Alaska (WINDSTORM; Kramer et al., 2001) for Cascade Head-Neskowin Crest. Maritime windstorm activity in coastal Oregon is similar in many ways to that of southeast Alaska. Both are driven by temperature instability between two large semi permanent air masses, the east Pacific High and the Aleutian low, the result being the development of occasional large extra-tropical cyclonic windstorms. WINDSTORM simulates linear airflow continuously through modification of a discrete airflow model (Boose et al., 1994; Kramer et al., 2001). Wind direction for winter storms was taken to be 180–225° (Ruth and Yoder, 1953). Soil stability class can take values of 1 (low) to 4 (high) depending on soil drainage and topographic position (Kramer et al., 2001). It was set to 1 because of uniformly steep terrain and relative uniformity of the parent material (Greene, 1982).

A comparison was made of structural variables estimated from the aerial photographs with information from ground measurements of tree DBH made in forty-two 0.1 ha circular permanent plots (see Acker et al., 2000 for additional methods and analysis of the permanent-plot data). First, the locations of 44 permanent plots were overlaid on the spatially-corrected 1993 and 1953 cover maps. Then each plot was classified according to the patch type into which it fell (fine, coarse, blowdown). Two plots for which classification was ambiguous because of proximity to an indistinct patch boundary were excluded from this analysis. Next, GPS coordinates of the permanent sample plots were mapped onto the photos using the spatial models. At each plot location, a 1/5 acre circular plot was superimposed and trees with crown width >30 ft were enumerated using a standard crown-width template. For medium trees (10–30 ft crown diameter), 'regeneration' (trees <10 ft crown diameter), and open ground, percent coverage of each plot was estimated. Finally, biomass for all plots for 1994, and biomass changes for the seven blowdown plots were calculated from measurements in 1979, 1984, 1989, and 1994 using the methods of Acker et al. (2000). The biomass changes were inspected for correspondence with blowdown times estimated from the photos taken in 1979, 1984, and 1993.

Comparisons of structural variables among the three plot types were made using analysis of variance. Where the overall ANOVA indicated significance ($P < 0.05$), post-hoc pairwise comparisons among the three plot types were made using Tukey's method.

3. Results

Large patches of the fine-textured cover class occupied approximately 50% of the 1953 forest cover map (Fig. 1); they occurred mostly in the southern and eastern parts of the study area, and were more prevalent on SE–SW-facing slopes (Fig. 2). Several of the boundaries appeared coincident with ridge lines or streams. They strongly overlapped with second-growth patches on the 1934 survey map (Fig. 3). Ring counts from disks of 12 fallen trees taken from one of the patches indicated that all of them recruited in the decade following 1845. All this information supports the idea that these stands represent roughly synchronous regeneration following the 1845 fire, which burned into the area from the east. Hereafter we refer to these patches as second growth.

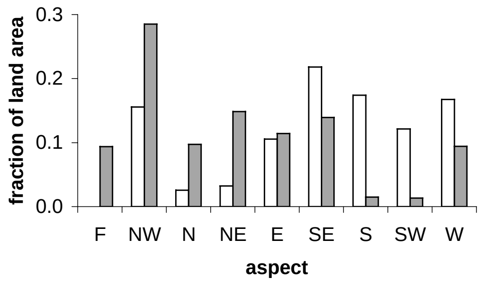

Fig. 2. Distribution of cover types (fine texture: open bars; coarse texture: dark bars) by aspect (F: flat).

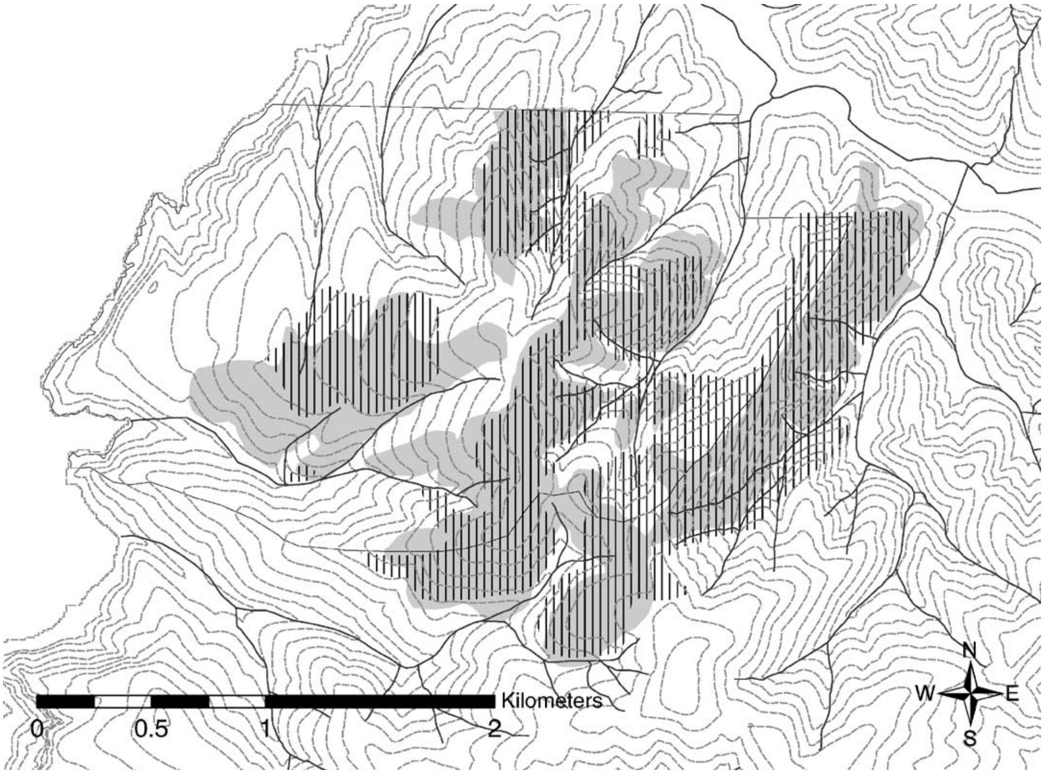

Fig. 3. Map of Neskowin Crest Research Natural Area showing overlap of fine cover type (gray shading) and area mapped as second growth in 1935 (vertical lines).

Coarse-textured patches were mostly concentrated in the steep north-trending ravines in the NW quarter of the site, with some additional areas in creek bottoms and W-facing slopes of the drainages on the eastern half of the site. The 1934 survey map portrayed them as old growth or mixtures of old growth and second growth. We interpret the mixtures as being lightly-burned patches which retained a substantial number of residual canopy trees. Hereafter, we lump the mixtures with old growth.

The large blowdown patch evident in recent photos was represented by only two tiny spots in the 1953 photos (Fig. 4). The spots grew larger and more numerous through 1979. By 1979, there was evidence of tree fall in the narrow fingers of forest between the blowdown patches. In 1984, new discrete blowdown patches were apparent, but they were separated from the 1979 blowdown margins by patches showing intermediate levels of tree loss. These latter areas were less well defined, and it was inferred that they had appeared by a more gradual process. This same distinction, between new, obviously discrete patches, and more diffuse patches was evident in the 1994 photo. This distinction is portrayed in Fig. 4 by adding two panels (1983 and 1992) which depict the areas of gradual, diffuse blowdown.

Visual inspection of the recent photographs showed that the large blowdown patch was quite heterogeneous by 1993. It was mostly made up of patches of small stems of varying sizes, which represented post-windthrow regeneration varying in date of origin, with remnant patches or individuals of the pre-blowdown second growth, and possibly even a very small number of old trees (>145 years). Increment cores taken in this patch showed breast-height ages that dated recruitment to the 1940s or even earlier (Greene et al., 1992), possibly as a result of small canopy gaps.

Several small gaps at ravine confluences were also noted; in general, their locations and sizes were reasonably constant over the full time series of photos.

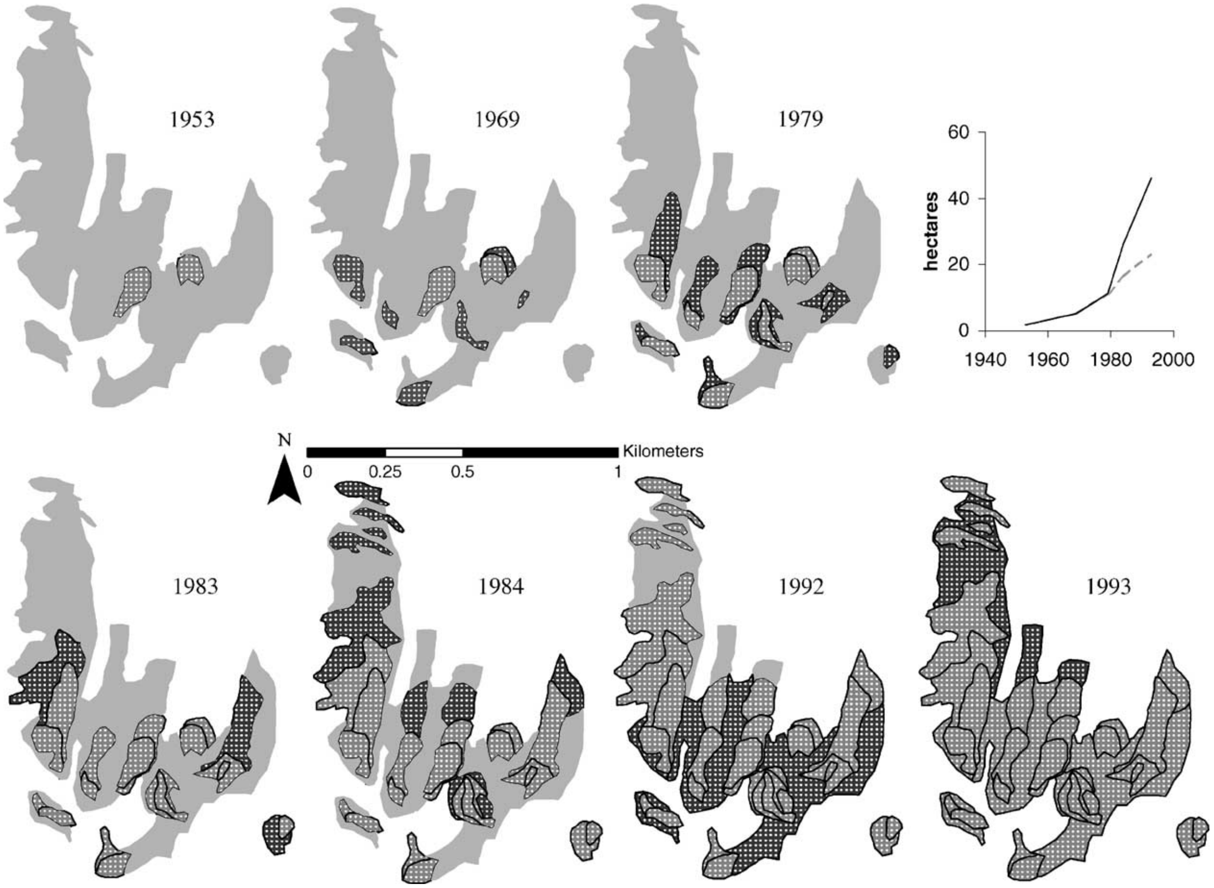

Fig. 4. Growth of blowdown patch from 1953 to 1993. Light gray outline is the blowdown area in 1993. Grey stippling is cumulative old blowdown evident on date shown. Black stippled areas were blown down in the interval between photos. Panels dated 1983 and 1992 show areas that appear to have blown down gradually rather than in discrete events (see text). Inset shows cumulative size of the blowdown area in hectares (dashed line indicates discrete blowdown patches; solid line indicates discrete patches plus gradual blowdown patches).

The lack of change plus their locations mostly in steep ravines or at the confluences of streams suggested that some of them were edaphic gaps (Lertzman et al., 1996) rather than windthrow features. Even smaller gaps too small or indistinct to map reliably appeared in the later photos.

Most of the large blowdown patch (67%) fell within the area predicted to have maximum blowdown probability (Fig. 5) by the WINDSTORM model, which was concentrated on south faces of secondary ridges west of the main N–S ridge which bisects the study area.

Field data from the permanent sample plots shows that the three classes of plots differed significantly in number of big trees and cover of all tree classes (ANOVA, Table 1). Old growth and second growth were distinguishable on the basis of number and cover of trees, and blowdown was distinguishable on the basis of regeneration cover (Tukey's method for pairwise comparisons). However, 1994 biomass in old-growth plots was in the same range as that in the second-growth plots (Table 1), and, even though blowdown plots had 50–60% less biomass than other plots, differences were not significant (ANOVA, $P = 0.052$), undoubtedly because of small sample size and high between-plot variability. Cumulative biomass loss by the blowdown plots over the period 1979–1994 was nearly four times greater than that of the plots outside the blowdown area (273 Mg/ha versus 73 Mg/ha). In spite of the high losses, all seven of

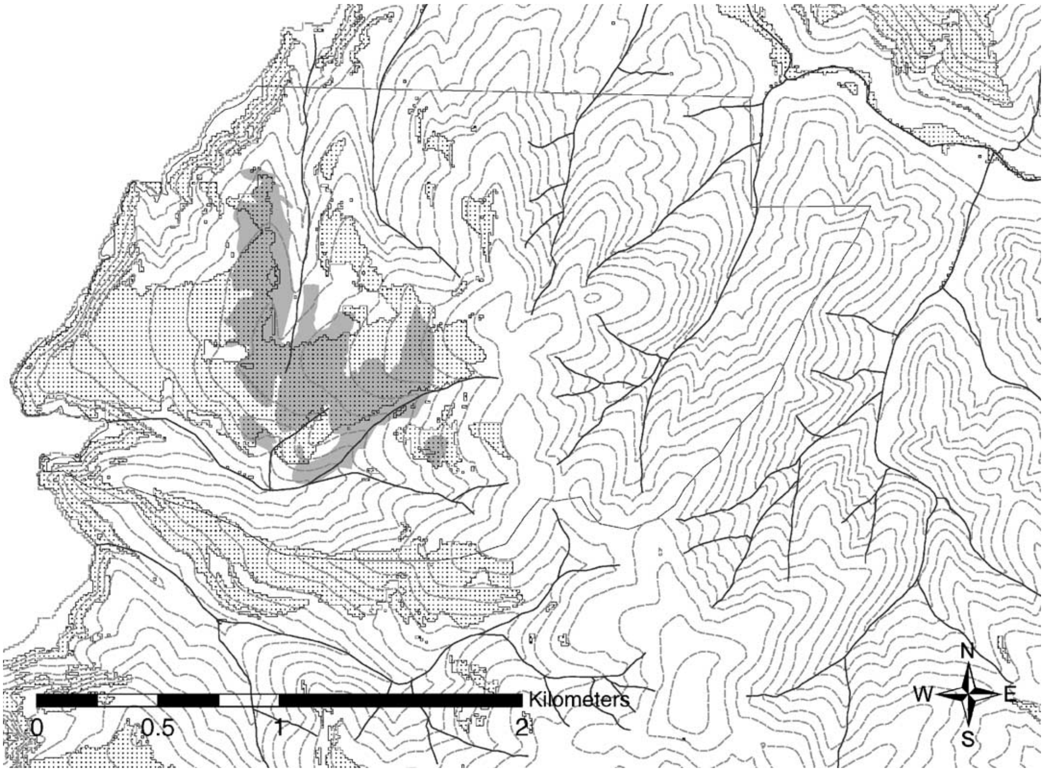

Fig. 5. Map of Neskowin Crest Research Natural Area showing overlap of blowdown area (gray shading) and area of highest susceptibility to wind damage according to WINDSTORM (stippled).

those plots retained many residual trees (biomass was 25–80% of the average for 'second-growth' plots). Also, there was weak consistency in time of apparent blowdown of plots between aerial photos (1979, 1983, 1993) and ground data (1979, 1984, 1989 and 1994). Interestingly, some of the plots showed substantial biomass loss before they were mapped as blown down on the aerial photos (Table 2). Finally, in six of the seven blowdown plots, biomass decline continued long after the initial blowdown. In a sense, gap

Table 1
Comparison of biomass estimated from permanent-plot data (1994) and vegetation structure elements estimated from aerial photographs

	N	Biomass (Mg/ha)	Big trees (no./plot)	Big trees (% cover)	Medium trees (% cover)	Regeneration (% cover)	Ground (%)
Old growth	28	522.54	8.71 a	46.25 a	25.18 a	7.14 a	21.79
Second growth	8	476.75	2.00 b	6.25 b	75.00 b	10.00 a	8.75
Blowdown	6	208.67	3.67 b	13.33 b	31.67 a	41.67 b	14.17
Old-growth stdev		317.1	4.7	26.0	23.2	13.2	15.8
Second-growth stdev		183.0	2.9	9.2	27.8	26.3	8.8
Blowdown stdev		64.3	3.3	15.1	23.2	28.4	20.8

Biomass calculation methods are given in Acker et al. (2000). Other definitions are as follows: big trees (>10 m crown diameter); medium trees (3–20 m crown diameter); regeneration (<3 m crown diameter); ground (percent of plot not occupied by tree crowns). Different letters denote significant differences using the Tukey's method for post-hoc pairwise comparisons where the overall ANOVA indicated significance ($P < 0.05$).

Table 2
Biomass estimates (Mg/ha) based on periodic ground measurement of tree DBH for the seven plots in the mapped blowdown zone

Plot	1979	1984	1989	1994	Map years
31	369	*350*	332	*377*	1983; 1993
32	*322*	207	128	126	1953; 1969
33	503	*487*	431	*171*	1979; 1993
34	*114*	143	201	206	1969; 1979
35	*359*	249	236	209	1969
13	656	*354*	130	136	1983
9	519	*338*	315	221	1983

The final column gives first photo year in which blowdown patch encompassed the plot. Italicized values represent measurements immediately following inclusion of the plot in a blowdown area. When plots were on edges between blowdown patches mapped for different years, both years are given.

formation by windthrow may be an event with a sharp beginning and an indistinct end.

4. Discussion

4.1. Fire

On the portion of the western edge of the Nestucca Fire of 1845 represented by this study, burning was patchy. The fire appears to have died down or gone out in the steep north-trending canyons on the northwest corner of the site. This provides additional evidence for the inference based on dendroecological and paleoecological data from Vancouver Island, British Columbia, where times since fire were much lower on south slopes than on north slopes in a coastal spruce–hemlock watershed (Gavin et al., 2003a). It adds to the list of studies cited in the Introduction showing that topography can be an important constraint on fire behavior. It also helps to explain the apparent anomaly of rapid, uniform post-fire regeneration reported for this area (Harcombe, 1986). In a patchy landscape containing remnant stands of mature trees, colonization of burned patches would not be limited by dispersal (Greene and Johnson, 1999, 2000).

The results contrast with evidence from a similar coastal spruce–hemlock stand less than 100 km farther south. There, topographic constraints were not evident, possibly because they were overridden by high fire intensity (Wimberly and Spies, 2001), as has been shown elsewhere (Turner and Romme, 1994; Lertzman and Fall, 1998; Heyerdahl et al., 2001; Wimberly and Spies, 2001; Gavin et al., 2003a). Taken together, the studies of coastal spruce–hemlock forest illustrate that high spatio-temporal variability in fire effects may occur through much of the range of coastal spruce–hemlock forests.

4.2. Blowdown

The large blowdown patch was the dominant wind-related feature, covering approximately 15% of the study area. Approximately 67% of the patch was within the area of predicted highest probability of blowdown, of which it covered 28%. This overlap supports the hypothesis that disturbance by major windstorms is constrained by topography. Strong topographic constraint on blowdown has been reported in other systems (e.g., Boose et al., 1994, 2001; Quine, 1995; Sinton et al., 2000), and also in spruce–hemlock forest (Kramer et al., 2001; Mitchell et al., 2001). In contrast, there was no relationship between blowdown and topographic position a short distance farther down the coast in the same forest type (Wimberly and Spies, 2001), possibly because that study was carried out in a protected valley where the range of exposure to winter storms would be much lower. Such low variation in exposure could account for the absence of an observed topographic effect in other studies, as well (e.g., Rebertus et al., 1997).

The time of initiation of the blowdown feature is of interest because it bears on the long-standing question of when during stand development a young stand of vigorous trees may get tall enough to be vulnerable to wind damage. This increase in vulnerability with stand age is often mentioned (e.g., Bormann and Likens, 1979; Harris, 1989; Everham and Brokaw, 1996; Wimberly and Spies, 2001), but few studies have investigated windthrow over time. Our results show that the blowdown patch first appeared at a stand age of about 100 years when it was approaching maximum stand height of 50 m and was in the late stem-exclusion stage (sensu Oliver and Larson, 1996; see Acker et al., 2000). This constitutes one datum to establish the putative threshold of blowdown susceptibility. It is remarkably consistent with values of 100–125 years reported for *Nothofagus pumilio* stands in Tierra del Fuego (Rebertus et al., 1997) and for *N. solandri* var.

cliffortioides in New Zealand (Jane, 1986). Nevertheless, many more studies of this phenomenon will be required, especially because the threshold is undoubtedly only indirectly related to age; it will be more directly influenced by species composition, causes of tree mortality other than wind, topography and stand structural attributes like canopy roughness (Ruel, 1995).

The rate of growth of the blowdown patch increased over time. Increasing edge area would contribute to this, since exposed edges tend to have a higher risk of subsequent blowdown (Ruth and Yoder, 1953; Harris, 1989; Ruel, 1995; Sinton et al., 2000; Mitchell et al., 2001). Increasing tree height and stand heterogeneity could also contribute. It does seem likely that the rate will drop, however, considering that the blowdown feature has reached the edge of the area of highest blowdown probability. Whether the blowdown patch has, indeed, reached its maximum extent is highly relevant to understanding the role of wind in this landscape and to the question of long-term biomass dynamics (see below). It also bears on conservation of natural forest remnants in a harvested and urbanizing landscape. The issue is whether the patch owes its size to location in a wind-susceptible site, or to the chance creation of gap 'nuclei' which expand as a result of edge effects. In our study, the several patches in the susceptible area appeared at different times and seemed to grow at different rates, not always along the north edge. Furthermore, there were small gaps in other parts of the study area that did not grow rapidly. In addition, many other papers (cf. Quine, 1995; Ruel et al., 1997, 1998; Sinton et al., 2000; Boose et al., 2001; Kramer et al., 2001; Mitchell et al., 2001) strongly support the idea that topographic position can be a primary determinant of disturbance extent and frequency. For these reasons, we suggest that, in this case, susceptibility to blowdown is more a consequence of location than of presence of edges, though the edges undoubtedly influenced the rate and local pattern of blowdown.

One of the most interesting results of this study is that the blowdown patch did not appear suddenly as a discrete feature in a single photo. Instead, it appeared over time by repeated windthrow. This temporal pattern is consistent with our earlier work that showed gradual loss of biomass from plots experiencing blowdown (Greene et al., 1992; Acker et al., 2000). At the same time, it demonstrates more clearly than was evident from the plot data that large, discrete blowdown patches are important landscape features. Viewing the system at a broader-scale clarified a pattern that was not evident at the finer scale—that is, small-patch processes dispersed in time can generate broader-scale patterns if there are spatial constraints. Conversely, viewing the system at the finer scale of the plots clarified the mechanism—large, discrete blowdown patches are not always the result of single storms, as seems to be frequently assumed (e.g., Wimberly and Spies, 2001; Boose et al., 2001; Kramer et al., 2001). The accreting patches may take a variety of forms, including well-organized waves and poorly-organized partial waves (see Rebertus and Veblen, 1993), or as the coalescing partial waves described here. The views at broad and fine scales are complementary; together they provide a more complete picture of the disturbance dynamics in one portion of the coastal North American temperate rainforest. As we gain more understanding of the spatial and temporal dimensions of wind damage, the uncertainty associated with wind disturbance will decline, and we may begin to conceive of it less as a source of 'noise' that reduces our ability to identify pattern and more as a 'signal' that can help explain spatial and temporal patterns.

This report represents but a single case study. However, in the framework of the regional wind model WINDSTORM, it also constitutes a test of the hypothesis that topography constrains windthrow and can generate large-scale blowdown patches from small blowdowns. In supporting the prediction, it strengthens the general hypothesis. Furthermore, the detailed site analysis provides new insight into the dynamics of blowdown in windstorm-susceptible topographic settings. With additional corroboration of model predictions from other case studies, a more robust picture of the regional disturbance regime will emerge, and it will become reasonable to make predictions about sites for which reconstructions are impossible. A more detailed understanding of regional patterns will have practical significance, as well, because of the relevance of the natural disturbance regime to forest management (cf. Franklin and Forman, 1987; Ruel, 1995; Mitchell et al., 2001, 2002; Franklin et al., 2002). The landscape patterns and biological legacies related to disturbance described in this paper provide valuable information for the development of silvicultural systems that emulate natural models in terms of locations, shapes, and sizes of management units, and identify management constraints based on knowledge of spatial and temporal patterns of blowdown susceptibility.

4.3. Spruce–hemlock long-term dynamics

Several studies spanning the geographic range of coastal spruce–hemlock forest have identified small-patch dynamic processes (Harcombe, 1986; Taylor, 1990; Alaback and Tappenier, 1991; Greene et al., 1992; Lertzman et al., 1996; Veblen and Alaback, 1996; Wells et al., 1998; Acker et al., 2000; Hennon and McClellan, 2003), while others have identified or alluded to large effects of individual windstorms (e.g., Ruth and Yoder, 1953; Greene et al., 1992). This study supports the assertion of Kramer et al. (2001) that in coastal regions neither of the two contrasting models of stand dynamics (catastrophic replacement or small-patch 'equilibrium' dynamics) applies to the exclusion of the other and that gradients of windthrow disturbance occur at the landscape scale, both in terms of variation in patch size, and also of variation within patches (e.g., Rebertus et al., 1997; Nowacki and Kramer, 1998; Boose et al., 2001). Even a relatively small landscape (ca. 500 ha) can be a mosaic, in which different structures and dynamics coexist, i.e., where different models of stand dynamics apply (Wimberly and Spies, 2001). Some areas will be dominated by big blowdown patches; others will exhibit small-patch dynamics. These areas may be substantially fixed in space—locations of big blowdown patches may occur more often in areas highly susceptible to maritime windstorm activity.

4.4. Long-term biomass dynamics

Acker et al. (2000) projected that biomass decline at this site over 20+ years would continue over the course of further stand development as a result of additional growth of the blowdown patch. A decline is consistent with the idea that there is a peak in biomass late in stand development followed by a decrease after the stand passes the wind-vulnerability threshold (Bormann and Likens, 1979; Shugart and West, 1981). While this study does give indication of such a threshold having been reached, it also suggests that susceptibility to blowdown varies with topography. Consequently, since much of the high-susceptibility area has already declined in biomass because of blowdown, continued loss at the same rate is unlikely. Instead, it might be predicted that because of asynchrony of mortality across the plots and the lack of a recruitment delay, biomass should approach a steady state (Peet, 1992; Acker et al., 2000). If, in fact, the site can be viewed as having two phases, one characterized by fine-scale, frequent disturbance, and the other by chronic disturbance, then theory (Turner et al., 1993) suggests that landscape biomass should level off and remain relatively stable at low variance. The prediction of relatively stable biomass near the current level is supported by the fact that there is little difference in biomass between the old-growth plots and the second-growth plots.

By identifying patterns related to past disturbance, this study helps to provide the necessary foundation for broad-scale analysis and modeling of the interaction of wind, topography and fire in controlling structure and productivity of coastal forest ecosystems of western North America, and also to rationalize theory and observation regarding long-term biomass dynamics.

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