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ABIOTIC CONTROLS ON LONG-TERM WINDTHROW DISTURBANCE AND TEMPERATE RAIN FOREST DYNAMICS IN SOUTHEAST ALASKA

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Abstract. We investigated the role of abiotic factors in controlling patterns of long-term windthrow in the pristine coastal temperate rain forests of southeast Alaska. Our objectives were to test the extent to which long-term patterns of windthrow can be predicted spatially at the landscape scale by using four abiotic factors (slope, elevation, soil stability, and exposure to prevailing storm winds), evaluate landform influence on windthrow, and compare stand age and structural characteristics in areas prone to and protected from windthrow. On Kuiu Island, southeast Alaska, we used field validation photo-interpretation procedures to identify forest patches likely to be of windthrow origin. A spatially explicit logistic model was then built from the windthrow data and other GIS data layers, based on slope, elevation, soil type, and exposure to prevailing storm winds. Landform influence on patterns of windthrow was examined by evaluating correct model classification by landform type. The model was cross-validated by extrapolating the Kuiu model coefficients to nearby Zarembo Island, and comparing model predictions to an independent large-scale windthrow data set. The model correctly classified 72% of both windthrown and non-windthrown forest. Field data collected in areas most and least prone to windthrow on Kuiu suggest that structural and age characteristics, as well as forest development stages, vary with the probability of windthrow across the landscape. We conclude that small-scale (partial-canopy) disturbance processes predominate in areas least prone to windthrow, and that large-scale stand-replacement disturbance processes predominate in areas most prone to windthrow. Our work suggests that a spatially predictable long-term wind-damage gradient exists on Kuiu Island. Before this research, gap-phase disturbances have been emphasized as the dominant disturbance process controlling forest dynamics in North American coastal temperate rain forests. We conclude that there is less naturally occurring old-growth forest regulated by gap-phase succession than previously believed, and that catastrophic windthrow is an important process driving forest development in southeast Alaska. To date, most timber harvest on Kuiu Island has been concentrated in storm-protected areas where gap-phase processes (old-growth forests) predominate; future management activities could be tailored to consider long-term natural disturbance patterns to better maintain historical ecosystem function.

Key words: coastal temperate rain forests; forest succession; landscape pattern; logistic regression; natural disturbance; spatially explicit modeling; stand dynamics; Tongass National Forest, Alaska (USA); windthrow.

Introduction

The role of natural disturbance in regulating forest dynamics is a widely recognized theme in forest ecology (Pickett and White 1985, Reice 1994). Disturbances, such as fire, catastrophic windthrow, and insect outbreak, may result in disturbance histories that interact both synergistically and stochastically with environmental gradients, such as soil or climate, to produce complex vegetation mosaics over the landscape (Romme and Knight 1982, Foster 1988*a*, Peet 1988, Veblen et al. 1992, 1994, Hadley 1994). In the past, many studies have emphasized a steady-state, gap-phase-dominated model of forest development (Bray 1956, Bormann and Likens 1979*a*) while others have stressed the role of broad-scale catastrophic disturbance processes in regulating forest characteristics (Franklin and Dryness 1973, Heinselman 1973). These apparently contrasting views on the role of disturbance in forest development may be attributed largely to differences in the rate, scale, and severity of disturbance processes over space and time (Pickett and White 1985, Reice 1994). Yet few studies have explicitly examined how these disturbance parameters (rate, scale, and severity) vary across the landscape (Boose et al. 1994) or have used abiotic factors to understand actual long-term disturbance dynamics over large spatial scales (Bergeron and Brisson 1990).

In this study, we investigated the role of four abiotic factors in controlling long-term patterns of windthrow in the coastal temperate forests of southeastern Alaska.

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Forests in the region are vast, relatively unlogged, and dominated by a single disturbance agent, windthrow, which make them well suited for such a study. Understanding and predicting long-term patterns of disturbance could lead to a better comprehension of how forest structure and ecosystem processes vary across the landscape through time (Dale et al. 1986). For example, if portions of the landscape are subject to more frequent severe disturbance, long-term differences in ecosystem processes, such as soil development, nutrient cycling, and forest productivity, may result (Vitousek 1985, Bormann and Sidle 1990, Vasenev and Targul'yan 1995). Seral trajectories could be different as well, which could affect old-growth dependent species (Carey 1985, Kirchhoff and Schoen 1987, Boyle 1996). These factors have important implications for understanding the impacts of traditional forest management and for developing a management approach based on disturbance ecology (Nowacki and Kramer 1998).

Many studies have recognized that forest dynamics are influenced by a wind-disturbance continuum ranging from small gap openings in the forest canopy to catastrophic stand-replacement events (Harmon et al. 1983, Frelich and Graumlich 1990, Runkle 1990, Spies et al. 1990, Deal et al. 1991). Unfortunately, complex interactions between biotic factors (species composition, canopy structure, size, age, disease, and vigor) and abiotic factors (precipitation, wind intensity and direction, soil and site properties, and the orographic effects of windflow patterns; Harris 1989, Mayer 1989) make a single wind-disturbance event particularly difficult to characterize and predict (Fosberg et al. 1976, Harris 1989, Attiwill 1994, Everham 1996). However, over larger spatial and temporal scales, abiotic factors may control rate, scale, and severity of disturbance. Few studies have explicitly addressed windthrow dynamics on a landscape scale (Boose et al. 1994, Rebertus et al. 1997), and none over both long periods of time and large spatial scales.

Wind-generated disturbance is the principal disturbance affecting the dynamics of coastal temperate rain forests of southeast Alaska (Veblen and Alaback 1996). The forests are comparatively low in tree-species diversity, relatively devoid of human influence, and experience few fires (Noste 1969, Harris 1989, Alaback 1996, Lertzman and Fall 1998). Catastrophic wind disturbance has been known to occur in the region (Harris 1989, Deal et al. 1991), but evidence of long-term catastrophic storm damage has been scant, and we know of no known quantitative studies on the subject. The role of small-scale tree falls in controlling and maintaining forest structure in coastal temperate rain forests of North America has been well studied (Alaback and Tappenier 1991, Boyle 1996, Lertzman et al. 1996, Nowacki and Kramer 1998). Lertzman et al. (1996) found that gap disturbances are common in both mature and old growth forests of coastal British Columbia, but that gap size and frequency patterns were different in each of these seral types.

Our objectives in this study were (1) to test the extent to which long-term windthrow patterns can be predicted spatially at the landscape scale by using four abiotic factors (slope, elevation, soil stability, and exposure to prevailing storm wind), (2) to evaluate the relative influence of landform type on patterns of windthrow, and (3) to compare stand age and structural characteristics in the areas most and least prone to windthrow around Kuiu Island.

METHODS

We combined remotely sensed data, statistical modeling, and field-based measurements to explore long-term windthrow patterns and forest dynamics. Remotely sensed data were used to construct and validate a spatially explicit predictive windthrow model. Field plots were used to ground truth our photo-interpretive windthrow classification, to determine storm dates, and to compare forest structure and age characteristics across the landscape. Our approach included seven steps: (1) quantify past windthrow on Kuiu Island through photo-interpretation and ground truthing, (2) assemble the database necessary to construct a predictive windthrow model, (3) construct the windthrow model, (4) account for spatial autocorrelation, (5) evaluate and validate the model, (6) quantify stand dynamics based on the results from the model, and (7) evaluate timber harvest on Kuiu Island relative to the probability of windthrow.

Study area

The extent of natural coastal temperate rain forest in the Alexander Archipelago of southeast Alaska makes it globally unique (Fig. 1). Twenty-nine percent of the world's unlogged coastal temperate rain forest can be found there. In excess of 3×10^6 ha of unlogged rain forest are thought to remain (Conservation International 1992), which is distributed principally in the vast region of the Tongass National Forest. The Tongass spans the entire extent of the Alexander Archipelago (Fig. 1), and is the largest, most intact national forest in the country. Forests in the Tongass are distributed throughout 7×10^6 ha of total area, located on >1000 islands that are diverse in geology and topography (Alaback 1996). Soils throughout the region are characteristically shallow, due to recent glaciation. Podzolization (Ugolini and Mann 1979) is common in these soils largely as a result of year-round precipitation and the cool maritime climate (Alaback 1986).

Six conifer species dominate the region (Pawuk and Kissinger 1989). On well-drained sites, productive western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Sitka spruce forests (*Picea sitchensis* (Bong.) Carr.) are common, with some mixtures of Alaska yellow cedar (*Chamaecyparis nootkatensis* (D. Don) Spach) and western red cedar (*Thuja plicata* Donn ex D. Don). At

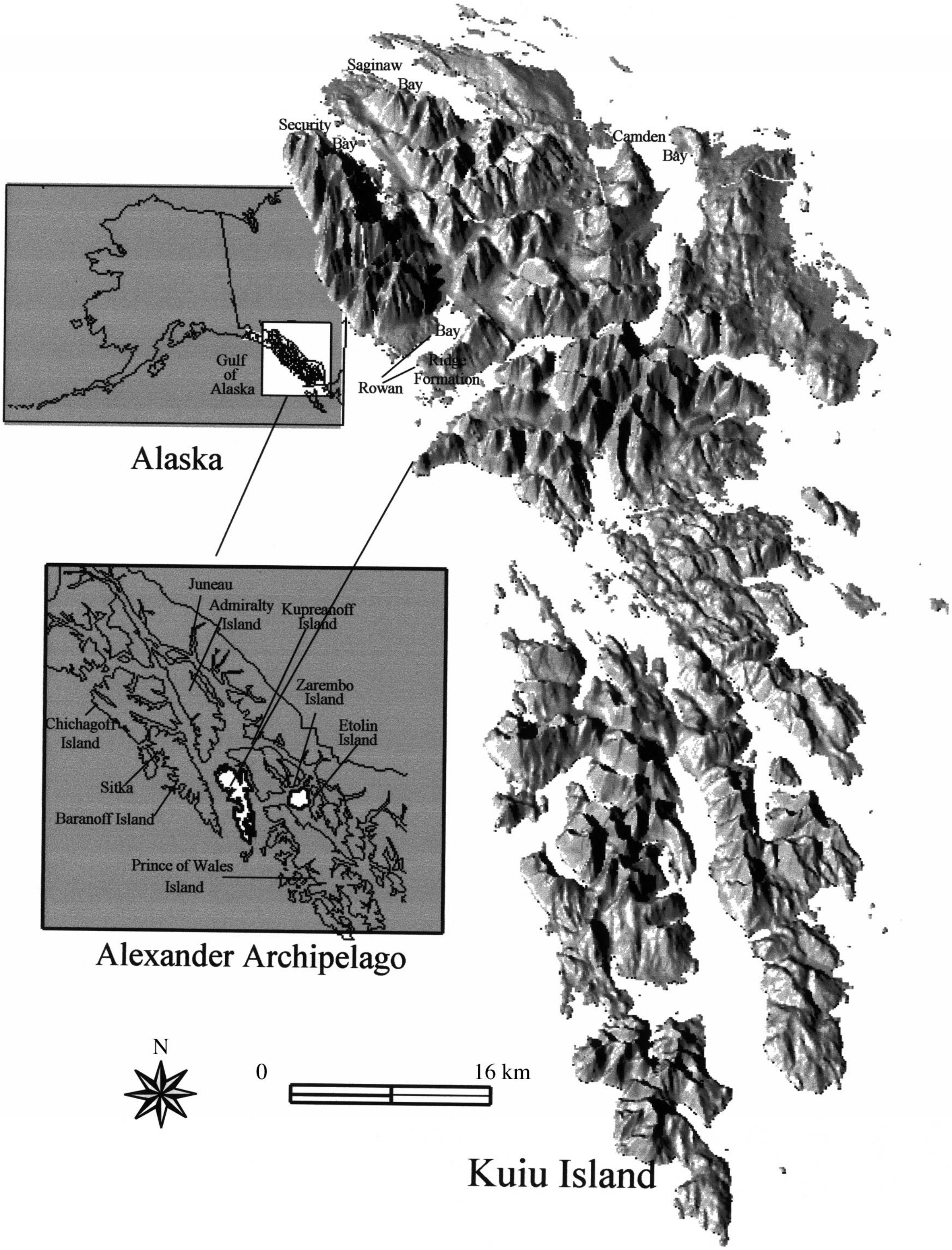

FIG. 1. Vicinity map and shaded relief of Kuiu Island.

higher elevations (>400 m), mountain hemlock (*Tsuga martensiana* (Bong.) Carr.) occurs, typically replacing western hemlock. Low productivity mixed conifer–scrub forests often dominated by lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. contorta), occur extensively on the landscape, along with muskeg (nonforest) on lower site hydric soils or wetlands (Pojar and MacKinnon 1994, Alaback 1996).

In southeast Alaska, the passage of extratropical cyclones dominates the meteorology, with a mean of one storm every four or five days during winter (Shumacher and Wilson 1986). Associated with these storms are winds up to and occasionally >40 m/s, persistent cloud cover, and up to 13 m of precipitation annually in the coastal mountains. Trajectories for these low pressure systems, referred to as the North Pacific Storm track, are largely determined by the location and strength of three semipermanent atmospheric features: the Aleutian low and Siberian high pressure systems in autumn, winter, and spring giving way to the east Pacific high pressure system in summer. Large interannual changes in storm frequency, intensity, and size may be expected as a consequence of El Niño, which can penetrate poleward into the Gulf of Alaska (Schumacher and Wilson 1986).

Extratropical cyclone frequency and intensity increases over the Alexander Archipelago from autumn to late winter due to a tightening gradient between the well-developed Aleutian low, and the weakened Pacific high (from November through March the Gulf of Alaska has the highest frequency of extratropical cyclones in the northern hemisphere; Klein 1957, Wilson and Overland 1986, Naval Pacific Meteorology and Oceanography Center [NPMOC] 2000). During this period, powerful and large extratropical cyclones, capable of producing hurricane force winds, can develop rapidly in the east Pacific Ocean through a process referred to as explosive cyclogenesis (Bullock and Gyakum 1993). Cyclogenesis in the east Pacific can occur several times per month from late autumn to early spring, with storms moving west to northeast as they approach the coastal mountain barrier along the Alexander Archipelago (NPMOC 2000). Associated with these large rapidly developing storms are high levels of precipitation, and counterclockwise vortices, which produce strong winds initially from the southeast direction, then from the southwest direction as the storms move northward or weaken along the coast (Wilson and Overland 1986, Harris 1989, NPMOC 2000).

Kuiu and Zarembo Islands (∼197 000 and 29 398 ha, respectively) are in the middle of the Alexander Archipelago in the Tongass National Forest. Kuiu Island, located 160 km from the mainland, is directly exposed to cyclonic storms that originate in the east Pacific. Zarembo Island, located 90 km from the mainland, is situated between four large island masses, but is still exposed to storm winds from the south and southwest. Timber harvest on both islands began in 1910 (M. McCallum, *personal communication*). Long-term timber contracts initiated by the USDA Forest Service (1991) began primarily in 1956. Only 8% of the forested area on Kuiu Island has been logged, concentrated on the northern half of the island (Fig. 2) and 23% of the forests on Zarembo. Although no towns or human populations persist on either island, a primitive road network associated with timber harvest has been developed on portions of the islands since 1956.

The larger Kuiu Island has four broad landform categories, with unique topographic, geologic, soil, and plant community associations (Fig. 3). Landform type can influence storm damage patterns in many ways, including channeling wind (i.e., through valleys), impeding windflow (topographic protection), and influencing patterns and productivity of vegetation (soil type and parent material; Swanson et al. 1988, Sinton et al. 2000). Landform types on Kuiu (Fig. 3) include the following:

1) Plutonic mountains. This area (26% of the island) consists of the major mountains on Kuiu Island. Landforms are typically smooth slopes below relatively extensive alpine areas. Slopes are generally steep, frequently dissected, and shallowly incised. Elevation ranges from sea level to ∼1105 m. Fifty two percent of the plutonic landscape is forested. Vegetation is dominantly productive western hemlock/blueberry/shield fern plant associations (Pawuk and Kissinger 1989). Muskegs and hydric soils occupy only 10%, and are found infrequently on lower slopes and in valley bottoms.

2) Sedimentary hills. This landform type (33% of the island) is characterized by long, smooth, forested hillslopes bisected by broad U-shaped glacial valleys. Hill summits are well rounded and most are <700 m in elevation. Nearly all of the well-drained hillslope positions are occupied by the highly productive western hemlock/blueberry/shield fern plant associations (Pawuk and Kissinger 1989). Most of the landscape is forested (85%). Alpine ecosystems are rare; hilltops commonly have subalpine (mountain hemlock) plant communities. Muskegs and hydric soils compose a small part of the landscape (20%), and tend to be concentrated in the broad glacial valleys.

3) Limestone ridges. Limestone features are relatively rare on Kiuu Island (6% of the area). Landforms are characterized by gently sloping to moderately steep hills that are abruptly broken by prominent limestone cliffs. The cliffs are generally parallel to each other, giving the landscape the appearance of a series of parallel ridges oriented in a northwest–southeast direction. The landscape has been severely modified by glaciation. Thick glacial till covers many of the moderate slopes, especially at lower elevations, but the white limestone cliffs remain the prominent landscape feature. Forest cover is extensive (83% of the area), and is dominantly highly productive western hemlock/blueberry/shield fern plant associations (Pawuk and Kissinger 1989). Hydric soils are patchy in distribution, and not very common (18% of area).

4) Greywacke lowlands. This landscape is most characteristic of Kuiu Island (61% of the total area). Landforms are low-lying rolling hills (typically <300 m elevation). Hillslopes are typically short, broken, and irregular in shape with well-rounded summits typical of glaciated terrain. Forests are less productive here than on other portions of the island, and tend to be concentrated on hillslopes (59% of the landscape).

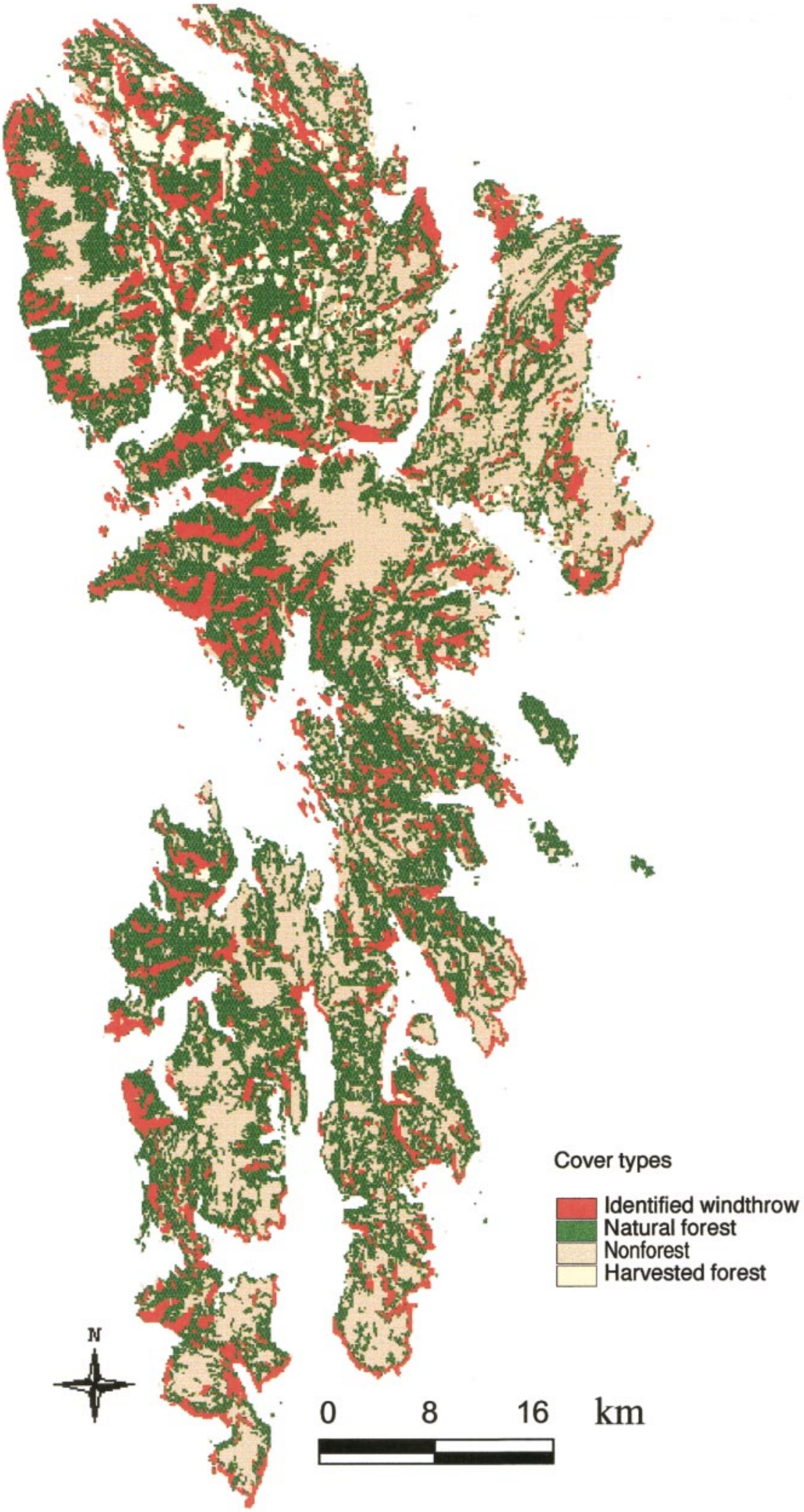

FIG. 2. Windthrown and non-windthrown forest on Kuiu Island. Nonforest area and timber harvest are also shown.

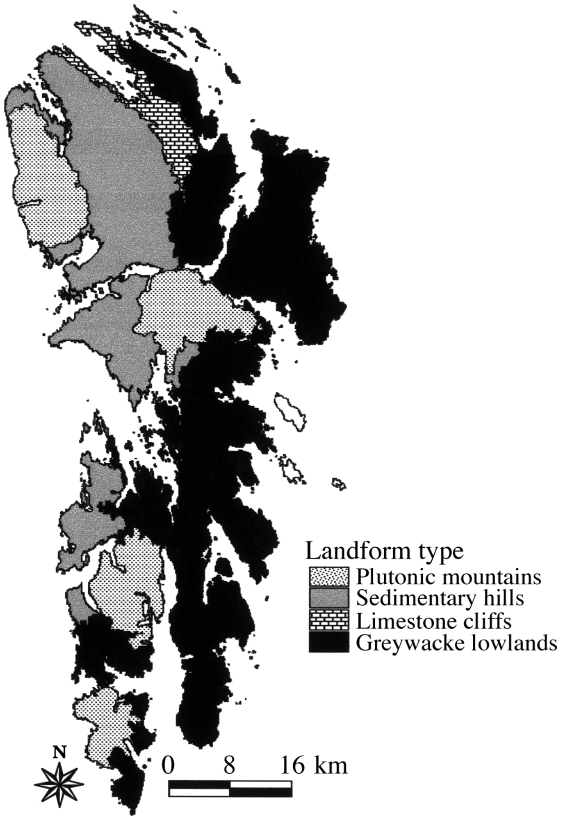

FIG. 3. Location and extent of major landform types found on Kuiu Island.

These are dominated by less productive western hemlock and western hemlock–Alaska yellow cedar plant communities (Pawuk and Kissinger 1989). Muskegs and mixed conifer plant communities (scrub timber) occur extensively on undulating terrain or valley bottoms, both of which tend to be excessively wet. Hydric soils occupy 49% of the landscape.

Zarembo Island can be regarded as a single landform characterized by long, smooth, sometimes moderately sloped forested hillslopes bisected by broad U-shaped glacial valleys. Hill summits are well rounded (<700 m elevation) and most are dominated by muskeg and subalpine scrub forests. Forest occupies 60% of the landscape. Nearly all well-drained hillslope positions are occupied by productive western hemlock/blueberry/shield fern plant associations (Pawuk and Kissinger 1989). Less productive western hemlock and western hemlock–Alaska yellow cedar plant communities (Pawuk and Kissinger 1989) occur on more moderately drained hillslopes, and in valley bottoms. Muskegs and hydric soils comprise 57% of the landscape, and tend to be concentrated in broad glacial valleys, and on higher elevation benches.

Quantification of historical windthrow on Kuiu and Zarembo Island

We used photo-interpretation of 1:32 000 high-altitude color infrared photographs (1979) to identify and delineate forest patches that appeared to be even aged and possibly of windthrow origin on Kuiu and Zarembo Island. Windthrow data from Kuiu Island was used in the model construction and evaluation portion of the study, and from Zarembo Island for model validation. Forest patches that were likely of landslide origin (based on patch shape, and topographic characteristics) were not mapped. All even-aged forest patches interpreted as windthrow were digitized into a geographic information system (GIS) in Alaska state plane coordinates.

Field sampling was focused on areas identified as even aged by photo-interpretation on Kuiu Island. Eighty-one plots were distributed randomly among the even-aged patches throughout the island, as logistics permitted. At each plot, we collected evidence that the forest originated from one or more catastrophic disturbance event by measuring forest age and size characteristics. We then searched for evidence of landslide activity, past windthrow, or alternative causes of disturbance, based on standing tree, forest floor, and soil characteristics.

The plot was confirmed to be of windthrow origin if dead and downed stems were present, and if they showed consistency in direction of fall (Gastaldo 1990). Stand stage (Spies and Franklin 1996) was visually estimated on the basis of canopy closure and structural characteristics (Kramer 1997). No forests >150 yr old (mature forests) could be confirmed as windthrow because decomposition made identification of dead and downed stems difficult. In these mature forests, we classified the plot as probable windthrow if we could not find evidence of landslide activity, fire, or alternative causes of disturbance.

Evidence of landslide activity included the shape of the disturbance patch, landform position (ridge top, midslope, or toe slope), the presence of headwalls, and unsorted landslide debris (angular rocks) on the forest floor or in soil horizons. If cut stumps were found, the cause of disturbance was identified as timber harvest. Other possible causes of stand-replacement disturbance in these forests include insect or pathogen outbreaks. However, there are no known reports of widespread catastrophic mortality events associated with fungal or insect attack, although these agents of disturbance have been studied in the region for some time (P. Hennon, *personal communication*). In addition, we found no evidence of recent catastrophic insect or fungal mortality in any of our plots (defoliation, bark beetle damage, catastrophic death of trees still standing).

In forests of confirmed or probable windthrow origin, we estimated the date of the storm from the age at breast height of a cohort of 5–15 trees that regenerated on windthrow mounds or rootwads (if present). Mortality since catastrophic disturbance may bias older storm dates (Fox 1989), so storms >150 yr were dated to the nearest 25 yr. Using this methodology we were able to estimate the age of forests that originated from a stand replacement disturbance as far back as 400 yr.

Database assembly

To construct a spatially explicit windthrow model, we began by looking at all forest lands on Kuiu Island. The delineation for these forest lands was based on productivity (USDA Forest Service, *unpublished data*). Less productive scrub forest and nonforest areas were not included in our analysis. These areas were thought to be minimally affected by catastrophic storms and did not show any identifiable evidence of catastrophic windthrow.

A digital map delineating all forest lands was obtained from the USDA Forest Service (*unpublished data*). Only forests not logged in the last 100 yr were considered (92% of the forest lands on Kuiu Island). A new digital layer was created by combining the windthrow GIS layer and the forest lands cover. Each forested cell was classified as either windthrow or nonwindthrow based on the presence or absence of windthrow (Fig. 2). We used a cell size of 0.8 ha because it represented the coarsest scale of available GIS data.

We selected a subset of four abiotic variables (slope, elevation, soil stability, and storm exposure) from a suite of many abiotic and biotic factors generally thought to influence windthrow (Swanson et al. 1988, Everham 1996). The four factors chosen were selected because they represented the best available GIS data thought to be most appropriate in predicting windthrow occurrence over both long time periods and large spatial scales. We did not include landform type as a variable in the model because of the diverse landform types (both geologic and geomorphic) between and within other islands, which are not well represented on Kuiu Island. In addition, even on Kuiu Island we could see no clear way to rank each landform type, since each has unique topographic, geologic, edaphic, and vegetation characteristics.

Slope, elevation, soil type, and storm exposure categories were created for each forested cell. Storm exposure was calculated by using a modification of the EXPOS model (Boose et al. 1994), and a 62-m resolution digital elevation model (DEM) of Kuiu (USDA Forest Service, *unpublished data*). The EXPOS model simulates linear wind flow over terrain from a specified direction. A specified inflection angle allows wind to bend (in the vertical plane) as it passes over any protruding surface (i.e., a ridge or peak). Each 0.8-ha cell in a DEM is then classified as either exposed or protected. To create a range of exposure values over Kuiu Island, we modified the EXPOS model to run iteratively, increasing the specified inflection angle by 2° each time, up to a maximum inflection angle of 14°. This resulted in nine categories of exposure.

Historical storm data was unavailable for Kuiu Island, and the exact direction of prevailing storms was unknown. Based on consultation with regional meteorologists, publications and primary station wind records, and on the direction of fallen stems in forests of windthrown areas on Kuiu Island, we determined that storm force winds on both islands came mainly from the south-southeast to southwest (160–220°) directions. To determine exposure from storm winds, which could from any of these directions, we ran the modified EXPOS model from the two outermost directions, south-southeast (160°) and southwest (220°), and calculated the mean exposure from those two directions.

Slope categories were created with the LATTICEPOLY command in Arc/Info software (Version 7.0.1; Environmental Systems Research Institute, Redlands, California, USA) and a DEM (62 m). Soil stability classes, based on soil drainage characteristics and topographic position, were obtained from digital USFS maps (USDA Forest Service 1992), and converted to a 0.8-ha cell grid size. The RECLASS command in Arc/Info GRID from a DEM (62 m) was used to calculate elevation classes. For each variable, the final ordinal class assigned reflected a range of possible values. For example, all cells with elevations between 124 and 185 m were assigned an ordinal class of 3. All possible variable values are covered in the ordinal class assigned (Table 1). These slope, elevation, soil, and exposure classes were then used as attributes for each forested cell in the GIS.

Model construction

Our primary modeling objective was to make spatially explicit predictions of windthrow across the landscape. Spatial models make statistical inference and interpretation of model coefficients difficult because assumptions regarding independent observations are difficult to meet (Cressie 1991). We examined each variable individually with windthrow occurrence, to confirm that it should be considered for inclusion in the model and to make exploratory interpretation of the relative influence of each of the four abiotic factors in predicting the occurrence of windthrow.

We selected a multiple logistic regression model to estimate model coefficients and generated a probability of windthrow occurrence for each forested cell on Kuiu Island. Each variable was normalized to zero. Because prediction was our primary goal, and not explanatory inference, second-order and interaction terms were added, resulting in 14 terms considered for inclusion in the model. An exploratory stepwise approach using maximum-likelihood estimation based on Akaike (1973) was used to select the best-candidate model (SAS Institute 1988). Our best-fit model, selected from a set of models, had minimum Akaike information criteria which asymptotically minimized prediction error (Stone 1977). Final model coefficients were standardized for relative comparison. Variance inflation factors (VIF) were calculated for each independent variable to detect for the presence of multicollinearity in the independent variables. Generally, a VIF <10 suggests

TABLE 1. For each of the four variables, a new GRID GIS coverage was created by collapsing the original data into one of nine ordinal values.

Ordinal number assigned (increasing value)	Slope (%)	Elevation (m)	Soil stability (class)	Storm exposure (by inflection angle)
1	0.00–0.99	0–61	0	never exposed
2	1.00–2.14	62–123	1	14
3	2.15–4.59	124–185	2	12–13
4	4.60–9.90	186–247	3	10–11
5	10.00–21.40	248–309	4 (highest)	8–9
6	21.5–46.3	310–372		6–7
7	46.4–99.0	373–433		4–5
8	100–1000	434–1111		2–3
9	>1000	>1111 (highest)		1 (most exposed)

moderate multicollinearity influence on least squares estimates (Neter et al. 1996).

Spatial autocorrelation

The presence of spatial autocorrelation in our dependent and independent model variables may influence parameter and prediction estimates (Manly 1991). While new methods have recently emerged that account for spatial autocorrelation in spatial data so that inferential assumptions are met few have been applied and used in spatial ecological modeling problems (Manly 1991, Pereira and Itami 1991, Augustin et al. 1996, Sinton 1996). Resampling of lattice data has been suggested by numerous authors as a technique to cross-validate prediction estimates, and obtain confidence intervals for model coefficients that account for spatial autocorrelation present in lattice data (Cressie 1991, Lele 1991, Manly 1991). Although resampling has been recognized for some time in the statistical literature (Cressie 1991, Lele 1991, Manly 1991, Sherman 1996), techniques such as the jackknife or the bootstrap have not been widely used in spatially explicit ecological problems (Heagerty and Lele 1998).

We used a jackknife cross-validation resampling approach to determine the degree to which high spatial autocorrelation was influencing our model predictions. Spatial autocorrelation in windthrown forest cells was measured using semivariance (Carr 1995). High spatial autocorrelation was found up to 1500 m east–west and 3000 m north–south. We then jackknifed out a 3000 × 6000 m block of data (1800 ha) centered on each prediction cell. The remaining data were used to estimate model coefficients and compute a probability of windthrow occurrence for that individual cell. The 1800-ha block was then centered on the next forested cell so that it would not overlap with the position of previous blocks. This resulting in running the model and estimating model coefficients 115 times, each time removing, or jackknifing out, data from a single 1800-ha block. Ninety-five percent prediction and coefficient confidence intervals for both windthrown and non-windthrown forests were then calculated based on these results. Because a spatial error (dependence) term was not included in the model, the 95% confidence intervals obtained from resampling represent a conservative estimate for both our predictions and coefficient estimates.

Model evaluation

The best-candidate model was evaluated on Kuiu Island as a whole and by each landform type to determine the relative effects of landform on windthrow. For each landform, a correct classification, percentage improved over random, and the corresponding cutoff value used was reported. We defined ‘‘correct’’ as the classification that best classified both response states (windthrown and non-windthrown forest) with equal success. ‘‘Percent improved over random’’ is a measure of improvement over a model that could correctly classify 50% of both the windthrown and non-windthrown simply through random selection. A model that correctly classified 60% of both windthrown and non-windthrown data would represent a 20% improvement over such a random model. The cutoff value is the probability value at which the model is correctly classifying both response states (windthrown and non-windthrown) with equal success. These criteria were chosen because our primary objective in developing this model was to predict windthrow occurrence on the landscape.

Model validation

The reality and utility of our best-candidate model was assessed via external validation (Hosmer and Lemeshow 1989), using an independent windthrow data set from nearby Zarembo Island. The digital data construction techniques described for Kuiu Island (second step) were repeated for Zarembo Island on all unlogged forest. The coefficients derived from Kuiu Island were then used to generate a map of the probability of windthrow for every 0.8 ha of intact forest on Zarembo Island. The windthrow data set developed from photo-interpretation of color infrared photography was used to compare predicted and observed windthrow. The same measures used to evaluate the model on Kuiu Island (correct classification, percentage improved over random, and cutoff value) were reported for Zarembo Island.

Stand age and structure

More detailed forest structure and age information was collected from field plots using a stratified random design in forest accessible from the road network (within 2 km) on the north half of the island. Seventy-three of the plots (those located in areas most prone to windthrow; probability of occurrence >0.2) already established to ground truth the remotely sensed windthrow data set on Kuiu Island were included in this comparison. An additional 38 fixed radius (0.l-ha) field plots were located randomly in 15-ha or larger forest regions that were either windthrow prone or protected (based on model results). In each of the 38 plots, dbh, tree species, and estimated canopy position (dominant/codominant, intermediate, suppressed) of all standing trees (dead or alive and >12 cm dbh) were recorded. Prominent rootwads (mineral mounds) and stumps (organic mounds) were counted. Ten to twenty codominant trees of representative diameter classes were cored at breast height in each plot to determine age. Cores were stored in a plastic core holder, then counted in the lab by using a dissection microscope. Cores that were difficult to count were mounted, sanded, and then counted.

For each plot, the coefficient of variation and mean tree age and diameter was calculated. We then compared the mean coefficient of variation of tree age and diameters from all plots in located in windthrow prone with those from windthrow protected forests. A regression of mean age on mean diameter was performed separately for plots most and least susceptible to windthrow. No hypothesis tests or P values were reported from those regressions. The comparisons between forest structure in windthrow-prone and windthrow-protected areas were purely exploratory because plots located in known even-aged patches were included in the comparison. We collected data from six plots randomly located in windthrow-prone areas that were not identified as even aged from the photo-interpretation exercise. The results from these plots were reported, but no inferential statistics were used because the sample size was small. We clustered data from all the fixed radius plots (from both windthrow prone and protected areas) using a Chebychev distance metric. Clustering was based on structural and age characteristics of the fixed-radius plots.

RESULTS

Identification of windthrown patches on Kuiu Island

Based on photo-interpretation, we identified 20% (26 588 ha) of the forest as even-aged stands which originated from windthrow (Fig. 2). Ground-truthing this remotely sensed data set resulted in forty-six percent of the even-aged forests being classified as younger (<150-yr-old) confirmed windthrow, with an additional forty eight percent identified as older (>150-yr-old) probable windthrow. No forests >150 yr old (mature forests) could be confirmed as windthrown because decomposition made identification of dead and downed stems difficult. We classified these mature even-aged stands as probable windthrow because we could find no evidence of landslide activity, fire, or logging. It is still possible that these forests originated from alternative causes such as catastrophic insect outbreak. However no evidence of insect outbreak was found in any of the younger forests sampled, and aside from localized spruce budworm outbreaks associated with islands located just off the mainland, no catastrophic outbreaks have been reported in the southeast Alaska region (B. Pawuk, *personal communication*). In 5 of 81 plots identified by photo-interpretation as windthrow, either evidence of a landslide or clearcut activity was found or catastrophic storm evidence was not discernible from forest structure and age characteristics.

Stands that originated from a storm event that occurred $\sim$110 yr ago comprised 40% of our plots (Fig. 4a). The remaining even-aged patches originated from at least four other major storms that occurred anywhere from 50 to 400 yr ago (Fig. 4a). The orientation of downed stems in recent (<150-yr-old) windthrow plots confirmed our assumption regarding prevailing storm direction (Fig. 4b).

Model construction

The increase in windthrown forest with higher EXPOSURE values suggests that this variable is a strong predictor of windthrow occurrence on Kuiu (Fig. 5a). Increase in SLOPE, SOIL, and ELEV are all accompanied by increasing windthrow occurrence (Fig. 5b–d); however, the rate of windthrow increase is not as strong as with EXPOSURE. The univariate results suggest that all four independent variables are appropriate for inclusion.

All four first-order variables, three second-order variables, and three interaction terms were selected in the best-candidate model (Table 2). The positive value of the first-order coefficient for exposure was consistent with results from univariate diagnostics. All selected interaction terms included the EXPOSURE term, again suggesting that EXPOSURE was one of the stronger predictors in the model. Akaike (1973) distance values and differences in the model performance suggest this best-candidate model represents a considerable improvement over either a single-variable model (using EXPOSURE) or the four-variable model (using the four abiotic factors alone). Variance inflation factors for each variable in the model were all <10 (Table 2), which suggest multicollinearity effects were not unduly influencing our coefficient estimates (Neter et al. 1996).

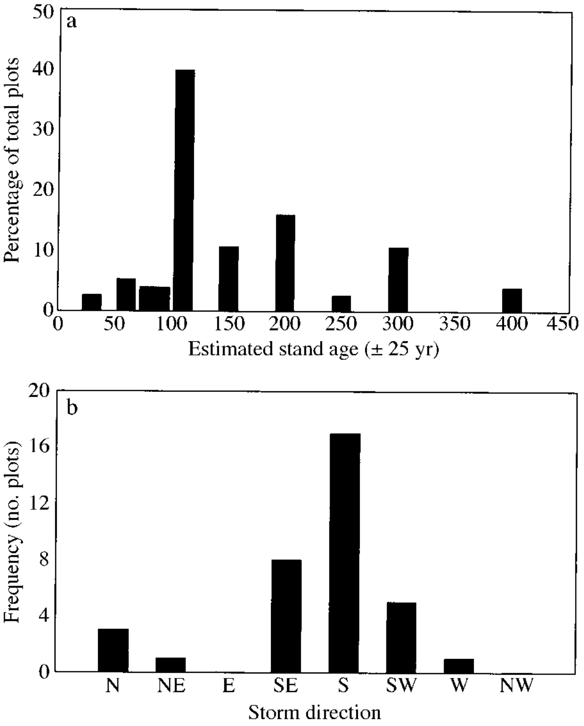

FIG. 4. (a) Frequency of estimated stand ages from 81 field-validation plots in forests identified as windthrown from photo-interpretation. (b) Frequency of storm direction of 37 field plots that experienced windthrow in the last 150 yr. Storm direction was based on the direction of fall of synchronously downed stems.

Prediction error due to spatial autocorrelation was <0.3% for both windthrown and non-windthrown forest. The tight range of 95% prediction confidence intervals and coefficient estimates (Table 2) suggests that high spatial autocorrelation did not unduly influence model predictions.

TABLE 2. Final model variables, and order selected in the best-candidate model, with 95% confidence interval coefficient values and variance inflation factors (VIF) for each variable.

Model variable	Lower 95% CI limit	Upper 95% CI limit	VIF
Intercept	1.65762	1.65491	···
Exposure	0.32057	0.32142	2.7
(Elevation)^3	0.02441	0.02423	1.6
(Slope)^2	0.04675	0.04718	1.1
Soil	−0.90812	−0.90463	5.7
(Elevation)^4	−0.00478	−0.00471	1.6
(Slope)^3	0.02316	0.02331	1.3
(Soil)^2	0.52016	0.52177	5.6
Exposure × (Elevation)^3	0.01964	0.01980	1.2
Exposure × (Slope)^3	0.05954	0.05993	2.2
Exposure × Soil	0.00266	0.00269	1.1

Model evaluation and validation

Model performance (correct classification and percentage improved over random) and the corresponding cutoff probability values that were specified are shown in Table 3. The model showed good agreement with actual patterns of long-term storm damage (68% correct classification) on Kuiu Island. However model performance varied considerably by landform type on Kuiu Island (Table 3). The 38% improvement over a random model on the entire island was considerably lower than the 58% improvement value in the sedimentary hills landform type. In this landform type, the model was able to explain 79% of the actual storm damage patterns. Correct classification in the three other contrasting landform types; plutonic mountains (67%), grey-

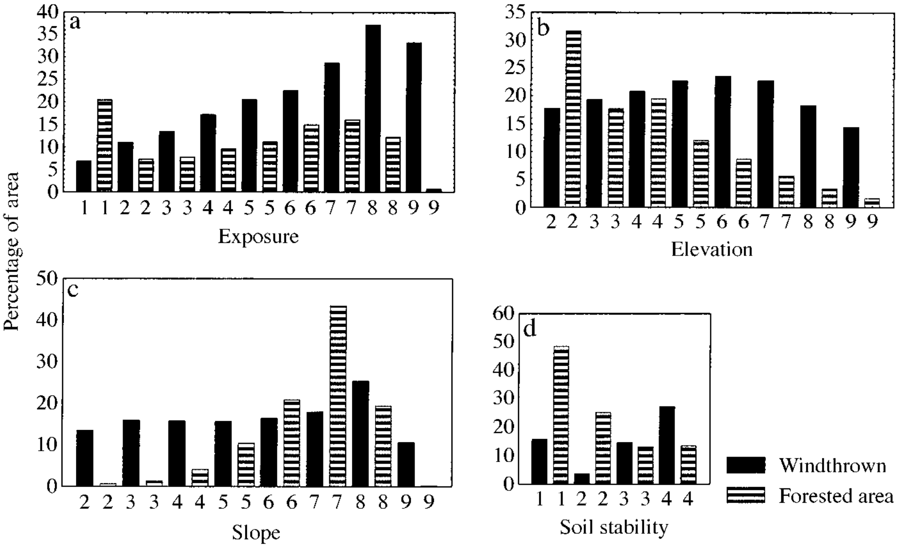

FIG. 5. The percentage of all forested area and windthrown forested area in each exposure, elevation, slope, and soil stability class. See Table 1 for definitions of classes.

TABLE 3. Model performance on Kuiu and Zarembo Island, and by landform type on Kuiu Island. The cutoff value is the probability value used to correctly classify both response states (windthrown and non-windthrown) with equal success.

Model performance	Correct classification (%)	Improved over random (%)	Cutoff value
Zarembo Island	72	44	0.21
Kuiu Island	68	38	0.18
Landform type			
Plutonic mountains	67	38	0.21
Sedimentary hills	79	58	0.28
Limestone cliffs	69	39	0.30
Greywacke lowlands	66	33	0.19

wacke Lowlands (66%), and limestone cliffs (69%); was considerably lower.

Model validation was performed by comparing actual patterns of damage on nearby Zarembo Island to predictions of windthrow-prone areas using Kuiu coefficients. Fifteen percent of the forested landscape on Zarembo Island was identified as even-aged probable windthrow from photo-interpretation (Fig. 6a, b). Our model validation exercise considered Zarembo Island as a single landform type, and was done for the island as whole. Overall there was good agreement between predicted and observed patterns of storm damage, with 72% correct classification (Fig. 7). Our predictions represented a 44% improvement over a random model, which is 7% higher than for Kuiu Island (38% improved over random; Fig. 7). No windthrow was observed in a relatively large forested area on the southeast portion of the island, which was predicted to be windthrow prone (Fig. 6a).

Stand structure

Stand age and structural characteristics were compared from data collected in storm-prone and storm-protected forests. Forest age and structural characteristics were found to be more homogenous in areas of high storm susceptibility. Mean coefficient of variation for forest age was 17 ± 1.49 (mean ± 1 SE) vs. 37 ± 2.06, respectively. Mean coefficient of variation for tree age was 26 ± 1.79 vs. 51 ± 1.71, respectively. Regression results between stand age and diameter in storm prone landscapes suggest a significant positive relationship between stand age and diameter (Fig. 8a). By contrast, no linear relationship between age and diameter could be found in storm protected landscapes (Fig. 8b).

Sixteen percent of the fixed radius plots collected in storm protected areas exhibited structural and age characteristics indicative of recent catastrophic disturbance. The six fixed-radius plots collected in areas the model predicted as windthrow prone but where no windthrow was detected from photo-interpretation, all showed evidence of at least one major catastrophic windthrow. However, all six of these stands originated from windthrow that occurred >200 yr ago, suggesting that our photo-interpretation methodology may not have detected all windthrows >200 yr, or possibly windthrows which occur in less productive sites. Poorer soil conditions and the older age of stands in those areas may have created a more heterogeneous canopy texture, which made detection via photo-interpretation difficult. However, the unimodal diameter and even-aged characteristics of these forest plots suggest catastrophic windthrow affected all of them.

Fixed-radius stem plots (collected in both storm-prone and storm-protected locations) were summarized and clustered to provide more detailed understanding of age and structural characteristics of forests in various stages of recovery from catastrophic disturbance. Clustering (using the Chebychev distance metric [Michalski et al. 1981]) was done based on stand structure (histograms of standing dead and alive) and population structure (age of trees cored) of the fixed-radius plots. This resulted in four distinct clusters, ranging from even-aged young stands to all-aged older forests. Most plots (33 of 38) exhibited age and structural characteristics indicative of late-seral-stage forests (clusters 2–4). Density of large trees (>120 cm) was relatively constant in these forests (15 ± 5 per ha; mean ± 1 SE).

Cluster 1.—Complete (6 plots). Plots in this cluster were located primarily in storm-prone locations and showed strong evidence of both recent (<150 yr) and older (>150 yr) catastrophic stand-replacement events. Ages were tightly grouped (Fig. 9a), and diameter distributions were normal (Fig. 9b), with a relatively tight range of diameter sizes found in the stand. The high number of small standing dead trees in these plots (Fig. 9b) suggests that self thinning is still a dominant mechanism for mortality.

Cluster 2.—Partial (6 plots). Plots in this cluster showed evidence of a partial canopy disturbance, which resulted in some tight clustering of age groups (Fig. 9a), but stand characteristics (bimodal, negative exponential, or uniform) were indicative of late-seral-stage forests. These stands may have experienced one or more partial canopy disturbance events, and be multi-aged stands.

Cluster 3.—Gap (21 plots). Plots in this cluster showed evidence of some partial canopy disturbance, and multiple small-scale disturbance events. Ages were variable (Fig. 9a), and diameter distributions were mostly negative exponential and uniform with a wide distribution of diameter sizes. Large standing dead trees could be found in most plots. Smaller trees (Fig. 9b) were uneven aged (Fig. 9a).

Cluster 4.—Low site (5 plots). Plots in this cluster showed evidence of many small-scale disturbances. Ages in these plots spanned a wide range (Fig. 9a), and diameter distributions were uniform (Fig. 9b). Standing dead trees (both large and small) were abundant. One especially long lived species, Alaska yellow cedar, was noticeably more abundant (20% of live stems on average) in two of the plots, which might explain the wider variation of age characteristics found in them.

Evaluation of timber harvest on Kuiu Island

We used our best-candidate model to predict the probability of windthrow in logged portions of Kuiu Island (Fig. 10.) Most timber harvest has occurred in areas where forests are protected from long-term catastrophic storm damage.

DISCUSSION

Long-term natural disturbance on Kuiu Island

Forests are most often influenced by multiple natural disturbance processes, including, in many cases, strong influence by human activity (land use conversion, timber harvest). As a result, the way in which natural disturbance dynamics (rate, scale, intensity) may be expected to manifest themselves over both long periods of time and at large spatial scales is not well understood (Peterson 2000). The forests on Kuiu Island, and surrounding islands, are particularly well suited to study the long-term effects of a single natural disturbance agent, windthrow, on the forested landscape. The limited logging that has occurred is not sufficient to have confounded or erased beyond recognition the natural disturbance history reflected in present day forests.

Many large catastrophic wind storms have affected Kuiu Island in the last 400 yr. These storms may have repeatedly blown down the same forested landscapes, so our conclusions regarding the extent of damage caused by each storm are limited. Our evidence of wind damage caused by multiple storms is consistent with evidence of catastrophic wind damage found in other windy environments such as Ireland, New Zealand, and Argentina (Anderson 1954, Gallagher 1974, Thomson 1976, Rebertus et al. 1997). A record of major gale-force damage in Ireland that dates as far back as 500 AD suggests that at least one major catastrophic storm occurred each century (Gallagher 1974). As in southeast Alaska, frequent maritime windstorms in coastal regions of New Zealand, Ireland, and Chile are reported to travel in characteristic prevailing storm directions due to persistent large-scale atmospheric features (Shumacher and Wilson 1986, McBean 1996, NPMOC 2000).

Windthrow has affected >20% of the forests on Kuiu Island. These catastrophic storms effect some portion of Kuiu Island every 100 yr (Fig. 4a), well within the lifespan of dominant forest species. Prior research has focused on the role of gap-phase disturbance processes in controlling forest structure and age dynamics in the coastal temperate rain forests of North America (Alaback and Tappenier 1991, Boyle 1996, Lertzman et al. 1996). Our results suggest that, while gap-scale disturbances may operate in both mature and old-growth forests, stand-replacement events control many of the age and size characteristics in coastal temperate rain forests, especially those most prone to catastrophic storm damage

Abiotic controls on windthrow

Landscape windthrow patterns that result from a single storm event are the consequence of complex and stochastic interactions between abiotic and biotic factors, which can make prediction of individual storm damage patterns difficult (Peterson 2000). At large spatial and temporal scales, topographic and edaphic conditions and prevailing storm direction appear to constrain the intensity of disturbance on some portions of the landscape, which results in a gradient of long-term storm effects across the landscape (Foster 1988*b*). This gradient can be made spatially explicit and predicted on a broad scale using multiple logistic regression. The good agreement between predicted and actual patterns of windthrow on Zarembo Island suggests that our model is generalizable to nearby islands, and that gradients of landscape-scale, long-term catastrophic windthrow damage occur on both Zarembo and Kuiu islands.

Our conclusion that disturbance rate, scale, and severity are constrained by relatively few abiotic factors may apply to other large-scale disturbances such as forest fire or insect outbreak related to drought stress. Numerous studies on fire have found variations in the return interval, intensity, and extent of fire over relatively large landscapes (Bergeron and Brisson 1990, Morrison and Swanson 1990). These differences may also be the result of relatively few abiotic factors, such as susceptibility to lightning strikes, fuel loading, or soil moisture differences (Foster 1988*b*), which could be used to predict and understand long-term disturbance gradients across a landscape.

Landform influence on windthrow

Landforms strongly influence long-term storm damage patterns on both Kuiu and Zarembo Island (Table 3). Each landform has unique geomorphic and vegetation characteristics that control windthrow occurrence on the forested landscape. The pronounced ridge and valley formations and contiguous highly productive forest cover in the sedimentary hills landform on Kuiu, for example, appeared to strengthen or accentuate this storm damage gradient (79% correct classification of both windthrown and non-windthrown forest). Many ridges run perpendicular (east–west) to prevailing storm directions, with well-defined valley and ridge formations that adequately protected some portions of the landscape from catastrophic windthrow. By contrast, the glacially smoothed topography, and less contiguous, less productive forested region of the greywacke lowlands weakened the storm damage gradient (66% correct classification of windthrown and non-windthrown forest). We observed leeward windthrows, possibly due to relatively low ridges (<300 m) that

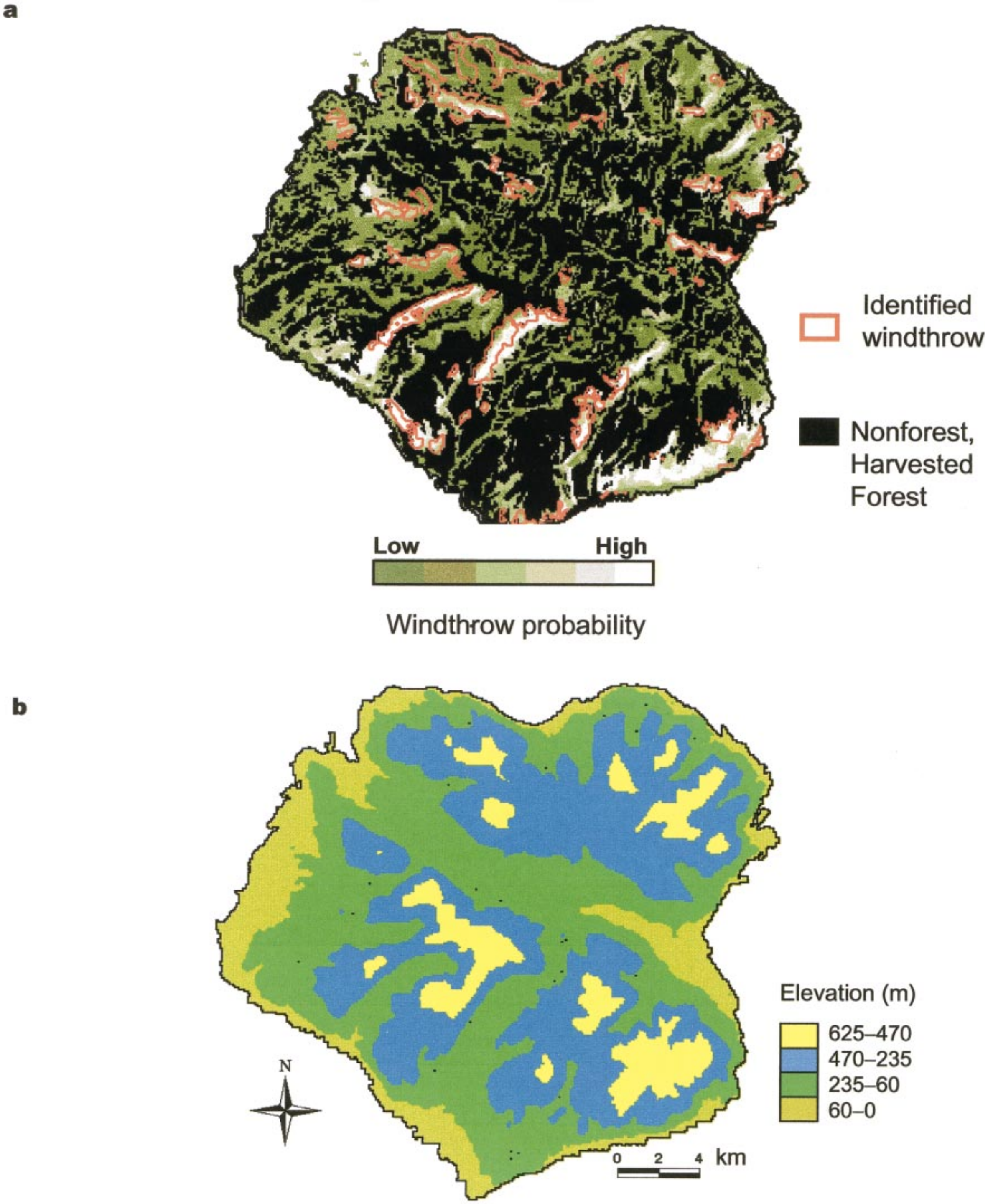

FIG. 6. (a) Comparison of predicted windthrow on Zarembo Island based on extrapolation of the Kuiu model and actual patterns of windthrow found on the island in nonharvested forests. Black areas (not included in the analysis) are harvested forest, or nonforest. (b) Elevation map of Zarembo Island.

were unable to protect lee slope and valley positions (Figs. 1 and 3). Although both landforms were similar, model performance on Zarembo Island was better (6% higher correct classification) than in the Kuiu greywacke lowlands. This may be due to the prevalence of steeper, higher hills on Zarembo and associated forest lands, which are thought to be more productive (E. Kissinger, *personal observation*).

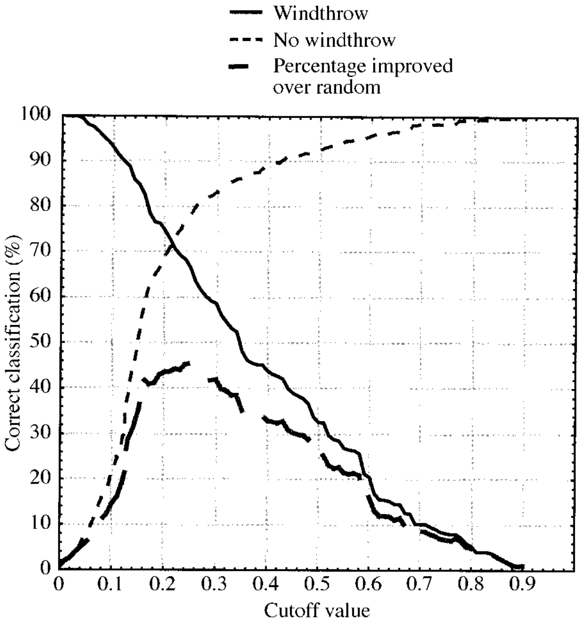

FIG. 7. Model validation results from Zarembo Island. Applying Kuiu model coefficients to Zarembo Island resulted in a 72% correct classification; a 44% improvement over random. This is a 7% improvement over the results for Kuiu Island.

Limitations

The simple assumptions made regarding wind dynamics over complex terrain, prevailing storm wind direction, and storm movement over forested regions may underestimate the proportion of landscape prone to windthrow. Unusual storm wind directions, eddies, channeling of wind through valleys, and other effects of complex wind–topography interactions such as downslope winds, may result in extensive windthrow not predicted by a simple linear windflow model. Such complex interactions between wind and topography can sometimes lead to substantial lee and valley damage from a storm (Everham 1996). Topographic barriers sufficiently high and contiguous, such as those present on the south island of New Zealand, may result in frequent lee-side windthrow from downslope winds (Reid and Turner 1997). The low-lying and fragmented nature of the topography in the Alexander Archipelago does not appear to have such an influence on storm wind behavior. Most of the windthrow we observed occurred on windward hillslopes, in topographically exposed locations.

Over long time periods, windthrow may be most widespread along ridges and valleys that run parallel to prevailing storm wind direction on Kuiu. On the northern portion of the island, windthrow was observed (based on fixed-radius validation plots and photo-interpretation) on both windthrow-protected and windthrow-prone portions of the Rowan Ridge formation (south of Rowan Bay; Fig. 1). This ridge system runs approximately parallel to the prevailing storm wind direction (southwest–northeast). Rebertus et al. (1997) concluded that valleys and ridges that ran parallel to direction of storm winds were most susceptible to a catastrophic storm that struck Tierra Del Fuego in 1972; however, their study area was one-tenth the size of Kuiu Island. Both Kuiu valleys, Rowan Bay to Saginaw Bay and Rowan Bay to Camden Bay, showed evidence of a valley effect, where windthrow may have resulted from bending and channeling of the wind in areas that our linear exposure model identified as low exposure (Fig. 1). No windthrow was observed on a relatively large southeast facing hillslope on Zarembo Island that was predicted to be prone to catastrophic windthrow (Fig. 6a). This may be due to the close proximity of this portion of Zarembo to Etolin Island (Fig. 1), which afforded topographic protection to this hillslope. We did not consider the topography and juxtaposition of Etolin Island when we ran the model for Zarembo. In spite of these model limitations, we found good agreement between predicted storm-prone locations and actual storm-damage patterns on both Kuiu and Zarembo islands (Table 3).

On a regional scale, long-term storm damage patterns could vary considerably from those found on Kuiu and Zarembo islands. For example, nearby Prince of Wales and Kupreanoff islands are both >400 000 ha in size and have a more circular shape. Storms may weaken

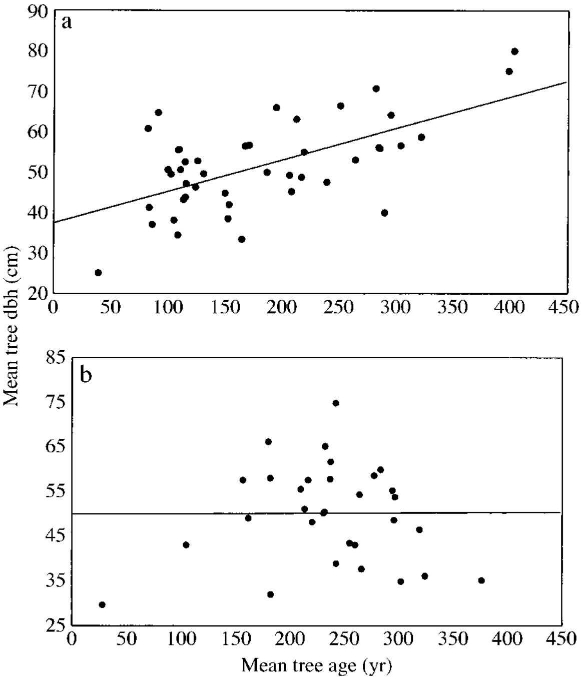

FIG. 8. (a) Regression results between mean tree age and mean tree diameter from windthrow validation plots; $N = 79$, $F_{1,77} = 46.4$, $R^2 = 0.38$, $P < 0.01$. (b) Regression results between mean tree age and mean tree diameter from fixed-radius plots in storm-protected areas; $N = 30$, $F_{1,29} = 0.01$, $R^2 = 0.001$, $P < 0.976$.

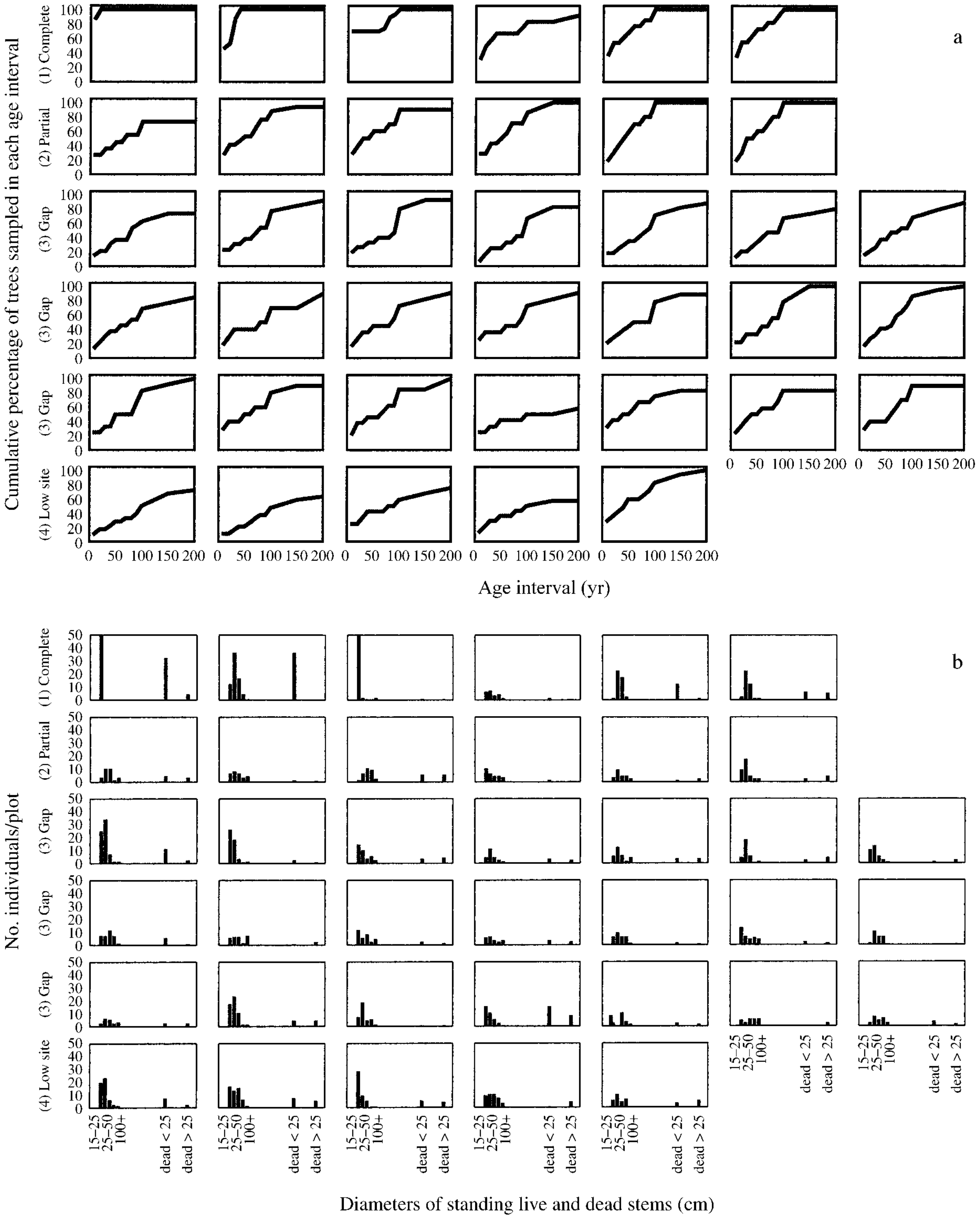

FIG. 9. (a) Age characteristics of individual plots grouped into one of four clusters, each in various stages of recovery from catastrophic windthrow. The cluster was based on age and size characteristics of each plot. (b) Size characteristics of standing live and dead stems from each plot, grouped into one of four clusters in various stages of recovery from catastrophic windthrow. The cluster was based on age and structural characteristics of each plot.

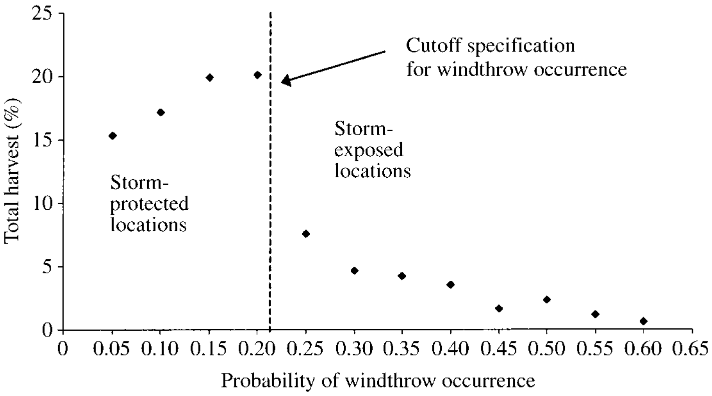

FIG. 10. The amount of logging (measured as percentage of total harvest) in storm-exposed and storm-protected locations.

as they pass over inland portions of these islands (Foster 1988*b*). In addition, wind deflection through narrow inland waterways may result in complex storm damage patterns. Evidence of windthrow has been found south of Kuiu Island on Prince of Wales (Harris 1989), and to the north on Chichagoff Island (T. Garvey, *unpublished data*). These islands are on the outermost portion of the archipelago, and may be more exposed to catastrophic winds as a consequence. However, they comprise a substantial portion of total area of the archipelago (35%).

Further inland, topographic protection may result in less damage from cyclonic storms, which may weaken as they approach the mainland. Some of the forests along the mainland however, are prone to windthrow from locally strong glacial winds associated with ice fields and glaciers of the coastal mountains (Harris 1989). Future work should include an analysis of regional meteorological data and actual observations of wind damage and wind speeds during a catastrophic storm, as well as an exploration of weakening storm patterns further inland.

Windthrow and stand structure

Our results suggest that as forests are more protected from storm damage they become increasingly all aged. This same trend was observed for tree diameters. Although largely exploratory, these results suggest dramatic differences in the competitive interactions and population dynamics of forests in these two landscape settings attributable to disturbance gradients in both space and time.

Forests most susceptible to windthrow may never reach a late-seral stage. The return interval of catastrophic storms appears to be sufficiently short to cycle these forests back to an early-seral, even-aged stand before the longest-lived trees die (~350–950 yr; Lertzman et al. 1996). It is possible that forests in these storm-prone landscapes may experience a stand replacement much sooner than that (50–100 yr) based on frequent occurrence of these stand ages in our plots.

By contrast, the wide range of ages and lack of a single identifiable cohort in storm- protected plots, such as those found in cluster 4 (Fig. 9a), suggest that at least one turnover cycle may have occurred in at least seven of our forest plots since the last stand-replacement event. Wind dynamics influenced by unusual storm wind direction, valley effects, bending, and complex effects of mountainous terrain likely explain the occasional catastrophic windthrow that was found in storm-protected areas (Fig. 9a, b). Evidence of larger scale, more intense events, that led to a distinct pulse of new recruitment in some clusters (2 and 3), suggest that late-seral-stage forests have experienced a range of disturbance intensities and frequencies (Fig. 9a, b); overall, however, wind disturbance was characteristically less intense in more protected forest landscapes.

Stand development patterns resulting from windthrow

A model of stand development (Spies and Franklin 1996) was used to describe development stages resulting from windthrow disturbance: an establishment phase, followed by an early-seral thinning phase, then a midseral mature phase, and finally a self-replacing late-seral all-aged forest (Runkle 1990) that has undergone complete turnover since the last catastrophic event. Characteristic stand development from plots in windthrow-prone landscapes include the initial establishment, early thinning, and midseral mature phases. Franklin et al. (*in press*) suggest that as forests develop after catastrophic disturbance mortality is largely a consequence of self thinning up to the mature phase of forest development, where noncompetitive mortality factors become increasingly important. The observed increase in mean plot diameter with stand age in our windthrow validation plots suggest that stands most susceptible to catastrophic storm damage are still at these early- to midseral stages of stand development (Fig. 8a). In mature forests, gaps created from individual tree mortality (both competitive and noncompetitive) are still predominantly filled by overstory neighbors, but interstitial space between adjacent crowns becomes common, and an understory begins to develop. The high representation of mature (>150 yr) stands in windthrown forests suggests forests may remain in a midseral mature stage for up to 400 yr if site conditions are poor and if no catastrophic windthrow occurs during this period. However most of the older midseral forests we sampled were between 200 and 300 yr old (Fig. 4a), which suggests a windthrow return interval of 300 yr in storm prone forests or, possibly, that they may advance to a late-seral stage after 300 yr. Site, and partial canopy disturbances are likely to be important factors in determining the rate at which forests advance to a late-seral gap-phase condition.

Forest plot data collected in protected areas suggest that complex lower-intensity winds (partial canopy disturbance and small-scale gaps) serve to maintain late-seral age and structural features in these forests. The lack of a relationship between mean tree diameter and age suggests that competition is less equal among individuals in these forests (Fig. 8b). As gaps open up, shade-tolerant individuals compete with overstory neighbors to fill the available light niche. This pattern of stand development has been studied extensively elsewhere and is consistent with a gap-phase or late-seral-stage model of forest development.

Long-term ecosystem consequence of windthrow

In addition to influencing forest stand dynamics across the landscape, windthrow disturbance over long periods of time could also have important consequences for ecosystem function and process (Shulze and Mooney 1994, Ulanova 2000). Ecosystem properties (productivity, diversity, and resiliency) may vary spatially and temporally across the landscape as a result of windthrow. If true, the forested areas we have predicted as most and least prone to windthrow may reflect these differences in ecosystem properties.

Forests more prone to catastrophic windthrow may be more productive (Bormann and Sidle 1990). Root throw may serve to disrupt soil development processes, which could in turn increase mineral weathering processes and increase nutrient availability (Skvortsova and Ulanova 1977, Peterson et al. 1990, Schaetzl et al. 1990, Bormann et al. 1995). Areas prone to stand-replacement events may also experience an increase in decomposition of organic matter through increased temperature (Bormann and Likens 1979*b*). Conversely, if disturbance frequency and intensity is sufficiently low, which may be the case in the most protected landscapes, forest productivity may decline, possibly leading to paludification (Zach 1950).

Differences in light (due to differences in stand structure) and soil nutrient conditions (due to differences in soil disturbance) may also lead to a difference in species diversity and composition in each of these landscape settings. Protected landscapes may have high plant and animal diversity due to heterogeneity in light and stand structure (Alaback 1982). Conversely, understory plant diversity and abundance may be considerably lower in areas most prone to windthrow because of a more light-limited, denser overstory canopy (Alaback 1982). Lower plant diversity, abundance, and simplified forest structure, in turn, may have long-term consequences for management of species dependent on late-seral-stage forests, such as the pine martin, Sitka black-tailed deer, or black bear (Kirchhoff and Schoen 1987, Boyle 1996; G. Degayner, *unpublished data*).

Management implications of long-term windthrow dynamics

To understand the impact of forest management, a good knowledge of disturbance history is essential (Peart et al. 1992). In southeast Alaska, late-seral-stage forests in particular are valued for their high structural and species diversity (Kiester and Eckhardt 1994, Boyle 1996). Our results suggest that there is less naturally abundant late-seral-stage forest than was previously believed, because some forests are very susceptible to windthrow disturbance. Yet a central goal in the Tongass Land Management Plan is to maintain late-seral-stage characteristics over much of the forested landscape (USDA Forest Service 1991). Past management activities have further reduced the amount of forest that is in a late-seral stage. On Kuiu Island most timber harvest has occurred in areas where forests are protected from storm damage (Fig. 10). Timber harvest in these areas has an additive effect, i.e., old-growth forests are converted to second-growth stands that will not develop beyond the stem-exclusion stage because of the planned 100-yr cutting rotation. Such early-seral stages are historically infrequent on such landscapes. The removal of standing biomass (by clear-cutting) is a substantial departure from small-scale turnover in the forest.

The amount of forests in later stages of development will be noticeably reduced if current harvest trends continue. An alternative approach may be to tailor management activities so that they are more compatible with prevailing natural disturbance processes (Hansen et al. 1991, Swanson and Franklin 1992, Nowacki and Kramer 1998). For example, greater emphasis could be placed on single-tree or small-group selection harvesting in areas where late-seral-stage forests occur, to maintain natural processes such as root throw and coarse woody debris inputs in the understory. One tradeoff, however, is that more frequent entries over large areas would be needed to maintain the current harvest volume. In areas most prone to long-term catastrophic storm damage, two-aged management may be more appropriate to maintain disturbance effects (via root throw of standing residual trees) and similar historical stand attributes (stem-exclusion, understory-reinitiation forests). Long-term windthrow patterns should be considered when devising management alternatives so that management practices can be tailored to better maintain ecosystem process, function, and habitat conditions that will assure viability of species common to those areas.

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LITERATURE CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce–western hemlock forests of southeast Alaska. Ecology **63**:1932–1948.

Alaback, P. B. 1996. Biodiversity patterns in relation to climate: the coastal temperate rainforests of North America. Pages 105–133 *in* R. G. Lawford, P. B. Alaback, and E. Fuentes, editors. High-latitude rainforests and associated ecosystems of the West Coast of the Americas. Springer-Verlag, New York, New York, USA.

Alaback, P. B., and J. C. Tappenier. 1991. Response of western hemlock (*Tsuga heterophylla*) and early huckleberry (*Vaccinium ovalifolium*) seedlings to forest windthrow. Canadian Journal of Forest Research **21**:534–539.

Anderson, K. F. 1954. Gales and gale damage to forests, with special reference to the effects of the storm of 31st of January 1953, in the northeast of Scotland. Forestry **27**:97–121.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management **63**:247–300.

Augustin, H. H., M. A. Mugglestone, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology **33**:339–347.

Bergeron, Y., and J. Brisson. 1990. Fire regime in red pine stands at the northern limit of the species' range. Ecology **71**:1352–1364.

Boose, E., D. R. Forest, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs **64**:369–400.

Bormann, B. T., and R. S. Sidle. 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. Journal of Ecology **78**: 561–578.

Bormann, B. T., H. Spaltenstein, M. H. McClellan, F. C. Ugolini, K. Cromack, and S. M. Nay. 1995. Rapid soil development after windthrow disturbance in pristine forests. Journal of Ecology **83**:747–757.

Bormann, F. H., and G. E. Likens. 1979*a.* Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist **67**:660–669.

Bormann, F. H., and G. E. Likens. 1979*b.* Pattern and process in a forested landscape. Springer-Verlag, New York, New York, USA.

Boyle, T. J. B. 1996. Biodiversity of Canadian forests, with particular reference to the west coast forests. Pages 353–378 *in* R. G. Lawford, P. B. Alaback, and E. Fuentes, editors. High-latitude rainforests and associated ecosystems of the West Coast of the Americas. Springer-Verlag, New York, New York, USA.

Bray, J. R. 1956. Gap phase replacement in a maple-basewood forest. Ecology **37**:598–600.

Bullock, T. A., J. R. Gyakum. 1993. A diagnostic study of cyclogenesis in the western North Pacific Ocean. Monthly Weather Review **121**(1):65–75.

Carey, A. B. 1985. A summary of the scientific basis for spotted owl management. Pages 110–114 *in* R. J. Guitierez and A. B. Carey, editors. Ecology and management of the spotted owl in the Pacific Northwest. USDA Forest Service. General Technical Report **GTR PNW-185.**

Carr, J. R. 1995. Numerical analysis for the geological sciences. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Conservation International. 1992. Coastal temperate rain forests: ecological characteristics, status and distribution worldwide. Conservation International, Washington, D.C., USA.

Cressie, N. 1991. Statistics for spatial data. Wiley & Sons, New York, New York, USA.

Dale, V. H., M. H. Miles, and J. Franklin. 1986. Modeling the long-term effects of disturbance on forest succession, Olympic Peninsula, Washington. Canadian Journal of Forest Research **16**:56–67.

Deal, R. L., C. D. Oliver, and B. T. Bormann. 1991. Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. Canadian Journal of Forest Research **21**:643–654.

Everham, E. M. 1996. Hurricane disturbance and recovery: an empirical and simulation study of vegetation dynamics in the Luquillo Experimental Forest, Puerto Rico. Dissertation. State University of New York, College of Environmental Science and Forestry, Syracuse, New York, USA.

Fosberg, M. A., W. E. Marlatt, and L. Krupnak, 1976. Estimating airflow patterns over complex terrain. USDA Forest Service, Research Paper **RM-162.**

Foster, D. R. 1988*a.* Species and stand response to catastrophic wind in central New England, USA. Journal of Ecology **76**:135–151.

Foster, D. R. 1988*b.* Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah Forest, south-western New Hamphshire, USA. Journal of Ecology **76**:105–134.

Fox, J. F. 1989. Bias in estimating forest disturbance rates and tree lifetimes. Ecology **70**:1267–1272.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service, General Technical Report **PNW-8.**

Franklin, J., T. Spies, R. Van Pelt, A. Carey, D. Thornburgh, D. R. Berg, D. Lindenmayer, M. Harmon, W. Keeton, and D. C. Shaw. *In press.* Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management.

Frelich, L. E., and L. J. Graumlich. 1990. Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. Canadian Journal of Forest Research **24**: 1939–1947.

Gallagher, G. J. 1974. Windthrown in state forests in the Republic of Ireland. Irish Forestry **31**:154–167.

Gastaldo, R. A. 1990. Tree orientation in response to cyclonic winds. Palaios **5**:472–478.

Hadley, K. S. 1994. The role of disturbance, topography, and forest structure in the development of a montane forest landscape. Bulletin of the Torrey Botanical Club **121**:47–61.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience **41**:382–392.

Harmon, H. E., S. P. Bratton, and P. S. White. 1983. Disturbance and vegetation response in relation to environmental gradients in the Great Smoky Mountains. Vegetatio **55**: 129–139.

Harris, A. S. 1989. Wind in the forests of southeast Alaska and guides for reducing damage. USDA Forest Service, General Technical Report **PNW-GTR-244.**

Heagerty, P. J., and S. R. Lele. 1998. A composite likelihood approach to binary data in space. Journal of the Royal Statistical Society B **93**:1099–1111.

Heinselman, M. L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Journal of Quaternary Research New York **3**:329–382.

Hosmer, D. W., Jr., and S. Lemeshow. 1989. Applied logistic regression. Wiley & Sons, New York, New York, USA.

Kiester, A. R., and C. Eckhardt. 1994. Review of wildlife management and conservation biology on the Tongass National Forest: a synthesis with recommendations. USDA Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.

Kirchhoff, M. D., and J. W. Schoen. 1987. Forest cover and snow: implications for deer in southeast Alaska. Journal of Wildlife Management **51**(1):28–33.

Klein, W. H. 1957. Principal tracks and mean frequencies of cyclones and anticyclones in the northern hemisphere. U.S. Department of Commerce, Weather Bureau. Research Paper **40.**

Kramer, M. G. 1997. Abiotic controls on windthrow and forest dynamics in a coastal temperate rainforest, Kuiu Island, southeast Alaska. Thesis. Montana State University, Bozeman, Montana, USA.

Lele, S. 1991. Jackknifing linear estimating equations: asymptotic theory and application in stochastic processes. Journal of the Royal Statistical Society B **53**:253–267.

Lertzman, K. P., and J. Fall. 1998. From forest stand to landscape: the impacts of disturbance. Pages 339–367 *in* D. Peterson and V. T. Parker, editors. Scale issues in ecology. Columbia University Press, New York, New York, USA.

Lertzman, K., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology **77**:1254–1270.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman & Hall, New York, New York, USA.

Mayer, H. 1989. Windthrow. Philosophical Transactions of the Royal Society of London B. **324**:267–281.

McBean, G. A. 1996. Factors controlling the climate of the West Coast of North America. Pages 27–41 *in* R. G. Lawford, P. B. Alaback, and E. Fuentes, editors. High-latitude rainforests and associated ecosystems of the West Coast of the Americas. Springer-Verlag, New York, New York, USA.

Michalski, R. S., R. E. Stepp, and E. Diday. 1981. A recent advance in data analysis: clustering objects into classes characterized by conjunctive concepts. Pages 33–56 *in* L. N. Kanal and A. Rosenfeld, editors. Progress in pattern recognition. Volume 1. North-Holland, New York, New York, USA.

Morrison, P. H., and F. J. Swanson. 1990. Fire history and pattern in a Cascade Range landscape. USDA Forest Service, General Technical Report **PNW-GTR-254-87.**

Naval Pacific Meteorology and Oceanography Center. 2000. Eastern Pacific regional forecasters handbook. Commander, Naval Meteorology and Oceanography Command. San Diego, California, USA.

Neter, J., M. H. Kutner, C. J. Nachtsheim, and W. Wasserman. 1996. Applied linear statistical models. Irwin, Chicago, Illinois, USA.

Noste, N. V. 1969. Analysis and summary of forest fires in coastal Alaska. USDA Forest Service, Institute of Northern Forestry, Juneau, Alaska, USA.

Nowacki, G. J., and M. G. Kramer. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. USDA Forest Service, General Technical Report **PNW-GTR-421.**

Pawuk W. H., and E. J. Kissinger. 1989. Preliminary forest plant associations of the Stikine Area, Tongass National Forest. USDA Forest Service, Alaska Region. **R10-TP-72.**

Peart, D. R., C. V. Cogbill, and P. A. Palmiotto. 1992. Effects of logging history and hurricane damage on canopy structure in a northern hardwood forest. Bulletin of the Torrey Botanical Club **119**:29–38.

Peet, R. K. 1988. Forests of the Rocky Mountains. Pages 46–101 *in* M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.

Pereira, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mount Graham red squirrel. Photogrammetric Engineering and Remote Sensing **57**:1475–1486.

Peterson, C. J. 2000. Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. Forest Ecology and Management **135**:237–252.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Pojar, J., and A. MacKinnon. 1994. Plants of coastal British Columbia. Lone Pine Publishing, Edmonton, Alberta, Canada.

Rebertus, A. J., T. Kitzberger, T. T. Veblen, and L. M. Roovers. 1997. Blowdown history and landscape patterns in the Andes of Tierra Del Fuego, Argentina. Ecology **78**:678–692.

Reice, S. 1994. Nonequlibrium determinants of biological community structure. American Scientist **82**:424–435.

Reid, S., and R. Turner. 1997. Wind storms. Tephra **16**:26–30.

Romme, W. H., and D. H. Knight. 1982. Landscape diversity: the concept applied to Yellowstone Park. BioScience **32**: 664–670.

Runkle, J. R. 1990. Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. Canadian Journal of Forest Research **20**:632–641.

SAS Institute. 1988. SAS guide for personal computers, Version 6.03. SAS Institute Inc., Cary, North Carolina, USA.

Schaetzl, R. J., L. K. Hendrie, and S. W. Kirsch. 1990. Tree uprooting: review of types and patters of soil disturbance. Physical Geography **11**:277–291.

Sherman, M. 1996. Variance estimation for statistics computed from spatial lattice data. Journal of the Royal Statistical Society B **58**:509–523.

Shulze, E. D., and H. A. Mooney. 1994. Biodiversity and ecosystem function. Springer-Verlag, New York, New York, USA.

Shumacher, U. D., and J. G. Wilson. 1986. On the atmospheric and oceanic environment of the Gulf of Alaska. Pages 135–178 *in* Proceedings, a workshop on comparative biology, assessment, and management of Gadoids from the North Pacific and Atlantic Oceans, June 1985. National Oceanic and Atmospheric Administration Pacific Marine Environmental Laboratory, Seattle, Washington, USA.

Sinton, D. S. 1996. Spatial and temporal patterns of windthrow in the Bull Run Watershed, Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.

Sinton, D. S., J. Jones, J. Ohmann, F. J. Swanson. 2000. Windthrow disturbance, forest composition, and structure in the bull Run Basin, Oregon. Ecology **81**:2539–2556.

Skvortsova, E. B., and N. G. Ulanova. 1977. Nekotorye aspekty vlyanya vyvalov na lesnoy biogeotsenoz (Effect of uprooting of trees on forest biogeoceonoses). Vestnik Moskovskogo Universiteta Serya 17 Pochvovedenie. **4**:3–8 (*in Russian*).

Spies, T. A., and J. F. Franklin. 1996. The diversity and maintenance of old-growth forests. Pages 296–314 *in* R. C. Szaro and D. W. Johnston, editors. Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York, New York, USA.

Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research **20**:649–658.

Stone, M. 1977. An asymptotic equivalence of choice of model by cross-validation and Akaike's criterion. Journal of the Royal Statistical Society B, Series B **39**:44–47.

Swanson, F. J., and J. F. Franklin. 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecological Applications **2**:262–274.

Swanson, F. J., T. K. Krantz, N. Caine, and R. G. Woodsmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience **38**:92–98.

Thomson, A. P. 1976. 500-year evidence of gales. New Zealand Forest Industries Review **7**:11–16.

Ugolini, F. C., and D. Mann. 1979. Biopedological origin of peatlands in southeast Alaska. Nature **281**:366–368.

Ulanova, N. G. 2000. The effects of windthrow at different spatial scales: a review. Forest Ecology and Management **135**:155–167.

USDA Forest Service. 1991. Tongass land management plan revision. supplement to the draft environmental impact statement. USDA Forest Service, Alaska Region **R10 MB-49.**

USDA Forest Service. 1992. Classification and correlation of the soils of the Stikine Area, Alaska. (SSA-645). Tongass National Forest, Petersburg, Alaska, USA.

Vasenev, I. I., and V. O. Targul'yan. 1995. A model for the development of sod–podzolic soils by windthrow. Eurasian Soil Science **27**(10):1–16.

Veblen, T. T., and P. B. Alaback. 1996. A comparative review of forest dynamics and disturbance in the temperate rainforests of north and south America. Pages 173–213 *in* R. G. Lawford, P. B. Alaback, and E. Fuentes, editors. High latitude rainforests and associated ecosystems of the West Coast of the Americas. Springer-Verlag, New York, New York, USA.

Veblen, T. T., K. S. Hadley, E. J. Mel, T. Kizberger, M. Reid, and R. Villalba. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Journal of Ecology **82**:125–135.

Veblen, T. T., T. Kitzberger, and L. Antonio. 1992. Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. Journal of Vegetation Science **3**:507–520.

Vitousek, P. M. 1985. Community turnover and ecosystem nutrient dynamics. Pages 325–332 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Wilson, J. G., and J. E. Overland. 1986. Meteorology of the northern Gulf of Alaska. Pages 31–54 *in* D. W. Hood and S. T. Zimmerman, editors. The Gulf of Alaska: physical environment and biological resources. Department of Conservation/National Oceanic and Atmospheric Administration, Anchorage, Alaska, USA.

Zach, L. W. 1950. A northern climax, forest or muskeg? Ecology **31**:304–306.