BLOWDOWN HISTORY AND LANDSCAPE PATTERNS IN THE ANDES OF TIERRA DEL FUEGO, ARGENTINA

ALAN J. REBERTUS, THOMAS KITZBERGER, THOMAS T. VEBLÉN, AND LYNN M. ROOVERS

1School of Natural Resources, University of Missouri, Columbia, Missouri 65211 USA
2Geography Department, University of Colorado, Boulder, Colorado 80309 USA
3North Central Forest Experiment Station, Columbia, Missouri 65211 USA

Abstract. The effects of periodic gales on Nothofagus (southern beech) stand development and landscape dynamics were studied in a 10.4-km² study area in the Sierra de las Pinturas, part of the Andes in Argentine Tierra del Fuego. We reconstructed blowdown history (patch sizes, dates of origin, return intervals) since the late 1700s to assess how periodic large-scale wind disturbance influenced landscape pattern in a relatively simple system. Most previous studies have focused on single storms in more diverse forests and in landscapes influenced by several disturbance types and human activities. Boundaries of post-blowdown stands were digitized from aerial photographs and analyzed within a geographic information system. Ages of blowdowns and return intervals were determined from scars, growth releases, and maximum tree ages. Discrete blowdown patches (0.1 to >100 ha) covered two-thirds of the study area and ranged from 19 to ≈200 yr of age, with 20–30 yr between major events. The meteorology of these storms was unknown, but we suspect they were caused by intense low-pressure systems originating in Antarctica. The mean return interval for 34 sites was 145 yr, with a range of 103–218 yr. Based on treefall size distributions, most stands blown over in the past 100 yr were even-aged, with mean tree dbh (diameter at breast height) between 20 and 32 cm. Aerial photographs taken in 1970 were used for before-and-after comparisons of a 1972 blowdown. Seventy-one percent of the area blown over in 1972 was even-aged, and 35% of the boundaries from this storm exactly coincided with previous stand boundaries. Damage patterns from storms in 1924 and 1972 suggested that forests located on valleys parallel to the wind, windward side slopes, and possibly upper leeward slopes were most vulnerable to blowdown, but few landscape positions escaped being hit by repeated storms. Return intervals were not significantly related to slope, elevation, or aspect, but surprisingly, shorter return intervals were associated with deeper soils. The landscape pattern of blowdown and recovery shifted over time because of variation among individual storms and because a small proportion of old-growth stands were converted to blowdowns and vice versa. Browsing by guanacos (Lama guanaco), a large native camelid, has severely inhibited tree regeneration during the past 75 yr in small blowdowns and the perimeters of larger ones, converting some stands to open meadows and incipient alpine communities. In the relatively simple Nothofagus forests of Tierra del Fuego, periodic gales are the main determinants of forest structure and pattern across a range of scales from small patches to entire landscapes.

Key words: blowdowns; browsing; disturbance; guanaco; interactions, disturbance-type; landscape pattern; Nothofagus pumilio; southern beech; Tierra del Fuego; treefalls; wind.

INTRODUCTION

Complete characterization of a disturbance regime requires means and variances for return intervals, sizes, shapes, and intensities, and information on how these factors vary across the landscape. Yet, such statistics have not even been determined for the simplest landscapes (Peet 1992). Among the best described disturbance regimes include studies of wildfire by Heinselman (1973) in Minnesota and Romme (1982, and others) in Yellowstone National Park, and fine-scale treefall gaps in eastern deciduous forests by Runkle (1985, and references therein), but even these studies focus on only a single type or scale of disturbance. To understand the role of disturbance in creating landscape patterns, the full range of disturbances affecting an area must be considered (e.g., Harmon et al. 1983, Veblen et al. 1992).

Wind creates a spatial-temporal mosaic of patches or gaps in different stages of recovery from disturbance. Forest turnover is dominated by fine-scale treefall gaps in much of the eastern deciduous forests of North America (Runkle 1990) and in neotropical rain forests (Brokaw 1985), where gaps are formed at ≈1% of the canopy per year. Simulations by Turner et al. (1993) suggest that such disturbance regimes allow
both persistence and constancy of seral types or patches at scales of "stand" or larger; i.e., a "steady-state mosaic." Coarse-scale blowdowns (>1000 m²) are much less frequent, with return-time estimates for many temperate and tropical forests generally >1000 yr (Lorimer 1977, Canham and Loucks 1984, Whitney 1986, Glitzenstein and Harcombe 1988, Schaetzl et al. 1989, Nelson et al. 1994). Return intervals (i.e., inverse of frequency; White and Pickett 1985) for destructive storms are much shorter in hurricane/typhoon or gale-prone areas of the Caribbean and eastern United States (Foster 1988a, Lugo and Waide 1993, Boose et al. 1994), Southeast Asia (Whitmore 1984), Australia (Webb 1958), New Zealand (Shaw 1983, Jane 1986), and the North American Pacific Northwest (Harris 1989). However, damage patterns from these storms are very complex, with partial and complete destruction occurring at various scales.

Landscape patterns of coarse-scale blowdowns are best known from detailed analyses of the 1938 hurricane in New England and several hurricanes in the Caribbean (Lugo et al. 1983, Foster 1988a, Foster and Boose 1992, Boose et al. 1994). Blowdowns tend to increase landscape diversity by creating a mosaic of patches of different ages and successional status (Webb 1958, Foster and Boose 1992). Variation in blowdown intensity also contributes to landscape heterogeneity by enhancing beta diversity (e.g., severe, intermediate, and light levels of disturbance fostering different communities; Savage et al. 1992). Blowdowns may also strike some aspects and slope positions more than others, modifying vegetation patterns along environmental gradients (Foster and Boose 1992). The landscape patterns created by hurricanes are very complex, reflecting interactions of biotic, edaphic, and historical factors with meteorological and stochastic processes (Foster 1988b, Foster and Boose 1992).

Most studies of blowdowns are limited almost exclusively to single events superimposed on relatively complex landscapes with many tree species, several disturbance types, and anthropogenic activities. In addition, these studies usually focus on recent storms and initial stages of stand recovery. Not surprisingly, the spatial and temporal dimensions of blowdown dynamics under these circumstances are often difficult to assess. In this study we describe a disturbance regime in 10.4 km² of Nothofagus pumilio (Poeppig and Endl.) Krasser (lenga, southern beech) forest in the Andes of Tierra del Fuego. The system is ideal for addressing how disturbances generate landscape pattern because there is a single dominant disturbance, catastrophic windthrow, which reoccurs frequently and creates very discrete patches, and there is a single modifying disturbance, herbivory by guanacos (Lama guanaco), a large native herbivore. Furthermore, this study area has not been significantly affected by human activities, and the presence of a single tree species simplifies the task of examining tree responses to blowdown. Evidence for blowdown persists for ≈200 yr, providing opportunities to examine the long-term effects of disturbance on landscape processes. The objectives of this study were to determine spatial and temporal characteristics of the wind-dominated disturbance regime in the southern Andes, and to investigate long-term stand and landscape development controlled by wind disturbance and interactions with guanacos.

**Study Area**

The combination of westerly atmospheric circulation and the southwest–northeast orientation of the Andes results in a strong precipitation gradient across Tierra del Fuego. The associated vegetation gradient comprises evergreen Nothofagus betuloides rain forest in the southwest, deciduous N. pumilio "summer green" forest in the interior, and deciduous N. antarctica and steppe in the northeast (Fig. 1). With the exception of the Andean rain shadow, the climate of Tierra del Fuego is similar to southern Alaska and western Scandinavia with average monthly temperatures ranging from −1°C to 10°C, annual precipitation of 450 mm, and prevailing winds and major windstorms from the southwest (Lyons 1983, Tuhkanen 1992).
The 10.4-km² study area is located in *N. pumilio* forest in the Sierra de las Pinturas, a range of the southernmost Andes running east–west along Lago Fagnano (54°30' S, 67°40' W; Fig. 1). Cerro Yakush (elevation 950 m; relief 600–700 m) dominates the northeastern part of the study area, with several smaller foothills (relief 100–200 m) occupying the southwest half. The shallow (<50 cm deep), acidic brown soils are slightly podzolized, and derived from sandstone and conglomerate parent material (Moore 1983).

Eighty-nine percent of the study area is forested and 11% is alpine tundra. There are only slight changes in forest structure with elevation, and the transition to alpine tundra is very abrupt. Timberline ranges from 400 to 700 m. Northeast of Cerro Yakush, the Sierra descends into the sparsely populated steppe ecotone. Cerro Yakush is at the edge of a vast, uninhabited, roadless area that extends to the Pacific Ocean. Recent logging prevented us from sampling farther down the northeast side of the mountain, but the study area proper was pristine and had little evidence of past human activities.

Guano browsing plays a major role in forest regeneration near the steppe ecotone. These animals are large (80–100 kg), polygamous camels native to forests, pampas, and steppe from Peru to Tierra del Fuego. Roughly one-tenth of the total guano population resides on Tierra del Fuego, where there are perhaps 10–20 thousand animals (Raedecke 1978). Based on ground and aerial sightings, we estimated that there were 5–10 guanacos/km² in our study area during summer. In Tierra del Fuego, their diet consists mainly of grasses and forbs, but they also browse leaves and twigs of *Nothofagus antarctica*, *N. pumilio*, and several shrubs (Raedecke 1978).

**METHODS**

**Mapping of blowdowns**

An orthophoto image and digital elevation model (DEM) were constructed from 1970 1:40 000 aerial photographs using ERDAS (1992) DIGITAL ORTHO module. The orthophoto image removes distortions caused by terrain and the oblique camera angle. No adequate topographic maps existed for the study area, so a DEM was created from the 1970 aerial photographs. In this procedure, image matching of stereo pairs automatically generates two corresponding grids of >4000 points, representing identical ground locations. Ground coordinates, including elevation, are computed from matched image pairs and known camera orientation. The coordinates were scaled from external control points taken from a 1950 1:200 000 topographic map that overlapped part of the study area.

Blowdowns were digitized directly off the orthophoto image using IDRISI (Eastman 1992), a geographic information system (GIS). Blowdowns <200 yr old are comprised of even-aged stands that appear as homogeneous, fine-textured patches on aerial photographs. Old growth (>225–250 yr) has a much coarser texture. Several hundred oblique 35-mm color infrared photographs were taken from ~2000 m altitude in 1990–1991 to aid in mapping blowdowns that occurred in 1972. The 1972 blowdowns were transferred to the 1970 base image by carefully locating corresponding landmarks on each photograph. The 1972 event also provided an opportunity for detailed before-and-after comparisons to assess (1) how much of the area blown down in 1972 was previously even-aged vs. old growth and (2) what percent of the 1972 blowdown boundaries matched older blowdown boundaries visible in the 1970 photographs.

Areas where browsing by guanacos had inhibited post-blowdown *Nothofagus pumilio* regeneration were identified on the 1970 and 1990–1991 aerial photographs, and with field checks. We mapped patches within blowdowns where guanacos had browsed nearly all stems <1.5 m in height. Guanacos typically browsed seedlings in discrete patches wherever treefalls did not block their access. Trees that remained unbrowsed for >20 yr grew out of reach of guanacos, but in areas where animals concentrated, seedlings became severely deformed and hedge-like after decades of persistent browsing. Patches of complete regeneration failure were still widespread in blowdowns that occurred in 1924.

**Field procedures**

**Blowdown dating.** — To quantify the temporal and spatial patterns of wind disturbance, stands of different origin were identified on the 1970 photographs and stand history and regeneration patterns were determined by field sampling and dendrochronology. Treefalls from blowdowns were visible for 150 yr after the event, and were confirmed by the even-aged stands (single cohort) and lack of charcoal. Several even-aged stands between 170 and 200 yr old having pit-and-mound topography were also assumed to be blowdowns. Stands that reach 225–250 yr gradually become old growth (sensu Oliver and Larson 1990), where a second cohort develops in small treefall gaps. In this paper, “old growth” is synonymous with “no evidence of previous blowdown.” We attempted to sample all blowdown patches within the study area, but some data were only available for a smaller subset of blowdowns; an overview is presented in Table 1.

Blowdowns were dated from scars, growth releases on remnant trees, and maximum age of post-blowdown regeneration. At 21 blowdowns, we cut wedges from 1–4 live trees (60 total) with bole scars formed from tree collision injury. These scars were usually several meters long and most common on live windthrown trees, apparently from windward trees “sliding down” their leeward neighbors in domino-like fashion. Samples were not cross dated, but they provided approximate dates used in conjunction with other methods. We
cored remnant trees within and along blowdown edges and examined the cores for abrupt increases in growth (release) associated with disturbance (Lorimer 1985). Release was defined as a 2.5-fold increase in growth when adjacent groups of five rings were compared (Veblen et al. 1992). Because many trees have delayed growth response to disturbance, we assumed that the oldest release date among a group of similar dates corresponded closely with the event (Lorimer 1985). Initially, 10–30 cores were taken per blowdown, but after we became familiar with the ages and appearances of blowdowns, fewer cores were needed to confirm a suspected date.

Nothofagus pumilio can live 300–375 yr (Rebertus and Veblen 1993), but trees >250 yr old are often unsound and it was not practical to core them for release dates. Therefore, dates of older blowdowns (150–200 yr) were assigned in 25-yr age classes based on maximum stem age of five to ten trees cored at 0.3–0.4 m above the soil surface (Heinselman 1973, Veblen et al. 1992). N. pumilio typically regenerates in even-aged stands after major canopy disturbance (Veblen et al. 1996) and maximum tree ages usually correspond closely with the time of disturbance (Veblen et al. 1992, Rebertus and Veblen 1993).

Approximate point return intervals were determined for 34 stands which represented a wide range of site characteristics and blowdown events. Return intervals were based on dates of two successive events from the same locale (≈1–3 ha). A common situation was a small blowdown patch that occurred within a much larger, older patch, but in most cases the return intervals only correspond to points and not whole stands. Return intervals were sampled opportunistically, wherever sufficient dendrochronological material was available to date overlapping events.

Stand response.—A rapid assessment of treefall characteristics and stand response was made at 61 blowdowns along a randomly oriented, 60-m transect, starting from an arbitrary point near the center. For larger blowdowns, one or two extra transects were used. In some cases where small patches were nearly connected, only one blowdown within the group was sampled (Table 1). For blowdowns <100 yr old, the first 30 treefalls intersecting the tape were measured for dbh, direction, mode of treefall, and whether the treefall was dead or alive.

Post-blowdown tree regeneration (≥4 cm dbh) was documented along the transects by the point-centered-quarter method, with 10 m between points. Two supplemental trees were sampled at the end of the transect, for 30 trees total. Many recent blowdowns were heavily browsed and lacked sufficient regeneration for sampling (Table 1). At three blowdowns ranging from 67 to 130 yr old, all trees along the transects were cored at 0.3–0.4 m above ground. These blowdowns were subjectively selected to demonstrate stand response.

Site variables collected at each site included slope, aspect, elevation, and depth to bedrock. Depth to bedrock was determined by pounding a 0.5 cm diameter steel rod in as far as possible. Ten measurements were taken from relatively undisturbed areas along each transect, avoiding pits and mounds whenever possible. Cobble within the profile may have sometimes prevented the rod from reaching bedrock, but the site average (D) is probably a good index of relative soil depth.

Data analysis

Circular means, angular deviations, and mean vectors were calculated for treefall direction in each blowdown patch (Batschelet 1981). The Rayleigh test was used to test whether treefall directions within patches differed from a random distribution. Differences in tree survival among blowdown age classes were analyzed
using the Kruskal-Wallis test with Dunn’s method of pairwise comparisons.

The areas and landscape distribution of blowdowns, old growth (no evidence of blowdown >225 yr), and browsed areas were analyzed using IDRISI. Blowdowns up to 100 yr old were assumed to have intact boundaries (i.e., not partially covered by more recent blowdowns), and were used in analysis of patch size distribution. Cole’s coefficient (Cole 1949) was used to test for association between blowdowns and aspect, slope, and elevation classes. This technique compares the presence or absence of two classes on a cell-by-cell basis (Foster and Boone 1992). In addition, we digitized the study area into several landform categories: valleys, ridges, and side slopes. Valley boundaries extended from a stream channel up side slopes 20 m and 30 m in vertical relief from first- and second-order streams, respectively. Ridges extended downslope 15 m in vertical relief from the crest. Valleys were subdivided into those oriented north–south and east–west; side slopes were subdivided into north, east, south, and west exposure.

Stepwise multiple regression (SAS 1988) was used to examine the relationship between return intervals and site variables: slope, elevation, and mean soil depth. Aspect, a circular variable, was analyzed separately using periodic regression (Batschelet 1981). Values of the site variables were based on the few hectares where tree-coring established the return interval.

Assuming a random sample of disturbance return intervals, the shape of their frequency distribution may suggest how often a blowdown is likely to occur. Although many functions could be used to describe such a distribution, we chose the Weibull because of its flexibility and traditional use in fire history studies. The probability density form of the Weibull function is \( Y = \frac{(c e^{-b t})}{b} \times \exp[-(t/b)] \), where \( Y \) is the frequency or probability of having disturbances with intervals of age \( t \) (in years), \( b \) is a scale parameter (in years) that has been called disturbance “recurrence,” and \( c \) is a dimensionless shape parameter (Johnson and Van Wagner 1985). When \( c > 1 \), the instantaneous rate of disturbance increases with age. This Weibull model assumes that the probability of disturbance is a power function of the time since the last disturbance, and that the disturbance regime is spatially and temporally constant, or reasonably so, at scales relevant to the study.

**RESULTS**

**Blowdown history and patch structure**

One-hundred and fourteen patches >0.10 ha, 65% (605 ha) of the forested part of the study area, were identified as post-blowdown in origin (Figs. 2 and 3A). The distribution of patch sizes for blowdowns <100 yr old was highly skewed right and approximated a power curve: 62% of 90 total patches were <1 ha and 90% were <6 ha (Fig. 4). Nevertheless, patches >6 ha comprised >70% of the total blowdown area. The largest single patch was <150 ha, of which 101 ha was within the study area.

Seventy-three percent of the 61 blowdowns <100 yr old had mean treefall directions within 60° of due north (Fig. 5). Treefalls were strongly directional within stands: all 61 stands had treefall directions significantly different from random (Rayleigh test, all stands \( P < 0.05 \)), and more than half had mean vectors >0.8 (a vector of 1.0 indicates all trees are oriented in the same direction). In contrast, treefall directions in an old-growth stand on the north edge of the study area were not significantly different from random (mean vector = 0.21, \( n = 40 \) trees, \( P > 0.05 \)).

Although most damaging winds from these storms were southerly, local topography clearly modified this general pattern. For example, winds from a 1972 event were deflected northwesterly, based on blowdowns along the windward flank of Cerro Yakush (Fig. 6A). Similarly, several stands were hit by winds from the east-northeast and northwest, apparently due to wind funnelling up curved valleys (Fig. 6A). Winds from a 1924 storm came from both the south and east-northeast (Fig. 6B). Hills in the southwest part of the study area deflected winds westerly, but differences in wind direction on opposite sides of Cerro Yakush were difficult to explain within the context of local topography. We also could not rule out a second event.

We had variable success in dating blowdowns to the exact year. Release and scar dates were often inconclusive, so we present the composite blowdown chronology in 25-yr classes (Fig. 3A). Over the entire area, major blowdowns have occurred fairly regularly, roughly every 20–30 yr, over the past two centuries (Fig. 3A). Nearly half of the study area consisted of stands <150 yr old, and two major storms, 1972 and 1924, affected 18% and 13% of the study area, respectively. Given that *Nothofagus pumilio* may reach >300 yr of age in old-growth stands (Rebertus and Veblen 1993), the preponderance of stands <150 yr old suggests a high disturbance rate.

There were some unavoidable problems in reconstructing this blowdown history. First, aerial photographs and “groundtruthing” probably failed to reveal some boundaries between older blowdowns of approximately the same age (see Heiniselman 1973). For example, a large 150-yr-old blowdown could easily “hide” many smaller imbedded or adjoining patches that were 10–20 yr younger or older. Second, both boundaries and sizes of older blowdowns were indeterminate, because these blowdowns were often partially or completely covered by younger events. There is good evidence from treefall sizes and point return intervals, however, that new blowdowns only occurred in stands >100 yr old, so the sizes and shapes of blowdowns occurring after 1890 are completely intact (Fig. 3A).
At 34 stands we were able to estimate the interval between two successive blowdowns at the same point. The mean return interval was 145 yr and ranged from 103 to 218 yr (Fig. 3B). The distribution of return intervals did not differ significantly from a normal distribution (Kolmogorov-Smirnov test, $P = 0.555$). The Weibull probability function (Johnson and Van Wagner 1985) provided a good fit to the return interval frequency distribution ($r^2 = 0.705$), and the expected return interval, $b = 147$ yr, was close to the mean. The Weibull shape parameter, $c = 5.922$, indicates an increasing hazard of blowdown with stand age (Johnson
and van Wagner 1985). Unlike most fire regimes where these models have been applied, blowdown hazard appears to increase between 100 and 200 yr post-disturbance, and then possibly decrease in older stands. No return interval was <100 yr, which is consistent with the behavior of the 1972 event. Blowdowns from this storm completely enveloped several 50- to 75-yr-old stands without causing significant damage. The distribution of return intervals probably overestimates the disturbance rate, because the dendrochronological record diminishes with stand age (Fox 1989). For example, to detect a return interval >220 yr in a patch created in 1924, we would have needed to find remnant trees >280 yr old, which is approaching the typical lifespan of N. pumilio.

Although return intervals were not randomly sampled, and despite the dendrochronological bias, it is reassuring that the return interval distribution is consistent with the treefall size distribution of 61 stands <100 yr old (Fig. 7). The structural threshold of vulnerability occurred when trees reached 18–20 cm dbh. Based on characteristics of live stands, post-disturbance cohorts reached this size between 100 and 125 yr after disturbance (Fig. 8A), which corresponds closely with the minimum estimates of return interval

Fig. 4. Distribution of blowdown patch sizes on Tierra del Fuego in 1991 for events <100 yr old. Original patch boundaries were assumed to be intact. Frequency data were fit to a power function: $Y = 0.22 + [18.82 \times (\text{Area})^{-1.95}]$ ($r^2 = 0.994$). Circles signify the cumulative percentage of total blowdown area contributed by each size class for the past 100 yr.

(Fig. 3B). Most of the treefall samples came from even-aged stands. Sixty-five percent of the treefall samples had mean dbh’s <32 cm (also upper quartile <40 cm), which is within the range of tree diameters found in post-blowdown stands <200 yr (compare Figs. 7 and 8). Thirteen percent of the treefall samples had diam-

Fig. 5. Distribution of mean treefall directions in 10-degree classes for 61 blowdowns on Tierra del Fuego. Each circle represents one stand; circle patterns indicate blowdown ages.
Fig. 6. Treefall directions in blowdowns from (A) 1972 and (B) 1924, illustrating the possible effects of topography on wind direction. Ground transect data (30 measured tree azimuths per locale) were supplemented with estimates of treefall directions from aerial photographs and "groundtruthed" estimates of general treefall direction (single azimuth measured per locale). The circled "1" in chart (A) refers to the area of greatest local impact.

Diameter >32 cm (upper quartile >40 cm dbh), and were structurally similar to the old-growth sample and other old-growth stands on Tierra del Fuego (Rebertus and Veblen 1993). Twenty-two percent of the samples had characteristics intermediate between even-aged post-blowdown stands and old growth. The transects only represented a small portion of some blowdowns; nevertheless, the treefall data further suggested that most
stands were destroyed by blowdown before they reached old-growth status.

Where do blowdowns occur?

Old-growth stands (no evidence of blowdown in >225 yr) were fairly evenly distributed with respect to topographic positions (Table 2). Old growth was negatively associated with ridges and positively associated with easterly aspects and elevations <300 m, but the relationships were relatively weak. Stands with no evidence of previous blowdown were more common 2–5 km northeast of Cerro Yakush, but we did not sample this area because it marked the transition to steppe and was more heavily impacted by human activities.

Damage from the 1924 blowdown was positively associated with east aspects and ridges, and negatively associated with valleys and south and west side slopes (Table 2). In contrast, the 1972 storm was positively associated with valleys oriented north–south, west-facing side slopes, moderate slope steepness, and elevations <300 m; and negatively associated with ridges. Sixty-four percent (108 ha) of the area destroyed in 1972 was associated with north–south valleys and east–west side slopes, oriented parallel to the predominantly southerly winds. Indeed, one blowdown followed a stream valley for >5 km before flaring out on the south-west flank of Cerro Yakush (Fig. 6A, solid black circle labeled “1”). Despite the negative association with north and east side slopes, a line of blowdowns occurred just below timberline on the northeast side of Cerro Yakush, some clearly in lee of slope positions, accounting for 28.6% of the damage from the 1972 storm.

We used the 1970 aerial photographs to better understand the damage patterns from the 1972 storm, which was carefully reconstructed from 1990–1991 photographs and groundtruthing. Before the storm, 60% of the study area was even-aged and 40% was old

![Fig. 7. Distribution of mean treefall diameters at breast height (dbh) from 61 blowdowns <100 yr old. Sample size for each blowdown is ~30 trees.](image)

![Fig. 8. Mean tree dbh (A) and basal area (B) of post-blowdown regeneration in 25-yr age classes. Individual blowdowns are plotted to show range and variation.](image)
growth. However, 71% of the area blown down in 1972 was comprised of even-aged stands and 29% was old growth. The before-and-after comparison also revealed that 35% of the total perimeter length of the 1972 blowdowns matched previous blowdown boundaries.

In the multiple regression model, variation in return interval was significantly related only to mean soil depth ($r^2 = 0.27$; $F_{1,32} = 11.9$; $P = 0.004$; Fig. 9). Elevation, slope, and interaction terms were not significant in the regression model. Surprisingly, higher disturbance rates were associated with deeper soils, although the relationship was highly variable. Return intervals also tended to be slightly shorter on north and east aspects (Fig. 10), but the correlation was weak and not significant ($r = 0.24$, $n = 34$, $P = 0.32$). Negative findings should be interpreted cautiously because any error associated with dating blowdowns (see Lorimer 1985, Norton and Ogden 1990) may have been compounded when determining return intervals.

**Stand response**

Of 1839 treefalls sampled in 61 blowdowns <100 yr old, 92% were uprooted, 5% were wind-snapped, and 3% were unknown. Survival of windthrown trees was observed in 8.1% of these 1839 treefalls <100 yr old and was more prevalent in stands <25 yr old (Kruskal-Wallis test, $P < 0.001$, 3 df; Fig. 11). Surviving trees were supported by both original and adventitious root systems.

In the three blowdowns where we cored trees for age structures, 67–97% (total $n = 30$ trees cored per blowdown) of *N. pumilio* originated within a two-decade span immediately after blowdowns (Fig. 12). The presence of occasional older, “open-grown” trees suggests that they were probably saplings when the storm occurred. Based on stand chronosequences, average dbh and basal area increase asymptotically the first 200 yr after disturbance, with basal area possibly declining slightly in old growth (Fig. 8B).

**Guanaco browsing in blowdowns**

In 1991, guanaco browsing inhibited *N. pumilio* regeneration in 130.7 ha (41.5%) of the area affected by blowdowns since 1915 (Fig. 2B). Persistent browsing, with nearly all stems pruned below 1.5 m in height, was visible in 62.4% of the area blown down in 1972, 61.5% of the area impacted in 1940–1965, and 6.9% of the areas hit in 1924. These older browse areas have now been partially converted to meadow. On Cerro Yakush the percentage of blowdown area severely browsed increased with proximity to timberline (Table

| Slope (°) | <10 | 10–20 | 20–30 | >30 | N–S valley | E–W valley | Ridge | North | East | South | West |
|----------|-----|-------|-------|-----|------------|------------|-------|-------|------|-------|------|------|
|          |     |       |       |     |            |            |       |       |      |       |      |      |
| +0.05    | 0.03 | –0.18 | 0.01  | 0.05 | –0.17      | –0.09      | –0.03 | –0.02 | 0.02  | 0.05  | 0.03  | 0.02  |
| (20.4)   | (44.2) | (31.6) | (3.8) | (13.6) | (6.0) | (5.7) | (25.2) | (21.7) | (7.0) | (7.0) | (20.9) |
| +0.02    | –0.03 | 0.00  | –0.19 | –0.11 | –0.51 | +0.10      | +0.05 | +0.09 | –0.35 | –0.65 | –0.65 | –0.65 |
| (17.7)   | (41.3) | (38.9) | (2.1) | (11.4) | (2.7) | (15.8) | (31.5) | (26.9) | (4.4) | (7.5) | (7.5) | (7.5) |
| –0.08    | +0.14 | –0.14 | –0.65 | +0.16 | +0.01 | –0.47      | –0.16 | –0.47 | –0.57 | +0.08 | +0.08 | +0.08 |
| (14.7)   | (50.8) | (33.5) | (1.0) | (26.6) | (6.2) | (10.3) | (23.3) | (10.3) | (2.9) | (27.2) | (27.2) | (27.2) |

**Fig. 9.** Linear regression model of the blowdown return interval ($t$) vs. mean soil depth ($D$) for 34 stands, $t = 179.38 – 1.33D$ ($r^2 = 0.27$); dotted lines are 95% confidence limits.

**Fig. 10.** Distribution of return intervals ($t$) across aspects, fitted with a trigonometric polynomial: $t = 147 + [9.0 \times \cos(\text{Aspect} – 229)]$. 

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3). Browsing was also negatively correlated with blowdown area for the 1972 event (Pearson rank order correlation, \( r = -0.64, P < 0.01, n = 32 \)). In blowdowns >5 ha, severe browsing was often restricted to discrete perimeter bands 10–50 m wide (Fig. 2B).

**Discussion**

**Regional dynamics of forests and wind**

The distribution of patch ages, return intervals, and treefall diameters provide three lines of evidence for periodic blowdowns every few decades and patch turnover times of \( \approx 150 \) yr for most of the study area. One-third of the study area is old growth, suggesting that the blowdown regime is not spatially homogeneous. Nevertheless, the disturbance rate is at least twice that reported for *Nothofagus pumilio* and similar species in old-growth stands dominated by fine-scale treefall gap dynamics (Veblen 1985, Rebertus and Veblen 1993, Veblen et al. 1996).

Because of the remoteness and limited aerial photogrammetric coverage of the interior, we do not know whether this blowdown regime is representative of other areas. The west end of the Sierra de las Pinturas forms a promontory in Lago Fagnano (Fig. 1), which may expose the range to more intense winds. Indeed, there appear to be fewer blowdowns in the Sierra Beauvoir, immediately to the west (A. J. Rebertus, personal observation). Extensive even-aged stands of probable windstorm origin have been documented in *Nothofagus* forests throughout Patagonia (Agostini 1941, Eskuche 1973, Mutarelli and Orfila 1973, Alvarez and Gross 1979, Schmidt and Urzua 1982, Armesto et al. 1992).

We have no direct information of what type(s) of storms were responsible for these blowdowns. However, Lyons (1983) described infrequent, intense Antarctic depressions that are consistent with the level of damage observed in this study. These storms develop rapidly offshore of Antarctica, move northeast into the Drake Passage, and sweep across Tierra del Fuego, generating winds >60 m/s (215 km/h), equivalent to a category 3 hurricane (Lyons 1983). The life cycle of these storms is extremely short and their genesis is poorly known, but they are most numerous in spring and fall when trees are in full leaf. Given the proximity of Tierra del Fuego to the Antarctic pack ice, it is likely

**Table 3.** Percentage of blowdown area heavily browsed as a function of travelling distance from timberline on Cerro Yakush, Tierra del Fuego. Total blowdown area (in hectares; browsed + unbrowsed) for each category appears in parentheses. The foothills in the southwest third of the study area usually lack timberline and were not included in the analysis.

<table>
<thead>
<tr>
<th>Blowdown period</th>
<th>Slope distance from timberline (m)</th>
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<tbody>
<tr>
<td></td>
<td>0–199</td>
</tr>
<tr>
<td>1965–1990</td>
<td>85 (17)</td>
</tr>
<tr>
<td>1940–1965</td>
<td>72 (4)</td>
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<tr>
<td>1915–1940</td>
<td>3 (6)</td>
</tr>
<tr>
<td>All</td>
<td>64 (28)</td>
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</table>
that this disturbance regime is highly sensitive to climate change (cf. Clark 1989). Global warming studies predict a decrease in the frequency of low pressure systems between 30° and 90° S latitude but an increase in their intensity (Lambert 1993).

Although wind explains the current landscape patterns, charcoal from bogs in Tierra del Fuego suggests a long history of fire on the island (Heusser 1987). Lightning is extremely rare in Tierra del Fuego (Veblen et al. 1996), and burning patterns would have been subject to vagaries of the nomadic Ona, who roamed the interior steppe and deciduous forests in search of guanaco (Goodall 1979). Most of the indigenous peoples were wiped out by measles and smallpox in the late 1800s, but extensive logging and burning has occurred north and east of the study area where estancias (ranches) were built by European immigrants in the early 1900s (Goodall 1979).

Stand response

Effective dispersal of *Nothofagus* seeds is often limited to distances of 50–80 m, rarely 200 m (Veblen et al. 1996), so most blowdowns are small or narrow enough to capture adequate seed from adjacent stands or remnant trees. In addition, *N. pumilio* stands >100 yr old have a short-lived pool of seedlings, most <10 cm high, that survive *en masse* following a blowdown (Rebertus and Veblen 1993; T. T. Veblen, unpublished data). The development of even-aged stands after blowdowns is similar to the response of *N. pumilio* after fire, although regeneration failure following large, intense fires or burns on steep slopes is a common pattern throughout its range (Veblen et al. 1996). Vegetative reproduction of any kind has not been previously documented for *N. pumilio*. Based on our data, >50 treefalls (15–40 cm dbh) per hectare will survive in a typical blowdown, and these stems may play an important role in establishing early vegetation and minimizing erosion and nutrient loss, particularly near timberline or in areas heavily browsed by guanacos.

Factors involved in blowdown susceptibility

Based on our treefall data and point return intervals, the threshold of stand vulnerability for *N. pumilio* occurred between 100 and 125 yr, when trees attained a mean dbh of ~20 cm, basal area of 50 m²/ha, and ~16–19 m in height, which is very similar to results reported from *N. solandri* var. *cliffortioides* in New Zealand (Jane 1986). Windfirmness is strongly related to stem taper but tends to decrease with tree size (mass, volume, and height; Frederiksen et al. 1993). As tree size increases, the additional strain on the root–soil interface may exceed the soil shear strength (Putz et al. 1983), and trees may have stem and root rots that further compromise their strength (Foster 1988b, Harris 1989).

There is no consensus in the literature whether old-growth or even-aged structural characteristics are more susceptible to blowdowns. Of the 61 treefall samples we took from blowdowns <100 yr old (Fig. 7), only 13% were unequivocally from previously old-growth stands. In addition, even-aged stands were disproportionately affected by the 1972 storm. *Nothofagus* establish in dense, even-aged stands, where trees tend to grow tall and thin, with poorly tapered stems—all factors that decrease windfirmness (Oliver and Larson 1990). Wardle (1984) also noted that *Nothofagus* in New Zealand were more vulnerable to windthrow in monospecific, even-aged stands.

The landscape distribution of individual blowdowns indicated that valleys parallel to the storm winds, windward slopes, and some upper leeward slopes were more vulnerable to storm damage than other landscape positions. However, few areas were completely sheltered and storms displayed only modest levels of discrimination (Table 2). The return interval model also suggests that blowdowns were likely to *reoccur* over a wide range of elevation, slope, and aspect. Nevertheless, once a blowdown occurred, the odds were in favor of future blowdowns on the same site. However, the landscape pattern of blowdown and recovery shifted over time because of variations among individual storms and because a small proportion of old-growth stands were converted to blowdowns and vice versa. The reciprocal pattern of damage for the intense 1924 and 1972 storms can partly be explained by differences in wind direction. In addition, some landscape positions hit hard in 1924, such as ridges, had mostly younger and less vulnerable stands in 1972 (Table 2). The lack of strong discrimination of these blowdowns is in marked contrast to hurricanes in New England and the Caribbean (Lugo et al. 1983, Foster and Boone 1992, Boone et al. 1994), where damage is concentrated on windward aspects and variation can be predicted from relatively simple wind sheltering models (Boose et al. 1994).

The location and shapes of blowdowns may indicate the types of destructive winds accompanying these storms. The association of the 1972 blowdown with low elevations, moderate slope steepness, and valleys oriented north–south is consistent with convergence of laminar flow. Channelization in valleys is accompanied by an increase in windspeed, particularly as winds are compressed moving upslope (Buck 1964, Jane 1986, Harris 1989). The elongate patches from 1972 (Fig. 6A, solid circle labeled “1”) were apparently caused by this phenomenon, comprising almost two-thirds of the damage. Harris (1989) also reported that most gale damage in southeast Alaska occurred in valleys and side slopes parallel to the wind. Turbulent wind flow may explain the extensive damage on the upper northeast (leeward) slopes of Cerro Yakush (Fig. 6A). Roll eddies form downslope of sharp ridges in mountainous terrain, but any abrupt change in topography will cause turbulence (Buck 1964, Jane 1986). In New Zealand, Jane (1986) also reported that wind damage to *Noth-
ofagus forests was often concentrated on leeward slopes.

Although soils were very shallow in the Sierra, we believe the unstable sandstone-conglomerate bedrock was a more critical predisposing factor. Root masses were often heavily laden with rock, indicating possible slippage. In addition roots may be susceptible to mechanical abrasion from wind-rocking in the shallow, rocky soils, leaving them vulnerable to compression breaks and/or fungal pathogens (Stone 1977). The association of shorter return intervals with deeper soils runs counter to the majority of the literature (Schaezler et al. 1989). The simplest explanation is that trees on deeper soils grow faster and become vulnerable quicker (Boyd and Webb 1981, Harris 1989:48), but unfortunately our treefall data were inadequate to address this hypothesis.

**Landscape pattern development**

In the Sierra de las Pinturas, the majority of the landscape was composed of discrete patches of complete blowdown (>99% mortality), creating a coarse-scale mosaic that closely resembled some landscapes dominated by wildfire. We suspect this reflected not only the intensity of the storms but also their lack of discrimination in simple, monospecific, even-aged stands lacking height differentiation. Canopy emergents and suppressed trees were relatively rare. The more diffuse damage pattern of hurricanes partly reflects differences in susceptibility among species or canopy positions within stands (Foster 1988b, Foster and Boose 1992). Lugo et al. (1983) also noted that structurally and compositionally “complex” tropical forests were resistant to hurricane damage. Despite the intensity of some hurricanes, the damage is best characterized as a heterogenous mixture of patches, mostly <2 ha but some much larger, in various damage classes (Foster and Boose 1992).

Cooper’s (1913) pioneering study of forest succession on Isle Royale, Michigan, presaged the shifting-mosaic steady-state concept (sensu Bormann and Likens 1979) in describing the blowdown patch dynamics of Abies balsamea as a “mosaic or patchwork [that] changes continually in a manner that may almost be called kaleidoscopic.” This implied landscape equilibrium, while appealing conceptually, has been very difficult to demonstrate empirically for any disturbance (Pickett and White 1985, Turner et al. 1993). Turner et al. noted that definitions and criteria for assessing equilibrium were not applied consistently, and temporal and spatial scales were often confounded. They proposed using a spatial parameter \( S = \text{ratio of disturbance size to landscape size} \) and a temporal parameter \( T = \text{ratio of disturbance interval to the recovery time required to reach a mature stage} \). Landscape size is arbitrary, as long as there are reasonable estimates for disturbance size and frequency. For our study area, \( S \approx 0.04–0.1 \) (4–100 ha/1000 ha) and \( T \approx 0.6–0.7 \) (150 yr/225–250 yr). Based on simulations by Turner et al. (1993), these values should permit an equilibrium or steady state in the proportions of the 1000-ha landscape in various age classes. The behavior of damaging winds in 1972, which followed along previous stand boundaries, also suggested that blowdown patterns may exhibit some degree of constancy with respect to patch location. Similar dynamics are characteristic of some fire-dominated landscapes, where the juxtaposition of young and old stands reduces the likelihood of fire spread and maintains patch diversity (Minnich 1983).

**Interactions between guanacos, wind, and landscape patterns**

Although guanacos are known to browse trees (Rae-decke 1978), their impact on forests has not been previously documented. Variation in browsing intensity across the landscape influenced patch development by creating persistent meadows in accessible and/or highly preferred habitat. Few small blowdowns created in the past 50 yr escaped being heavily browsed; however, for blowdowns >200 m across there is a threshold of obstacles beyond which guanacos gave up and browsed solely the perimeter. This browsing pattern created conspicuous linear meadows between adjacent stands (Fig. 2), which may persist for centuries because they are favored by guanacos as travel corridors long after they cease being a significant source of browse (unpublished data). “Seedlings” survive persistent browsing for at least 60 yr, eventually becoming hedge-like, but many areas kept open since 1924 have gradually been converted to meadow and thickets of a thorny shrub, Berberis buxifolia.

Guanacos had greatest impact near timberline, where they concentrated in summer for browse and grazing in the tundra above (Table 3). The near-timberline portions of several blowdowns have been kept open for >60 yr, whereas lower parts have regenerated normally. Regeneration failure probably arose from a combination of browsing pressure, climatic stresses, and seed dispersal limitations. There was circumstantial evidence of longer-term conversion of blowdowns to alpine throughout the Sierra, some of which may be attributable to blowdowns and guanaco browsing: sharp timberlines lacking krummholz, stranded tree islands, wedge-shaped alpine intrusions, and dead wood fragments above timberline. Timberline was typically 600–700 m in nearby interior ranges (A. J. Rebertus, personal observation), but in many peaks of the Sierra de las Pinturas, blowdowns and guanaco browsing together have probably depressed timberline >200 m below its climatic limit. Indeed, we have found nascent colonies of Bolax gummifera, the dominant alpine cushion plant growing in old blowdowns 200–300 m below this plant’s typical alpine limit.

**Conclusions**

There is growing realization of the importance of coarse-scale windthrow in forest dynamics worldwide.
In Tierra del Fuego we found a system where periodic gales from Antarctica dominated many characteristics in Nothofagus pumilio forests, from microsite to landscape. The distribution of patch ages, treefall sizes, and return intervals across the landscape all indicated that vulnerability to blowdown increased acutely when stands reached ages of 100–125 yr. Although major valleys parallel to the prevailing storm winds, windward side slopes, and upper leeward slopes appeared to be most vulnerable to blowdowns, we could not detect any major differences in return intervals due to aspect, slope, or elevation. Some areas may have been more vulnerable to blowdowns, but the cumulative damage from 200 yr of repeated storms had affected most landscape positions. Guanacos also played a major, synergistic role in the disturbance regime, influencing forest regeneration and creating persistent open patches along edges of stands and adjacent to treefall line.

Most disturbance regimes were difficult to characterize because of the multiplicity of disturbance types, the fuzziness of their effects, and the confusing influence of historical factors. The overwhelming dominance of wind as the coarse-scale disturbance agent and the relatively simple forests of our study site on Tierra del Fuego, however, revealed a relatively clear relationship between forest patterns and the disturbance regime.

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