

WIND DAMAGE AS AN ECOLOGICAL PROCESS IN MOUNTAIN BEECH FORESTS OF CANTERBURY, NEW ZEALAND

Summary: Sites in four areas of Canterbury, New Zealand were examined to determine the principal factors influencing wind damage, and study sites at two areas were used to investigate forest age-class structure and stand dynamics. At all sites large-scale topographic features funnelled storm winds to produce recurrent damage, and smaller-scale topographic features determined precise points affected by winthrow.

Lee slopes provide shelter to susceptible sites during normal weather conditions and therefore permit better stand growth, but stand damage increases in storms. Stands on exposed windward slopes form a wind-shaped canopy which is constrained by stem breakage during minor storms.

Damage occurs in stands over a critical height of about 18 m and where stem diameter is large. Wind-damaged forests have restricted age-distribution compared with those of partially damaged and vulnerable forests. Wind damage is little cause for concern as it must be viewed in a framework of short-term forest stability. Periodic mortality in mountain beech forests can be seen as a regeneration strategy of a light-demanding species, since it produces ideal conditions for forest perpetuation. Forest collapse, followed by rapid massed regeneration is thus an effective competitive mechanism against a more shade-tolerant canopy species.

Keywords: wind damage, competition, disease, regeneration strategy, mountain beech, dendrochronology.

Introduction

Windthrow frequently occurs in mountain beech (*Nothofagus solandri* var. *cliffortioides*) forests and casual records extending back to earliest European settlement are reported by Thomson (1936) and Moorhouse (1939). Gale force northwest winds are common in upland Canterbury, exceeding 240 km/h two or three times a year in places like Mt St John and Craigieburn (McCracken, 1980). Wind damage to plantations on Canterbury Plains was reported in 1945, 1968, and 1975 (Jolliffe, 1945; Prior, 1959; Wendelken, 1966; Thomson, 1976; Wilson, 1976; Sommerville, 1980), but less attention has been given to concurrent damage in upland indigenous forests reported by staff at Arthur's Pass National Park.

Numerous factors determine severe wind damage location in forests. Many detailed field and laboratory studies are reviewed by Gloyne (1968) and Papesch (1974) but the studies are concerned with site susceptibility within plantations and managed forests (Bush by, 1965; Kennedy, 1974; Saville, 1983; Smith, 1946) and thus may be of limited applicability in natural stands.

Widespread damage observed in the present study occurred from Lake Ohau north to Lake Sumner during a storm on 4-5 October 1981 (Norton, 1983). Areas of damage, extending over hundreds of hectares, occurred in Moa, Poulter and Cox Valleys and smaller scale damage was particularly evident

throughout Arthur's Pass National Park, Craigieburn State Forest Park and Temple State Forest.

The current study attempts to deduce factors contributing to vulnerability of particular stands through examining stand and site parameters. It also attempts to interpret the role of windthrow in mountain beech forest regeneration and stand development.

Methods

Sites were visited, sketched and photographed at Temple State Forest, Lake Ohau (Temple, 4 sites); Hamilton Creek, Craigieburn State Forest Park (Hamilton, 3 sites); and Andrews Stream (Andrews, 24 sites) and Poulter River (Poulter, 6 sites), in Arthur's Pass National Park (Fig. 1). Detailed studies were made on sites at Andrews Stream and, to a lesser extent, in Poulter River valley.

In the Andrews and Poulter study areas 30 sites were examined in 8 localities. At each study site a whole windthrow and adjacent topography was sketched. Several points were then assessed by one of two sampling strategies: nearest neighbour plots (Batcheler and Hodder, 1975); or fixed area plots (Allen and McLennan, 1983).

Four stand types were recognised:

1. *Windthrown stands* containing no standing trees. Measurements were made on fallen stems at points

LOCATION MAP

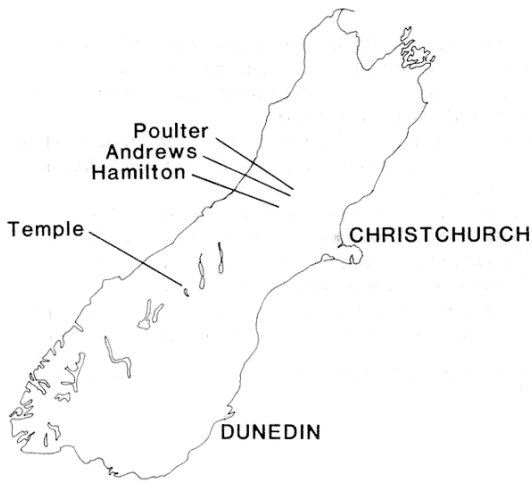


Figure 1: Location of study areas.

approximating those used on standing trees.

2. *Partially damaged stands*, usually part of a larger windthrow, where up to half the trees remained standing. Both standing and windthrown trees were measured.

3. *Vulnerable stands* close to wind-damaged sites, showing evidence of past damage by pit and mound micro-topography. (Pits are caused by removal of soil which is carried in the upturned root plate and which in turn decays to form the mound on the down-wind side of the pit).

4. *Intact stands* on similar sites but away from wind-damaged areas, showing no evidence of current wind damage and an absence of pit and mound micro-topography or fallen stems which might indicate past damage.

Nearest neighbour plots

Each plot consisted of three cells spaced at 10 m centres and arranged in a line across the direction of travel or five cells arranged as a cross with one axis the same as the direction and the other at right angles. Each cell was defined as three standing, recently dead or windthrown stems. The first stem was that nearest to the centre point of the cell, the second was nearest

neighbour to the first stem, and the third was the nearest neighbour to the second stem.

Four or six plots, each with five cells, spaced along lines at 20 or 40 m, were used to compare windthrown and unaffected stands. Lines originated from a pre-selected starting point, and were placed at right angles to a stand edge in wind damaged and undamaged areas. The first plot was placed 10 m from a line start to reduce bias inherent in selecting a starting point and subsequent plots were spaced by an interval determined by distance across a stand or wind damaged area. To compile vegetation transects across topographic features such as ridges and gullies, plots of three cells were spaced at 10 m intervals along a compass line.

Distance from cell centre to centre of the nearest stem base and distance between two subsequent nearest stems over 10 cm dbh (diameter at breast height) were measured to obtain stand density estimates. All three stem diameters were recorded. Trees less than 10 cm dbh were not included because it was thought that smaller stems could easily be overlooked in windthrow. Height (or length if windthrown) of the second tree from the centre in each cell was measured. Site parameters including slope, aspect, altitude, drainage and notes on old windthrow evidenced by pit and mound micro-topography were recorded.

Fixed area plots

Rectangular 20 x 10 m plots were established to follow long-term changes in vegetation. Within each plot five strata were recognised:

1. Old age-class trees: stems probably over 150 years old, recognised by bark type and usually over 30 cm dbh.
2. Trees: stems over 10 cm dbh. A stratum used for comparability with temporary plots.
3. Poles: stems 2-10 cm dbh. Recognised to make data comparable with Forest Service standard 20 x 20 m plots (Allen and McLennan, 1983).
4. Saplings: stems 135 cm tall to 2 cm dbh as in Forest Service standard 20 x 20 m plots.
5. Seedlings: plants 20 cm to 135 cm tall as in Forest Service standard 20 x 20 m plots.

Diameter of all trees and poles over 2 cm dbh were measured, even if a stem was windthrown or recently dead. Within each plot, heights of the three smallest, three largest and three average diameter stems were measured with a clinometer.

Density of old trees, shrubs and seedlings was

assessed using nearest neighbour technique (Batchelor and Hodder, 1975). Seedling and shrub densities were assessed at nine points, the four corners plus the five points midway between corners. Density of old age-class stems was measured at the plot corner furthest from the point beginning the plot layout. Density measurements were made regardless of plot boundary or measurement from a previous point (selection with replacement). At many sites only scattered seedlings or shrubs were present over wide areas but if one stem of any stratum appeared within a 20 x 10 m plot the stratum was regarded as present and an infinite search radius assumed for all measurements.

At each plot a standard reconnaissance description was completed as set out by Allen and McLennan (1983). Particular attention was given to windthrow history and factors such as nearness to a ridge and general topography.

Dendrochronology

Discs were taken from windthrown trees at Temple State Forest and three localities at Andrews stream. Discs were cut as close as possible to the stem base and prepared by planing and sanding. No precise chronology was determined, consequently tree ages may have an error of a few years, perhaps up to five years in older stems.

Results

Damage patterns at study sites

Small-scale damage was initiated on lee slopes or stand edges, producing broken or windthrown stems. At 2 of 30 sites examined damage was propagated from edges of previous windthrow but generally each storm resulted in a new damage site since there are uniform but different ages of regeneration at each site of windthrow (Fig. 2). This pattern is evident in the upper Poulter River, where damage has occurred in several years near the junction of the Thompson Stream.

1. Temple

Damage at Temple appeared to have resulted from a counter current to redirected northwest flow which was canalised down the Hopkins valley. At one critical point in the Temple valley, wind crossing at right angles over a ridge at about 1500 m appeared to be trapped by a high down-wind range 2100 m high and redirected down-slope towards the prevailing wind in a vertical vortex. This released some pressure up-river but the main thrust passed down-river causing extensive damage (Fig. 3).

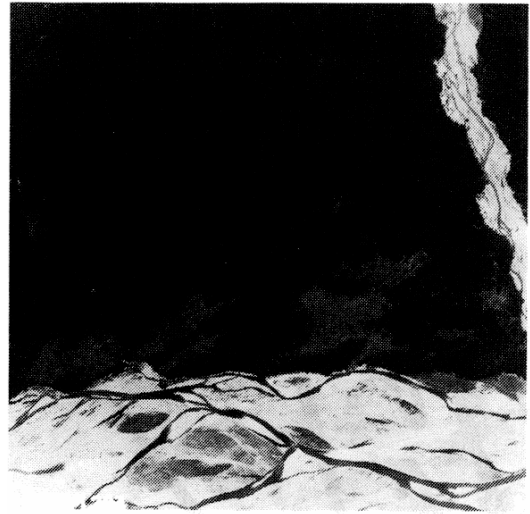


Figure 2: Aerial view of wind damage near the Thompson Stream junction. Several different ages of wind damage are apparent. Apart from the recent damage, an area with a low and slightly broken canopy at the centre (along the river) marks a windfall swath a few years old, and to the right an area with a low and even canopy marks one several years older.

2. Hamilton Creek

Similar circular damage patterns of three distinct ages were observed at the same general locality in Hamilton Creek suggesting similar damaging vortices and a predisposition to damage of this type at one particular point in the valley. Rapid downstream widening of the valley apparently allowed wind force to dissipate, causing little further damage.

3. Poulter

Damage began in the upper Poulter River at Thompson Stream junction (Fig. 4). At this point damage was found on a river terrace directly opposite and pointing away from the main river fork. Further down-river windthrow direction of 6 wind damage swaths of differing ages gradually changed to parallel the main valley. Damage at each site was associated with recent river bank erosion and removal of the stand edge, apparently because undercutting exposed trees of the stand interior which had lower wind stability. Each fresh episode of river bank erosion had resulted in a new area of wind damage. From

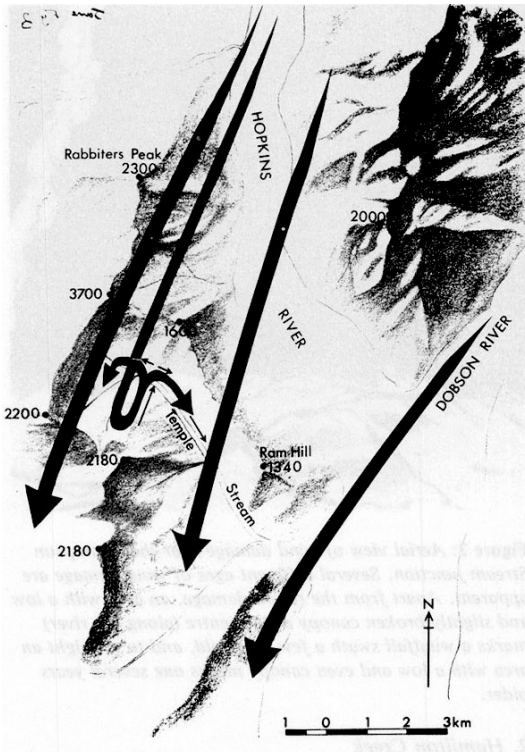


Figure 3: Schematic diagram of wind flows in the Temple valley showing probable deflection both up and down stream.

Thompson Stream junction sporadic damage was noted down-river until a major constriction below Casey Stream. There, wind was strongly canalised and damage was intensified by a venturi effect as the valley narrowed. Damage extended almost to the tree line and continued along the full forested valley length on the true left.

4. Andrews

Damage at the main Andrews study area consisted of several scattered patches with many predominant windthrow directions (Fig. 5) in a pattern which is best explained by air flows from Andrews Stream and Waimakariri River meeting and interacting (Fig. 6). Along Waimakariri River, upstream from Andrews Stream junction, windthrow direction was parallel with wind direction, (i.e. down the main river), but

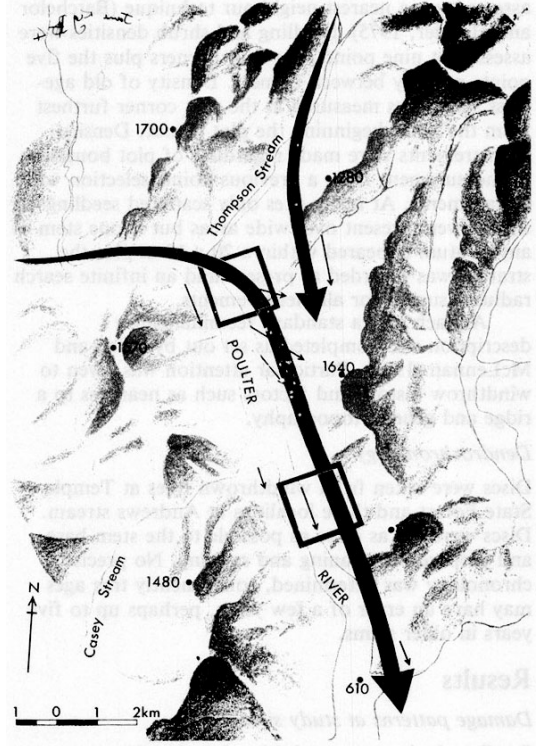


Figure 4: Schematic diagram of wind damage sites in the Poulter River. Small arrows indicate the direction of windthrow and large arrows indicate probable main wind direction.

near the mouth of Andrews stream, direction paralleled the stream because wind flow was deflected by wind canalised down the Andrews valley. Further downstream, windthrow direction gradually changed to parallel the main valley.

Site parameters

Little wind damage was observed at the tree line (1200 m), but windthrow occurred to within 150 m of the tree line in the Poulter Valley. At other localities, partial windthrow occurred on lee slopes of major ridges from river terraces to near the tree line. Sites affected were closely related to topographic focusing of wind intensity as described earlier.

Slope was highly variable at affected sites, ranging from flat to slopes of 250. A sharp change in slope occurred to windward of damaged areas at all

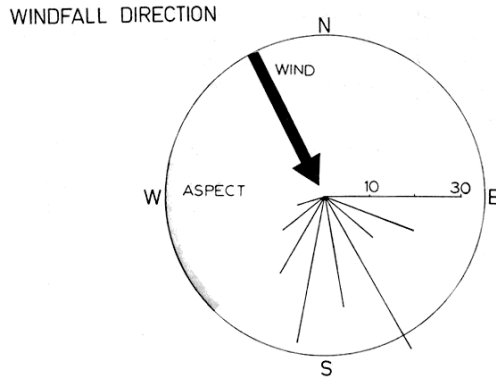


Figure 5: Wind rose percentages derived from measurements of lay of fallen trees at the Andrews study site. Note that although the predominant direction of lay is from the northwest, northeasterly and almost westerly directions are also prominent.

except two sites. At 20 sites windthrow began 2 or 3 tree heights from a ridge crest, above a deep gully or steep bank. At 5 sites recent stream bank erosion had removed trees on the edge of the stand which were naturally strengthened against strong winds, and exposed less resistant trees to the full wind force. Here windthrow began at the stand edge at the top of the bank.

Windthrow was absent on ridge or rocky sites with little soil, but elsewhere occurred with no break or transition where soil changed, on shallow soils derived from greywacke on slopes, or on deep alluvial gravels and loess on river terraces. Depth of soil overturned varied greatly, from a few centimetres on wet sites to over 1 m on deep alluvial gravels. Anchorage ability in a substrate was not important because wind forces at affected sites were so high that if windthrow did not occur stem breakage probably occurred. Even in healthy stands, tree sway, including tipping of root plates, was frequently caused by strong winds during the study.

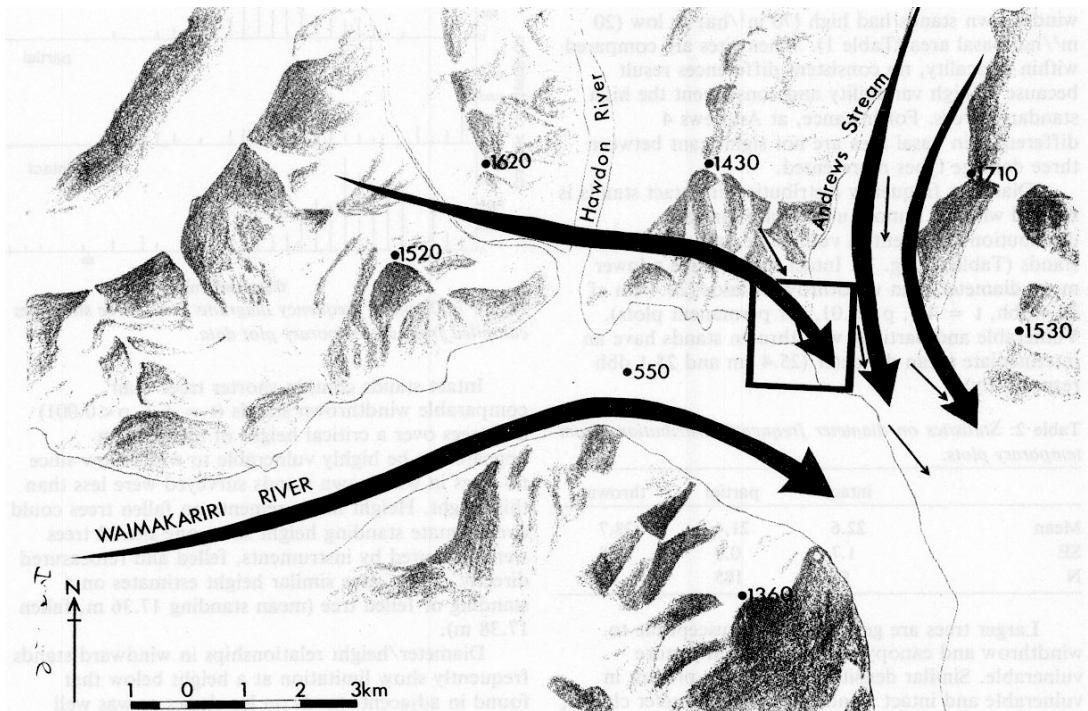


Figure 6: Schematic diagram of damage at the Andrews stream study site. Small arrows indicate general directions of wind damage.

Table 1: Basal Area (m²/ha) of trees over 10 cm dbh in mountain beech stands grouped by wind damage types on comparable sites. Data from permanent plots grouped into sets from the same wind damage site: intact - showing no evidence of current or past windthrow; vulnerable - showing evidence of past windthrow but otherwise intact; partial - up to 50% of stems windthrown; windthrown - more than 50% of stem windthrown; - no data; SE standard error of mean.

Locality		Stand type				Mean	SE
		Intact	Vulnerable	Partial	Windthrown		
Andrews	1	41.1	35.9	40.9	50.6	46.9	11.0
	2	63.6	-	49.0	-	56.3	10.1
	3	-	56.7	66.2	-	66.6	11.6
	4	-	68.2	69.5	68.4	68.7	0.7
Poulter	1	74.2	64.0	-	74.5	71.7	7.1
	2	72.3	30.6	-	27.5	43.7	7.1
Mean		46.6	49.0	52.2	48.8	55.9	17.8
SE		11.6	13.6	18.5	16.9	17.8	
No of Plots		14	10	12	12	48	

Stand Parameters

No difference in basal area was evident between stands ($t = 0.4$, $p > 0.50$) and even individual windthrown stands had high (70 m²/ha) or low (20 m²/ha) basal area (Table 1). When sites are compared within a locality, no consistent differences result because of high variability and consequent the high standard errors. For instance, at Andrews 4 differences in basal area are not significant between three damage types represented.

Diameter frequency distribution in intact stands is skewed whereas a more unimodal (normal) distribution is present in vulnerable and windthrown stands (Table 2, Fig. 7). Intact stands have a lower mean diameter than windthrown stands (20.4 cm cf 28.4 dbh, $t = 4.1$, $p < 0.01$, for permanent plots). Vulnerable and partially windthrown stands have an intermediate mean diameter (25.4 cm and 25.1 dbh respectively).

Table 2: Statistics on diameter frequency distributions from temporary plots.

	intact	partial	thrown
Mean	22.6	21.4	28.7
SE	1.7	0.9	0.8
N	56	185	88

Larger trees are generally more susceptible to windthrow and canopy trees are certainly more vulnerable. Similar densities of trees are present in vulnerable and intact stands at higher diameter classes, although more trees in intact stands are over 25 cm dbh (25% cf 33% $p < 0.05$; Fig. 7).

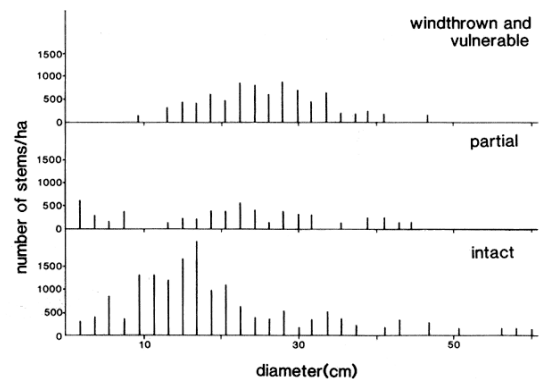


Figure 7: Diameter frequency diagrams from three site types compiled from all temporary plot data.

Intact stands contain shorter trees than comparable windthrown stands ($t = 5.7$, $p < 0.001$) and trees over a critical height of about 18 m appeared to be highly vulnerable to windthrow since no trees in windthrown stands surveyed were less than this height. Height measurements on fallen trees could overestimate standing height so at one site 12 trees were measured by instruments, felled and remeasured directly. These gave similar height estimates on a standing or felled tree (mean standing 17.36 m, fallen 17.38 m).

Diameter /height relationships in windward stands frequently show limitation at a height below that found in adjacent stands on lee slopes as was well demonstrated at the Andrews 3 site (Fig. 8). Windward trees over 20 cm dbh have a mean height

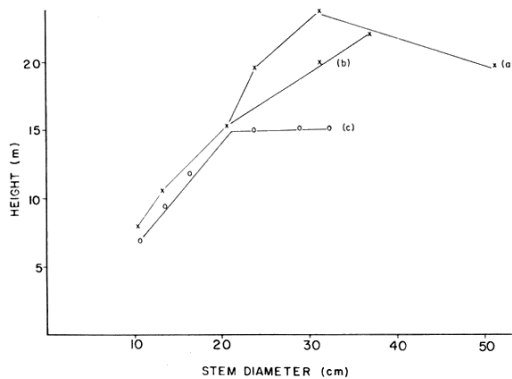


Figure 8: Patterns of diameter height relationship from three adjacent 20 x 10 m plots at Andrews stream: a) at the ridge crest; b) on the lee slope; c) on the windward slope.

of 12.9 m whereas lee slope trees were 20.8 m tall ($t = 6.7, p < 0.001$). Wind breakage has apparently limited height growth in exposed intact stands (Fig. 8). At a ridge crest, where wind strength is likely to be greatest, stem breakage of taller trees is common and apparently occurred at several different times in old trees 40-60 cm in dbh. Stand height on lee slopes did not decrease with altitude. Greatest difference between windward and lee slopes was found in two stands at

1200 m where height ranged from 5 to 1 m on the ridge to 20 to 5 m on wind damaged lee slopes.

Windthrown stands have approximately half the density of adjacent vulnerable stands ($t = 5.7, p < 0.001$) and sometimes less than a quarter the density of adjacent intact stands more remote from damage sites in the same locality (Table 3). Profiles from 2 sites in the Andrews area show that tree density increases gradually towards a ridge crest on both windward and lee slopes (Fig. 9). However, this general trend is broken by a reduction in density immediately to windward of a crest, and by a particularly high density in its immediate lee (Fig. 9). Fall in density at the ridge crest on these two sites is accompanied by a fall in height resulting in an open stand (Fig. 9), but on lower slopes a transition in stand density is not obvious and is visually masked by simultaneous changes in dbh and tree height.

Spacing/Height Ratio

Spacing height ratio (S/H) was calculated directly from (mean radii derived from cells)/(average height) at each temporary plot. Average values for intact and windthrown sites are similar (intact S/H = 0.16; windthrown S/H = 0.15, $t = 0.04$) and no unique threshold value or range of values can be associated with wind-damaged sites. Closer examination shows a fall in S/H ratio on ridge crests at all sites, and a rise on both windward and lee slopes (Fig. 10). On lee slopes near windthrown sites a fall in density is

Table 3: Stand density (stems/ha) of trees over 10 cm dbh in mountain beech stands grouped by wind damage types. Main data from permanent plots grouped into sets from the same wind damage site, temporary plot data grouped only as intact or windthrown: intact - showing no evidence of current or past windthrow; vulnerable - showing evidence of past windthrow but otherwise intact; partial - up to 50% of stems windthrown; windthrown - more than 50% of stem windthrown; - no data; SE standard error of mean.

Locality		Intact	Vulnerable	Partial	Windthrown	Mean	SE
<i>Permanent plots</i>							
Andrews	1	1150	775	500	850	828	280
	2	1720	-	300	-	1430	912
	3	-	1075	1050	-	1055	247
	4	-	1300	850	800	1075	988
Poulter	1	2370	875	-	350	1580	333
	2	1200	300	-	400	633	490
Mean		1356	920	950	617	1138	
SE		779	402	693	250	709	
N Plots		14	12	10	12	58	
<i>Temporary plots</i>							
Mean		1690	-	1161	563		
N Plots		85	-	58	143		

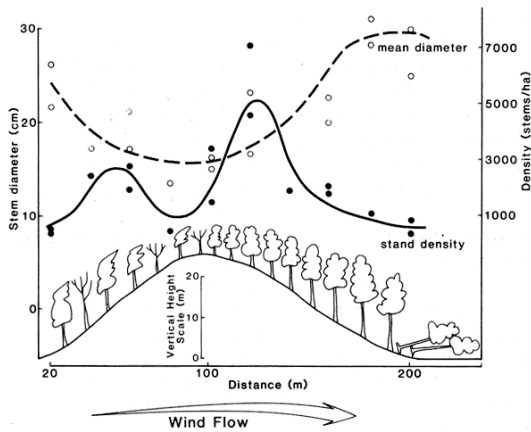


Figure 9: Variation in mean diameter and density over a minor ridge. Stand height indicated by tree height, relative mortality intensity by dead trees and wind clipping by flagging on trees. Diagram is a composite of two transects, each point representing a mean of 6 cells.

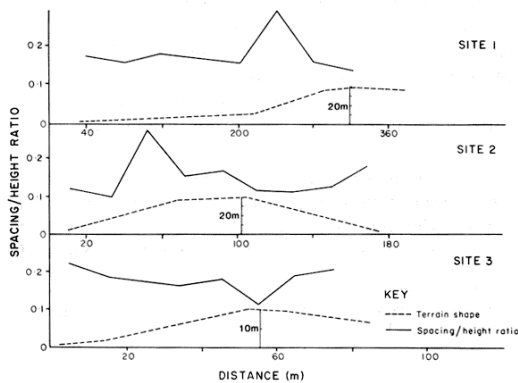


Figure 10: Variation of SIR Ratios across the topography on three transects at the Andrews study area. Predominant wind direction is from the left.

apparently compensated for by increased height so that damage is independent of S/H ratio.

Stand Mortality

Prior to windthrow the proportion of dead trees is similar on windthrown and partially damaged sites, averaging 21 % for all localities. Mortality apparently

arose following snow damage in 1968 and 1972 (Wardle and Allen, 1983). Wide variability occurs between stands even in the same locality, ranging from zero to over 40% in closely adjacent and similar localities and stand types, resulting in a large standard error for the mean (19.9 overall). Mortality on topographic profiles increases to a peak of about 30% on ridge crests (e.g. plot 3.1). Mortality affects all size classes but large and small stems tend to be more strongly affected (cf plots 2.1, 2.3 where 5 stems of 44 cm mean dbh and 21 of mean 11.6 dbh were affected).

Visual evidence at partially damaged sites did not suggest that tree death occurs from disease following windthrow or spread of mortality from partial or totally wind damaged sites at Andrews Stream, Poulter River or Temple Stream site. At many localities mortality occurred well away from wind damaged sites and, conversely, stems surviving windthrow in wind-damaged areas were not subsequently killed.

Regeneration

Seedling and shrub densities were highly variable (Table 4). In dense old stands seedlings were absent or confined to light wells where many mountain beech less than 20 cm tall were present. Death or windthrow of individual trees or small groups led to abundant plants up to 2 m tall within a few years (Table 4). Bud scars showed that growth of 50-100 cm was common with many plants passing from the less than 20 cm category into shrub category between windthrow in 1981 and 1983 (Table 4). At all windthrow sites dense, essentially even-sized regeneration will lead to well stocked pole stands within 20 years.

In partially opened stands, presence of seedling groups is well shown by the aggregation parameter A of Batcheler and Hodder (1975), which is greater than 2 (Table 4). In highly competitive, dense regeneration, stems are almost evenly spaced ($A = 0.8-0.9$) and in older stands, random ($A = 1$).

Stand age

Discs for stem dating were taken at four localities but samples were small - some 150 discs in all. Difficulty in finding sound large stems at most windthrow sites restricted information on older age-classes. Age distributions at each site varied, but peaks in the data suggest that disturbances have occurred at one or more sites at about 100, 125, 145, 180 and perhaps 240 years ago (Fig. 11). The age-classes are not totally disjoint for many reasons including errors in stem dating and the inclusion of stems which originated

Table 4: Stand densities and other parameters from four plots in wind damaged mountain beech forest - located within 50 m of one another. Trees, plants over 10 cm dbh; saplings, plants of 2 -10 cm dbh; shrubs, plants 135 cm tall to 2 cm dbh; seedlings, plants 20 -135 cm tall. A is a measure of non-randomness (Bateheler and Hodder, 1976); BA is basal area of trees.

Type	BA m ² /ha	Height (m)	Trees No/m ²	Saplings No/m ²	Seedlings No/m ²	Shrubs No/m ²	Seedlings A value	Shrubs A value
High Density	41.8	14.6	2400	1450	0.20	0	0.90	no data
Some opening	44.8	12.8	1050	650	3.68	0.10	1.97	2.63
Windthrown	43.4	18.2	1150	0	5.88	6.84	2.13	2.45

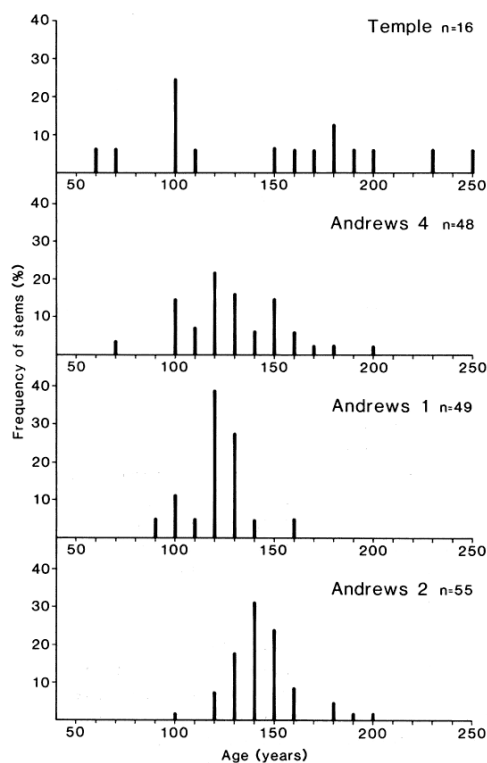


Figure 11: Age class structure of stands at four sites.

before postulated disturbance (being present as shrubs at the time) or in seed years immediately following the event. Nevertheless the sites examined within two years of windthrow suggest that most plants of the new generation develop from seedlings less than 16 cm

tall at the time of canopy disturbance and seedlings are frequently seen in adjacent undamaged stands (Table 4).

Differences in dates of peak disturbances are probably caused by differences in growth rates between sites because slower growing trees take longer to reach the critical height. This is shown in Fig. 12, where a population with slower growth rate, Andrews true left (including sites in localities 1 and 4), has a greater age at windthrow (144 cf 135, $t = 2.0$, $p < 0.05$).

Studies of size-class distributions in stands of many other species and also large populations of all-aged stands of mountain beech show a semi-logarithmic relationship between size-class and stem frequency (Wardle, 1984) but this is certainly not the case for the data in Fig. 7, because the stands consist of only a few age classes. Stand age-classes can be inferred from the size-class peaks using the diameter/age regressions in Fig. 12. Data from vulnerable and windthrown areas suggest peaks at 6, 16, 23 and 32 cm dbh corresponding with 80, 105, 125 and 150 age-classes. Other peaks occur at 45 and 50 cm (190 and 205 years) although data from larger size-classes are limited. The larger data set from temporary and permanent plots at Andrews 1 site (Table 2), with slower growth rates, suggests peaks at 25 and 30 cm dbh (125 and 145 years) whereas at all other sites peaks occur at 20, 30 and 45 cm dbh with strongest representation of the 20 and 30 cm peaks and few stems over 30 cm. This suggests that damaged sites are completely affected at intervals not greater than 130 years.

Discussion

Site factors

Both large and small scale topographic features were important in determining wind damage location. On a large scale, mountain ranges and valley patterns redirected winds and enhanced velocity in wind flows (Grace, 1977). Reports from local Rangers suggest

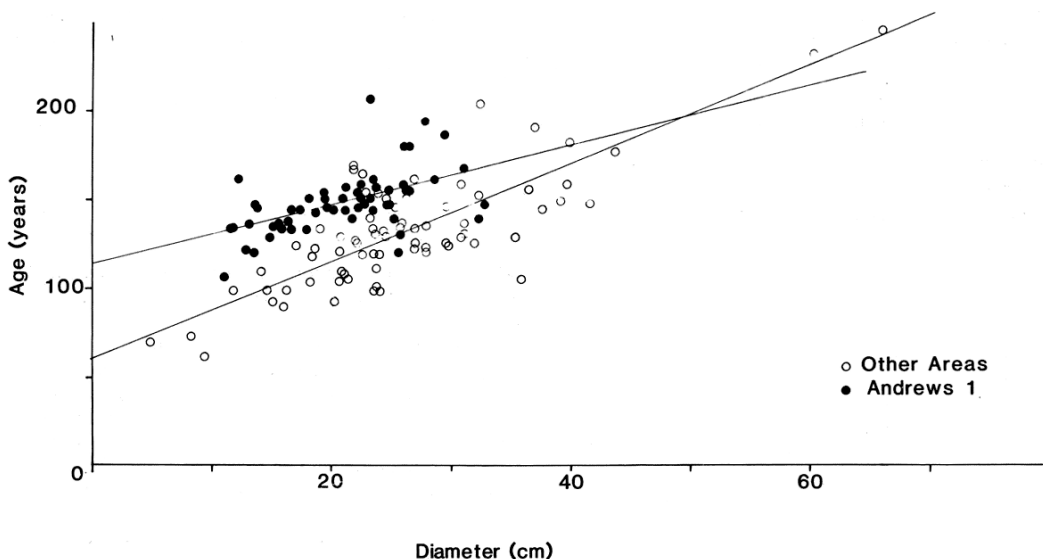


Figure 12: Relationship between diameter and tree age from sites on opposite sides of the same stream. (main area, Age = 2.9 diameter + 58.9, $r^2 = 0.57$, $n = 77$, $p .01$; opposite side of stream (Andrews 1), Age = 1.68 diameter + 114, $r^2 = 0.28$, $n = 55$, $p .01$; slopes significantly different, $p .001$).

that damage occurs particularly during northwest storms. On a local scale minor gullies increased damage risk on lee slopes by focusing wind impact. Laminar wind flow over ridges during a northwest wind led to maximum enhancement of wind velocity on upper lee slopes with sharp changes in slope, and caused damage. Similar damage has been widely noted elsewhere (Buck, 1965). Wind strength during gusts is likely to be enhanced by lee slope turbulences (Ruth and Yodder, 1953; Hutte, 1968) but lee slope turbulence leads to windthrow against the wind direction, whereas on all sites examined windthrow occurs with the wind. Consequently wind damage appears to arise from enhanced wind flow caused by a venturi effect in laminar flows, initiated by topographic features such as a deep gully in a manner similar to that portrayed by Buck (1965).

The most susceptible sites to windthrow are lee slopes protected from prevailing winds. On windward slopes, stature is kept low by wind shear and periodic breakage, possibly by non-storm winds. Similar wind-shaping of forest canopies has been widely reported (Lawton, 1982). Growth rates on exposed sites are also probably severely restricted by water stress rather

than substrate differences, particularly during northwest conditions when humidities can be low (less than 12% RH) and temperatures high (McCracken, 1980). Lower growth rates will result in smaller ring widths and greater wood density and strength. As a result, not only are stems kept below critical height on exposed sites, but wood strength factors may aid in resisting peak gusts during severe storms and reduce damage.

Susceptible stands were characterised by above-average growth rates resulting in large stem diameters and a greater stand height. This was in turn related to stand shelter through topographic position during normal weather conditions which permit better growth rates. Density in windthrown stands is about half adjacent stands at wind damage (Table 3), but lower density was associated with greater stem size which occurs through a natural trend in normal stand development in even-aged stands, and so basal area was frequently similar to adjacent stands.

Concurrent mortality and windthrow at a site may be merely coincidental, although even a low degree of mortality caused by pathogens such as *Armillaria* (Wardle and Allen, 1983) could lead to

increased root damage in live trees. When annual recruitment is subtracted and average rates of mortality taken into consideration, Wardle and Allen (1983) found mortality rates of 1% per annum over a 10 year period remaining, which was attributable to disturbances. But evidence presented here indicates high mortality rates (30%) since 1972 at ridge sites and less rates on lee slopes, where windthrow has occurred.

Wind tunnel studies of forest plantation models have suggested that spacing/height (S/H) ratio is more important than stand height alone in determining plantation susceptibility (Papesch, 1974) but the ratio was not found to be important in natural stands. S/H ratio on topographic profiles does not exhibit a critical value at damaged sites. In fact it may show minimum values at a ridge crest where wind damage is minimal and wind shear is predominant. Reasons why wind tunnel models (Papesch, 1974) and observations from plantations do not apply to natural stands probably relate to effects on small scale turbulence arising from two factors. Firstly, in natural stands tree size may cover a wide range with mixed age-class so that individual trees forming a canopy will not create the same turbulence as even-sized tended or plantation trees at the same top-height. Taller trees are also sheltered by smaller trees to a far greater extent by a natural multi-tiered forest structure.

Secondly, mortality in natural stands cannot be directly equated with thinning of plantations since tree death may only gradually result in a canopy gap. This is because during tree decay a dead crown slowly disintegrates and a gap may be rapidly filled by ingrowth of adjacent trees. At the same time roots of adjacent trees may become stronger. In managed

Table 5: Population Age Class Statistics. Populations are 1 Andrews 1; 2 Andrews 2; 4 Andrews 4; 5 Temple. Andrews localities are the same as used in previous tables, but sample size from Andrews 3 was too small to include here. SE, standard error of mean; s^2 /mean, variance/mean ratio.

	Populations			
	1	2	3	4
Mean age (years)	144	135	125	141
SE	4.5	5.3	3.9	14.3
S^2 /mean	0.23	0.28	0.13	0.41
Skewness	0.25	0.42	0.33	0.44
N	55	49	18	16

stands prone to wind damage thinning techniques which slowly open the stands in this way (e.g. tree poisoning) have a similar effect and are regarded as giving better protection from wind damage (Saville, 1983).

Recurrence of events

Partially damaged stands on the periphery of windthrown areas resulting from either past or current windthrow episodes, often showed development of two or occasionally three peaks in the age-distribution. Mature, intact, non-susceptible stands also showed evidence of periodic disturbance leading to a limited age range. Age-class and diameter data suggest that individual stands are severely damaged about every 120-150 years and minor damage may occur at intervals of 20-30 years (Fig. 7 and 11), but several factors may cause the damage. Peak damage during stand development probably corresponds with stand maturity, and a narrow age range in windthrown stands suggests single significant events. Wardle and Allen (1983) suggest that recent windthrow and mortality followed major storms in 1968 and 1972, but other authors suggest that drought is generally more important in initiating plant disease outbreak (Manion, 1981; Skipworth, 1981; Kershaw, 1980; Gilmour, 1960; Jane and Green, 1984).

Table 6: Dates of important snowfalls and droughts reported in Canterbury since 1850 by Burrows and Greenland. (1979) and estimated dates of disturbance derived from direct dating of stems (Fig. 11) and size class data (Fig. 7).

Snowfalls	Drought	Dates of disturbance From data
1862	1859	1865
1888/9	1890	1888
1918	1919	1920
1945	1947	1954 (actual)
1973/4	1971/2	1970 (actual)
1978	1978	1981 (actual)

Several types of extreme events likely to cause severe forest damage may occur in the same or consecutive years and the occurrence of several different extreme events near suggested dates of forest damage do not permit identification of the causes of disturbances from climatic information alone (Table 6). The concurrence of extreme events arises because changes in atmospheric circulation patterns can result in periods of extreme events followed by wetter, more benign weather conditions (Burrows and Greenland, 1979; Jane and Green, 1984). Major storms or

droughts are infrequent events and appear to have a characteristic return period of about 30 years (Jane and Green, 1983a).

Key dates suggested for wind damage are similar to those found in other studies (Grant, 1981, 1984; Jane and Green, 1983b; Skipworth, 1981). This lends credence to suggestions of widespread climatic changes providing conditions suitable for disease or wind damage. However, explanation and linkage of dates would require precise chronologies and dendroclimatic data, both of which can only arise from intensive study.

Concurrent windthrow and episodes of natural mortality occur when trees are reaching maturity, suggesting some form of senescence syndrome as described by Mueller-Dombois *et al.*, (1980) in Hawaiian Ohaia forests and elsewhere (Mueller-Dombois *et al.*, 1983). Overstocking of stands through continuing growth but limited mortality appears to reach a point where basal areas may be twice normal and competitively-induced stresses may place a stand at severe risk to disease (Manion, 1981). Stress is in part contributed to by slower growth rates and by low root/shoot ratios so that responses to stress may also be limited. Stand damage is then triggered by climatic events. Minor events may occur at short intervals, but severe mortality follows and reaches a peak as trees reach maturity and the maximal height that a site allows, at about 100-120 years for mountain beech in this region (Wardle, 1984; p287).

Regeneration strategy

Seedlings greater than about 20 cm tall are generally rare in fully stocked mature mountain beech stands, and yet when the canopy opens regeneration is rapid and prolific, sometimes from established seedlings less than 20 cm tall and directly from seed (Wardle, 1970). Beech seed falls occur sporadically and are heaviest in a year following drought (Poole, 1955). Most stands examined already contained a carpet of seedlings less than 20 cm tall. These were in small clearings resulting from partial canopy damage or single tree mortality and were the main source of regrowth in wind damaged stands.

Major seed falls linked with occurrence of disease, drought and concurrent storm -damage in a year following drought are also an ecological advantage. Physiological and other studies by Wardle (1970) show that, once established, mountain beech seedlings are strong light demanders. Occurrence of widespread windthrow or disease outbreaks can then be looked upon as strategies for stand replacement by

massed regeneration.

In some areas, periodic disturbance followed by massed regeneration may be a means by which a mono-specific association is maintained on a site in competition with other major forest associations. For instance, in Wilberforce catchment a sharp ecotone occurs between mountain beech and cedar/Hall's totara (*Libocedrus bidwillii*/*Podocarpus hallii*) forests. In cedar/Hall's totara forest, small scale forest turnover by shade tolerant species such as Hall's totara and broadleaf (*Griselinia littoralis*) largely precludes mountain beech, whereas large scale windthrow followed by rapid regrowth of beech, repeated at relatively short intervals (100-150 years), ensures that cedar/Hall's totara forest is precluded from mountain beech areas. Periods of site stability in mountain beech forest however, could be expected to favour cedar/Hall's totara forest. In other areas less extreme examples of forest succession proceed through invasion of the current forest by species of a later stage, followed by mortality of current canopy species. Transition from kamahi (*Weinmannia racemosa*) to podocarp/tawa (*Beilschmeidia tawa*) forest and kamahiltawa to pure tawa can be seen as examples of this trend (McKelvey, 1963; Knowlton *et al.*, 1982).

Hence in mountain beech forests where no successional trend is present, stand development proceeds until height growth indicates stand maturity is reached. Then, if windthrow does not occur, natural mortality will reduce stand density, creating ideal conditions for stand replacement. Optimal basal area (that which all stands tend towards under natural conditions) of 50 m²/ha is close to 250 sq ft/acre arrived at as an optimal basal area for unthinned plantation crops such as radiata pine *Pinus radiata* plantations parasitised by *Sirex noctilio* in New Zealand (Beekhuis, 1953), and suggest that these are also critical values beyond which stand susceptibility increases sharply.

Similar critical basal areas have been reported more recently for Douglas fir (*Pseudotsuga menziesii*) plantations affected by *Phaeocryptopus gaeumanii* at Kaingaroa forest, New Zealand. In both cases stem density under natural conditions declines logarithmically with age, but sporadic insect attack regulates density in steps from basal area above an ideal to those considerably below it, in much the same way that natural beech stand density is moderated. Hence severe mortality can be expected to reduce basal area by one third and densities perhaps by 50% or more if the interval between disease outbreaks is large.

Large scale wind damage and mortality events are

currently common in New Zealand indigenous protection forests and have been variously reported over the last 50 years (Shaw, 1983a, b). Mortality has often resulted from climatic aberrations and been exacerbated by browsing from introduced animals (Grant, 1984). Such events have occurred in the following places: Mt Moehau (Moore and Cranwell, 1934); Pirongia (Clayton-Greene, 1977); Ruahine Ranges (Elder, 1965; Grant, 1984); Urewera National Park (Grant, 1963); Tararua Ranges (Esler, 1969); Mt Ruapehu (Skipworth, 1981); Mt Egmont (B.D. Clarkson, pers. comm); Westland (Chavasse *et al.*, 1955; Veblen and Stewart, 1982); Canterbury mountain beech forests (Wardle and Allen, 1983); Maruia red beech forest (Kershaw, 1980); Stewart Island (Veblen and Stewart, 1980); and many others in both North and South Islands for which no formal reports have been written. Similar repeated disturbances have been observed widely overseas and are recognised as important ecological processes (White, 1979; Miergroet, 1979). Consequently, relatively short term forest stability is probably the norm in New Zealand protection forests. However, in mountain beech, large scale disturbance appears to form an integral part of regeneration strategy.

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