REVIEW

Wind damage and response in New Zealand forests: a review

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Abstract: The literature on wind damage in New Zealand forests is reviewed to investigate how abiotic and biotic factors influence damage severity, damage type, and forest recovery. Winds that damage forests tend to result from extra-tropical depressions or from topographically enhanced westerly air flows. Severe wind damage can occur when wind speeds exceed c. 110 km/hr, although investigating the relationship between damage and wind speeds is difficult, as gusts, for which speed is usually unrecorded, are important. Damage is often quantified by estimates of area affected, with some authors detailing the size and species of damaged trees within a given area. Key abiotic factors that influence damage patterns are topographical position, edaphic conditions, and disturbance history. Important biotic factors are tree height, tree health, position of the tree within the stand, and species. Damage type (uprooting or breakage) is primarily controlled by canopy position and rooting depth. Forest responses to wind damage include sprouting, recruitment, release, and suppression, with the dominant mode of forest recovery being strongly influenced by the severity of damage, and the species composition of the stand. As noted in international literature on wind damage, a lack of consistent methods, combined with poor species and spatial coverage, makes identifying general trends difficult. Investigating the role of wind damage in New Zealand forests has focused to date on *Nothofagus* forests and plantations of exotic trees and few studies have investigated long term dynamics following wind disturbance events.

Keywords: wind damage; wind-throw; uprooting; forest disturbance; *Nothofagus*; edaphic conditions; topography; sprouting; recruitment; release; forest dieback

Introduction

The effect of wind on forests is determined by complex interplay between many biotic and abiotic factors (Everham and Brokaw, 1996). However, differences in methodologies among studies often obscure dominant patterns, and many studies are of a descriptive nature, with a focus on the type of wind damage and immediate vegetation responses, and no consideration of longer term effects (Everham and Brokaw, 1996; Whigham *et al*., 1999, Burslem *et al*., 2000).

The effects of wind damage on forests have been extensively reviewed in the international literature (Schaetzl *et al*., 1989; Everham and Brokaw, 1996; Webb, 1999; Whigham *et al*., 1999; Peterson, 2000; Ulanova, 2000), and considerable research has been conducted on the reconstruction of forest disturbance following wind damage (e.g. Boose *et al*., 1994, Doyle and Gorham, 1996; Foster, 1988b). Several generalisations regarding wind damage appear to be valid across a diverse range of forest communities (Everham and Brokaw, 1996; Peterson, 2000; Webb, 1999). Topography and soil characteristics are often the key abiotic factors influencing wind damage, and tree density, canopy height variability, tree size, and species (including differences in rooting depth and wood strength) are usually the key biotic factors (Peterson, 2000). The most consistent finding of previous reviews is greater damage with increasing tree size (Everham and Brokaw, 1996; Peterson, 2000; Webb, 1999). The relative height of trees, in comparison with surrounding vegetation, is also likely to be an important factor (Peterson, 2000). Accompanying this trend, due to the correlation between tree size and age, is increasing damage with age (Everham and Brokaw, 1996; Peterson, 2000). Unlike fire, wind damage often causes low levels of mortality. This leads to forest regeneration often being dominated by the recovery of damaged stems and by release, rather than the recruitment of new individuals (Everham and Brokaw, 1996; Webb, 1999). This review seeks to answer whether these generalisations apply to New Zealand forests, or if the literature currently available allows for other generalisations to be made.

The literature on wind damage in New Zealand forest has not previously been reviewed in detail, and forms the basis of this paper (Table 1). Relevant theses, reports, and papers that did not focus on the effects of a known storm, or that covered wind damage indirectly, are also reviewed but not listed in Table 1. The literature reviewed covers storms between 1898 and 1988. The majority focus on damage to native forests, and descriptions of the storm of 1936 and Cyclone Bernie (1982) account for almost half of all papers published. Literature focused on wind effects in forests composed of exotics is included, as several of these sources included discussion of predisposing factors that increased wind damage.

To gain a more detailed understanding of the role strong winds play in New Zealand forests, the review investigates the following aspects of wind damage and forest response: 1) the relationship between wind speed and severity of damage; 2) the influence of abiotic factors on wind damage; 3) the influence of biotic factors on wind damage; 4) factors that influence damage type; 5) forest responses to wind damage (recruitment from seed, release, suppression, repression, sprouting).

For the purposes of this review, wind damage is defined as injury to the tree caused by strong winds, resulting in canopy opening; wind-throw is defined as trees being felled by wind either through uprooting or stem breakage; and uprooting is defined as trees being felled with stem and root plate intact. Measurements and units are converted to metric where appropriate. Botanical nomenclature follows Nicol (1997).

The wind disturbance regime in New Zealand

New Zealand's weather, in a global context, is subject to considerable variability (Fitzharris, 2001), and this variability results in North Island forests being frequently disturbed by climatic extremes such as severe winds, flooding, drought, and heavy snowfalls. Strong winds are probably the most widespread

Table 1. Forest damaging winds in New Zealand: key references, year of wind damage occurrence, forest type, and location

Reference	Year	Forest type	Location
Hosking and Hutcheson, 1998	1982	*Nothofagus*	Kaimanawa Range, Central North Island. Whirinaki Forest Park, Central North Island
Jane, 1986	1981	*Nothofagus*	Lake Ohau - Lake Sumner, Canterbury, South Island
Martin and Ogden, 2005	1982	*Nothofagus*	Mount Ruapehu, Central North Island
Norton and Wilson, 1981	1979	*Nothofagus*	Arthurs Pass, South Island
Reid, 1948	1938	*Nothofagus* podocarp-broadleaf	Tararua Range (Fields Track), southern North Island
Shaw, 1983b	1982	*Nothofagus*, podocarp-broadleaf	Urewera National Park, eastern North Island
Zotov *et al*., 1938	1936	podocarp-*Nothofagus*	Tararua Range, southern North Island
Foster, 1931	1898	podocarp-*Nothofagus*	Reefton, Nelson Province, northern South Island
Thomson, 1936b	1936	podocarp-broadleaf	Tararua Range (Mangahao/Ohau), southern North Island
Ogden *et al*., 1991	1986, 1988	podocarp-broadleaf	Hauhungatahi, Central North Island
Mason, 1950	1936	podocarp-broadleaf	Tararua Range (Waiopehu-Makaretu), southern North Island
Dawson, 1970	1968	coastal broadleaf	Kapiti Island, south western North Island
Conway, 1959	1959	kauri-podocarp-broadleaf,	Northland, northern North Island
Chandler, 1968	1950's	*Pinus radiata* plantation	Tapanui District (South Island), south Otago, South Island
Conway, 1959	1959	*Pinus radiata* plantation	Northland, northern North Island
Irvine, 1970	1963, 1968	*Pinus radiata* plantation	Nelson, northern South Island
Littlejohn, 1984	1982	*Pinus radiata* plantation	Central North Island
Prior, 1959	1945	*Pinus radiata* plantation	Canterbury, South Island
Wilson, 1976	1975	*Pinus radiata* plantation	Canterbury, South Island

disturbance agent in many New Zealand forests. While site and vegetation characteristics may result in a forest stand being particularly vulnerable to wind damage, studies of ex-tropical cyclones such as the storm of 1936 (Thomson, 1936a; Zotov *et al*., 1938) and Cyclone Bernie in 1982 (Shaw, 1983a) suggest that all North Island forests are periodically affected by extreme wind events. Major ex-tropical cyclones have a recurrence interval of c. 10 years and have a key role in modifying forest structure and pattern (Shaw, 1983a). Prevailing winds also play an important role in New Zealand forests; New Zealand has an oceanic position and lies astride the circumpolar westerly wind-belt (Brenstrum, 1998). Vegetation in many west-facing areas is characterized by a dense, wind-shaped canopy (Wardle *et al*., 1973). In these environments wind pruning by small branch breakage is frequent but catastrophic destruction is likely to be rare due to structural adaptation to wind.

Cyclical changes in climate influence the frequency, severity and direction of winds (Basher and Xheng, 1995; de Lange and Gibb, 2000; Fowler *et al*., 2000). Cyclone frequency in the south-west Pacific varies with changes in oceanic and atmospheric conditions, associated with variations of El Niño-Southern Oscillation (ENSO) (Basher and Xheng, 1995). Cyclones tend to form further west in the Pacific when the Southern Oscillation is in its negative phase (La Nina). As cyclones usually track south eastwards across the Pacific, cyclones formed during La Nina are more likely to track over or close to New Zealand. Additionally, the lessening of westerly winds during La Nina can steepen the latitudinal track of cyclones and increase cyclone incidence at lower latitudes (Sinclair, 2002). In contrast, during periods dominated by El Niño, south westerly winds prevail (Fowler *et al*., 2000). Under these conditions, the incidence of catastrophic wind-throw may lessen; there is greater dominance of prevailing winds to which trees are accustomed and reduced incidence of ex-tropical cyclones in the New Zealand region.

Wind speed and severity of damage

Nine papers quantitatively described the wind speeds recorded during storm events (Table 2). The storm of 1936, responsible for severe damage in the southern North Island, was estimated to have wind speeds of 110–160 km h^{-1} (Thomson, 1936a); a cyclone in 1959 caused winds of up to 175 km h^{-1} over Northland (Conway, 1959); and the highest mean wind speed recorded during Cyclone Bernie was 114 km h^{-1} (Revell and Ward, 1983). Severe winds may also result from westerly air flows passing over mountain ranges, with gales exceeding 240 km h^{-1} several times per year in

Table 2. The quantification of intensity and damage for wind events in New Zealand forests

Reference	Intensity	Quantification of damage
Chandler, 1968	severe	Wood volume loss per acre
Conway, 1959	up to 175 km/h	Number of uprooted trees, wood volume loss
Dawson, 1970	gusts to 170 km/h	% contribution of fresh litter for each species
Foster, 1931	heavy gale	Number of wind-thrown trees within a given area
Hosking and Hutcheson, 1998	-	% of canopy removed
Irvine, 1970	strong winds, severe gale	Estimates of forest area destroyed and wood volume loss
Littlejohn, 1984	frequent >130 km/h	Estimates of forest area destroyed and wood volume loss
Martin and Ogden, 2005	-	Number, size and species of uprooted trees within a given area
McCracken, 1979	>240 km/h	-
Norton and Wilson, 1981	severe	Number, size and species of uprooted trees within a given area
Ogden *et al*., 1991	-	Gap area, root mound area, and basal area loss per hectare; dimensions of fallen trees
Prior, 1959	gusts to 135 km/h	Estimates of forest area destroyed and wood volume loss
Revell and Ward, 1983	114 km/h (mean wind speed)	-
Shaw, 1983b	170 km/h	% of forest with severe, moderate or minor damage
Steel, 1989	-	Basal area and density loss per ha for main tree species
Thomson, 1936a	110-160 km/h	Estimate of forest area destroyed
Wilson, 1976	Gusts to 170 km/hr	Estimates of forest area destroyed and wood volume loss

upland Canterbury, South Island (McCracken, 1979). The remaining authors simply described wind speeds as severe (e.g. Chandler, 1968; Norton and Wilson, 1981), and concentrate on the forest damage rather than the cause.

A major difficulty in determining wind speed thresholds for forest disturbance is the variability in wind speeds over small spatial scales, due to factors such as topography and local meteorological changes (Everham and Brokaw, 1996). Few New Zealand-based studies indicated the distances between the study sites and the location where wind speed measurements were made, and this has also been noted in the international literature (Everham, 1995). The most damage during a storm may be caused by wind gusts, making the relationship between wind speed and damage difficult to determine (Everham and Brokaw, 1996). Individual wind gusts, which for two overseas studies had ratios of maximum gusts to mean wind speed of 1.3 (Hsu, 2002) and 1.75 (Burt and Mansfield, 1988) may significantly exceed mean wind speeds. Gusts during Cyclone Bernie reached 170 km h^{-1} at East Cape, and 157 km h^{-1} at New Plymouth Airport (Revell and Ward, 1983), giving ratios of 1.5 and 1.4 respectively.

The most frequent method of quantifying damage was the estimation of area affected. Estimates of area damaged by storms range from two hectares (Norton and Wilson, 1981) to more than 12 000 hectares of damage to *Pinus radiata* plantations from Cyclone Bernie (Littlejohn, 1984). Shaw (1983a) assessed the significance of Cyclone Bernie damage to mixed-podocarp-beech forest in Urewera National Park. By examining aerial photographs, he estimated the percentage of the forest with severe, moderate, or minor damage, and found that 20% of the forests in the park were visibly affected by this event, with severe canopy destruction of areas up to 40 hectares. Damage was also commonly quantified by recording the species, diameter at breast height (dbh) which, when stated, was either 1 m (Martin and Ogden, 2005) or 1.35 m (Steel, 1989) in height, and number of uprooted trees within a given area (Norton and Wilson, 1981; Steel, 1989; Martin and Ogden, 2005). Conway (1959) simply counted the number of uprooted kauri within different forest areas.

Inter-site comparisons of wind damage assessments for New Zealand studies are hampered by the diversity of methods employed. Groups of studies with similar methods, such as those that recorded species, diameter and number of uprooted trees within a given area, are more suited for comparison, but even for these studies, a lack of 'control' sites is apparent. Similar difficulties in damage assessments are highlighted in other reviews.

Influence of abiotic factors on wind damage

Topographical position

Variation in damage severity is often attributed to changes in topography (Table 3). Wind speeds usually peak above ridge crests, and the leeward side of hills experience increased turbulence (Finnigan and Brunet, 1995). However, there is no consistency in the literature as to which topographical positions are more or less prone to wind disturbance; wind damage can be either more or less severe on lee slopes and in valleys (Everham and Brokaw, 1996; Webb, 1999).

The most frequent New Zealand finding was increased severity of damage on lee slopes for plantation

Table 3. The influence of topographical position on wind damage in various New Zealand forest types (+ represents increased damage severity; – represents decreased damage severity).

Reference	forest type	lee slopes	slopes	ridges	valleys	gully heads	plateaus
Jane, 1986	*Nothofagus*	+					
Reid, 1948	*Nothofagus*, podocarp-broadleaf			+			
Shaw, 1983b	*Nothofagus*, podocarp-broadleaf	+		+	+		
Zotov *et al*., 1938	podocarp-*Nothofagus*		+		+		
Thomson, 1936b	podocarp-broadleaf		+				
Mason, 1950	podocarp-broadleaf		+	+			
Dawson, 1970	coastal broadleaf	-		+			
Conway, 1959	plantation					+	+
Irvine, 1970	plantation	+	+			+	
Littlejohn, 1984	plantation	+					
Chandler, 1968	plantation	+			+		
Somerville, 1995	plantation	+					
Wilson, 1976	plantation			+			

forests (Chandler, 1968; Irvine, 1970; Littlejohn, 1984; Somerville, 1995), *Nothofagus* forest (Jane, 1986), and mixed podocarp-beech forest (Shaw, 1983b). One study concluded that *Nothofagus* forests on lee slopes protected from prevailing winds were particularly susceptible to wind damage (Jane, 1986). However, Cyclone Giselle in 1968 caused less damage to coastal forest on lee slopes on Kapiti Island (Dawson, 1970). Greater wind damage may also occur where winds increase as valleys narrow (Somerville, 1995), with an accompanying decrease in damage where winds dissipate as valleys broaden (Jane, 1986). Ogden *et al*. (1991) recorded greater severity of damage in subalpine areas (17.6 tree-falls ha^{-1}) compared to adjacent montane forest (10.3 tree-falls ha^{-1}).

Topography may also influence tree vulnerability indirectly by governing tree growth rates and the nature of the canopy. In Canterbury, *Nothofagus solandri* forests on windward slopes were less vulnerable to wind damage as they typically grew more slowly, so that stands were comprised of smaller, more densely spaced trees, and the canopy was often wind shaped due to small branch breakage. In contrast, trees on lee slopes were regarded as more vulnerable as they were faster growing with associated lower wood density. They were also larger and taller, and canopy height was more variable (Jane, 1986).

The effect of topography on wind damage is often confounded with changes in soil type, tree architecture, and vegetation characteristics (Webb, 1999; Whigham *et al*., 1999). Whigham *et al.* (1999) regarded topographic position as influencing root anchorage, which is also influenced by edaphic conditions such as soil moisture and soil structure. They predicted that forests on slopes will have higher rates of damage only if soils are unstable or rooting is shallow.

Edaphic conditions

Everham and Brokaw (1996) categorized the main edaphic factors that interact with wind damage as soil depth, moisture content, and texture. These factors influence the stability of the root plate, and therefore whether damage is stem uprooting or breakage. There is common agreement that trees growing on wet soils are more vulnerable to wind-throw (Table 4). This is attributed to a reduction in root anchorage, and, if the soil has a high water table, also to restriction of rooting depth (Everham and Brokaw, 1996; Peterson, 2000). Storms accompanied by extreme rainfall have been documented as causing greater severity of forest damage (Everham and Brokaw, 1996). The relationship between soil type and wind-throw vulnerability is more ambiguous. Jane (1986) found an absence of *Nothofagus* wind-throw on ridgeline or rocky sites with little or no soil, but no relationship between other soil types and wind-throw vulnerability. However, within *Pinus radiata* plantations, one study attributed greater severity of damage to growth on gravel soils, which contained soil nutrients near the surface, thereby encouraging shallow rooting (Irvine, 1970), and a further study found no relationship between soil depth and damage severity, but only compared soils between 45 and 80 cm deep (Chandler, 1968).

Disturbance history

New Zealand studies often reported increased severity of wind damage to indigenous and plantation forests that had been recently disturbed (Table 4). Trees are more likely to be damaged if a previous disturbance has exposed formerly ‘stand interior’ trees on a stand edge (Prior, 1959; Wardle, 1984; Jane, 1986). However, this effect may be temporary, as stand edge trees can develop a form resistant to wind-throw (Wardle, 1984; Jane, 1986) and a larger root system (Chandler, 1968; Wardle, 1984). Thus, stand interiors can be wind-thrown by a storm leaving the edges intact (Littlejohn, 1984; Carter, 1989). Past disturbances can also lead to the development of dense, even-aged cohorts (Wardle, 1984; Ogden, 1988) which reach maturity, and therefore peak vulnerability, simultaneously. Severe damage is

Table 4. The influence of edaphic conditions and disturbance history on wind damage in various New Zealand forest types (+ represents increased damage severity; - represents reduced damage severity).

Reference	forest type	wet soils	gravel soils	peaty soils	rocky soils	recently disturbed
Jane, 1986	*Nothofagus*				-	+
Wardle, 1984	*Nothofagus*	+				
Ogden *et al*., 1991	podocarp-broadleaf	+		+		+
Rogers, 1999	podocarp-broadleaf	+				
Conway, 1959	kauri-podocarp-broadleaf					+
Carter, 1989	plantation					+
Chandler, 1968	plantation	+				+
Prior, 1959	plantation	+				+
Irvine, 1970	plantation	+	+			+
Littlejohn, 1984	plantation					+
Wilson, 1976	plantation	+				+

therefore typically episodic in nature, occurring when vulnerable cohorts, synchronised by past storm events, are subjected to extreme winds. The significance of infrequent, extreme events is highlighted by Ogden *et al.* (1991). They found that during three years on Mount Hauhungatahi, central North Island, 75% of tree deaths were caused by only two storm events.

Recently disturbed stands can have increased or decreased vulnerability to wind damage, depending on the nature of the disturbance and its effect on stand structure. If a disturbance increases canopy height variability, turbulent air flow and the potential for further damage are enhanced. Alternatively, if a disturbance results in a more even canopy, for example by the uprooting of emergents, wind resilience of the stand may be increased (Everham and Brokaw, 1996). If disturbance removes the vulnerable individuals within a stand, it may then experience a period of minimal disturbance, due to the decreased vulnerability of the surviving individuals (Everham and Brokaw, 1996; Whigham *et al*., 1999).

The influence of biotic factors on wind damage

Tree size

Within New Zealand *Nothofagus*-dominated forests, stands become increasingly vulnerable after the crowns of trees merge to form a canopy (Wardle, 1984). There appear to be relationships between tree size and vulnerability (Table 5). Jane (1986) found no trees less than 18 m tall in wind-thrown *N. solandri* var. *cliffortioides* stands, and he regarded this height as the critical threshold above which the stands became highly vulnerable. Jane (1986) estimated this height is reached when the trees are 100–130 years old and 20–30 cm dbh. Estimates of peak age and size vulnerability are probably species-specific; for example, a storm in 1898 near Reefton uprooted shallow rooted *N. fusca* trees c. 1 m dbh (Foster, 1931). The relationship between tree size and wind-throw vulnerability for non-*Nothofagus* forest types is poorly documented. Within exotic plantations, *Pinus radiata* becomes highly vulnerable to wind-throw when height exceeds 12–14 m and age exceeds 10 years (Prior, 1959; Wilson, 1976; Carter, 1989; Studholme, 1995). Strong winds may cause young *Pinus radiata* trees to be blown into lean without uprooting them (Conway, 1959; Wilson, 1976).

Height is probably of greater importance in determining vulnerability to wind damage than age. Height thresholds are generally 12–18 m, for both plantation and indigenous forests, while the age range of vulnerable stands varies widely. This is presumably because tree age is an indirect factor, wind vulnerability instead being directly influenced by age related trends such as tree size, structural soundness, and vigour (Everham and Brokaw, 1996; Peterson, 2000).

Tree health

Several authors noted a relationship between declining tree health and vulnerability to wind damage. Conway (1959) assessed damage from the 1959 cyclone in Northland and found that many of the uprooted kauri (*Agathis australis*) had unsound or hollow butts, and Foster (1931) described uprooted *N. fusca* as being "over mature", implying the trees had declined in health due to old age. However, neither of these studies assessed the health of trees that were unaffected by the storms;

Table 5. The influence of tree size and form on wind damage in various New Zealand forest types (+ represents increased damage severity; 0 represents no effect).

Reference	forest type	larger diameter	older stems	taller stems	stems in canopy
Jane, 1986	*Nothofagus*	+		+	
Martin and Ogden, 2005	*Nothofagus*	+		+	
Norton and Wilson, 1981	*Nothofagus*	+			
Steel, 1989	*Nothofagus*	+			
Reid, 1948	podocarp-broadleaf				+
Foster, 1931	podocarp-*Nothofagus*	+	+		
Zotov *et al*., 1938	podocarp-*Nothofagus*	0	0	0	
Conway, 1959	kauri-podocarp-broadleaf	+	+	+	
Dawson, 1970	coastal broadleaf		+	+	+
Carter, 1989	plantation		+		
Chandler, 1968	plantation			+	
Irvine, 1970	plantation		+	+	
Prior, 1959	plantation			+	
Studholme, 1995	plantation		+	+	
Wilson, 1976	plantation			+	

therefore it is possible that both wind thrown trees and surviving trees were equally characterised by stem rot or over-maturity and that other factors resulted in the tree falls. There is also some conflicting evidence that once a tree has declined in health to the extent that its foliage load is significantly reduced, or indeed that it is dead, vulnerability to wind decreases. Thomson (1936b) assessed damage in the Ohau Valley, Tararua Range, after the 1936 storm and noted that in an area of severe damage "nearly all over-mature and dead rimus (*Dacrydium cupressinum*) remained upright". He suggested that the cause of this was reduced wind resistance due to the development of a stag-headed crown and loss of foliage. He implied that few rimu in this state were felled by the storm, but presented no quantitative data about the species composition or health of the destroyed trees.

Trees with stem or root rot are more vulnerable to damage (Everham and Brokaw, 1996; Peterson, 2000; Webb, 1999). However, separating the role of tree size and health is difficult, as trees often begin to senesce and lose vigour upon reaching maturity. The reported decrease in vulnerability of over-mature or dead rimu, if indeed it is a valid finding, is difficult to discern from possible influences of tree size or species. If the surviving rimu had sound trunks, it is possible that survivorship conformed to a model proposed by Everham and Brokaw (1996) where large but structurally sound trees have reduced mortality due to a preconditioning to wind exposure.

Species

Species appear to differ in their vulnerability to wind damage. Presumably there is a continuum of vulnerability, and variation associated with age and species association also. Thus the dichotomy presented in Table 6 is a first approximation only.

Nothofagus spp. may be more vulnerable than podocarps to wind damage; Foster (1931) found that in Nelson Province, areas of *Nothofagus* were severely damaged by gales but *D. cupressinum* escaped damage, and Wardle (1984) stated that in mixed forests *Nothofagus* are more susceptible to wind-throw than the podocarps.

A cyclone in 1959 caused considerable damage to Northland kauri-podocarp-broadleaf forest. Using conservative estimates of wood volume loss, the proportional loss of kauri to the combined total for *D. cupressinum*, *Prumnopitys ferruginea* and *Podocarpus totara* was 18:1 (Conway 1959). This led the author to regard *Agathis australis* as a species vulnerable to wind damage. The study did not present the composition of the forests in which the damage occurred, and this casts doubt on the conclusions drawn. The author attributed the higher proportional loss of kauri to its emergent nature, and trees being knocked down by falling dominants. However, the data presented failed to exclude the possibility that more kauri were uprooted simply because they accounted for a greater proportion of the trees in the stand.

One podocarp, *D. cupressinum,* is considered less susceptible to wind damage than other species in wind-damaged areas (Foster, 1931; Thomson, 1936b; Zotov *et al*., 1938; Mason, 1950). Both Foster (1931) and Zotov *et al.* (1938) attributed its resistance to its strong root system; but its form, with pendulous branches, may also lessen wind effects (Zotov *et al*., 1938).

The susceptibility to wind damage of 242 species in 61 families was reviewed by Everham and Brokaw (1996). No New Zealand species were included, but the review provided further evidence for the susceptibility of *Pinus radiata* and *Salix* spp., and regarded the four exotic species noted by New Zealand authors (Table 6) as resistant as suffering high or intermediate levels of damage. Everham and Brokaw identified two possible trends: greater vulnerability of conifers than angiosperms, and greater vulnerability of species that characterize early successional stages of forest development. Whether these hold true for New Zealand forests could not be determined from the literature reviewed, although the scanty evidence suggests that some New Zealand conifers are relatively wind-resistant. Assessments of interspecies differences

Table 6. The resistance and susceptibility of some New Zealand forest species and some exotic species to wind damage in New Zealand. *denotes exotic species.

Resistant species	Susceptible species
Cyathea medullaris [1]	*Agathis australis* [7]
Dacrydium cupressinum [1,2,3,4]	*Cordyline indivisa* [5]
Griselinia littoralis [5]	*Halocarpus biformis* [5]
Metrosideros robusta [3]	*Kunzea ericoides* [6]
Myrsine salicina [6]	*Libocedrus bidwillii* [5]
Nothofagus (overmature) [1]	*Metrosideros robusta* [6]
Podocarpus hallii [5]	*Nothofagus fusca* [2]
Podocarpus totara [7]	*Nothofagus solandri* var. *cliffortioides* [5,12]
Prumnopitys ferruginea [7]	*Phyllocladus alpinus* [5]
Pseudopanax spp.[5]	
Rhopalostylis sapida [1]	
Weinmannia racemosa [6]	
* *Eucalyptus* (ash group) [8]	**Cupressus macrocarpa* [1]
**Pinus nigra* [9]	**Pinus contorta* [9]
**Pinus ponderosa* [9]	**Pinus muricata* [9]
**Pseudotsuga menziesii* [9,10,11]	**Pinus radiata* [1,7,8,10,13]
	**Salix* spp. [1]

[1]Thomson, 1936b; [2]Foster, 1931; [3]Zotov *et al*., 1938; [4]Mason, 1950; [5]Steel, 1989; [6]Dawson, 1970; [7]Conway, 1959; [8]Carter, 1989; [9]Prior, 1959; [10]Studholme, 1995; [11]Wilson, 1976; [12]Jane, 1986; [13]Irvine, 1970.

in wind damage susceptibility are limited by the lack of studies that sampled forest composition prior to the storm (Webb, 1999).

Factors influencing damage type

Several authors explained damage type with regard to stem size. Thomson (1936b) reported that small stems not uprooted by the 1936 storm were broken by the fall of larger trees, and Stewart *et al.* (1991) found that *N. menziesii* were often broken by the fall of larger *N. fusca*. Ogden *et al.* (1991) found that for every tree uprooted by storms on Hauhungatahi, a mean of 1.3 tree-sized stems (>10 cm diameter), and in some cases up to six stems, were broken by the fall of canopy trees. This may be an underlying explanation for species differences in damage type, according to whether a species most commonly has a canopy or subcanopy growth form.

However, damage type is also influenced by edaphic conditions. Montane *N. menziesii* and *N. solandri* var. *cliffortiodes*, growing on shallow, wet soils, are generally uprooted rather than bole snapped (Ogden *et al*., 1996). In contrast, Jane (1986) noted that montane *N. solandri* var. *cliffortiodes* on rocky soils were felled by stem breakage rather than uprooting. Greater rooting depth increases the incidence of bole snap relative to the number uprooted, and some tree plantation management regimes in Canterbury encourage shallow rooting, in order to decrease wood damage when trees are felled by wind (Studholme, 1995). Trunk form also influences damage type, with buttressed species, for example *N. fusca*, tending to be felled by bole snap (Ogden *et al*., 1996).

The New Zealand studies suggest similar findings to other reviews regarding factors that influence damage type. The breaking of small stems by the fall of larger trees is commonly reported in the international literature (Everham and Brokaw, 1996), but tree fall by stem snap or uprooting for stems of similar size appears to be strongly influenced by species differences and edaphic conditions (Everham and Brokaw, 1996; Whigham *et al*., 1999).

Characteristics of forest response to wind damage

The responses of forest to severe wind damage differ according to site and species composition, but often include sprouting from damaged stems, recruitment of new individuals, release of individuals previously experiencing intense competition, and repression of canopy species by vines, herbs, and shrubs (Schaetzl *et al*., 1989; Everham and Brokaw, 1996).

Sprouting

Some New Zealand canopy and sub-canopy angiosperms are capable of sprouting when uprooted (Table 7). Tree ring analysis of *N. solandri* var. *cliffortioides* uprooted by Cyclone Bernie showed a dramatic decline in diameter growth rate in the growing season following the storm, but then an increase in growth rate to former levels (Martin and Ogden, 2005); this was interpreted by the authors as a direct result of sprouting, with subsequent canopy attainment. In New Zealand, the only conifer species recorded as sprouting following uprooting is *Phyllocladus alpinus* (Ogden *et al*., 1991). Sprouting ability may not be related to shade tolerance for New Zealand species; species recorded as sprouting included *Beilschmiedia tawa*, a shade-tolerant, late-successional species (Smale *et al*., 1997), and *Nothofagus solandri* var. *cliffortioides*, which is shade-intolerant (Ogden, 1988). The tendency for broken stems to sprout more than uprooted stems (Everham and Brokaw, 1996) is also not evident for the New Zealand literature. Sprouting from both uprooted and snapped stems was noted following the 1936 storm in the Tararua Range, and with the exception of the conifers, if part of the root system of fallen trees remained anchored in the ground, new shoots were produced by most species (Thomson, 1936b).

Sprouting can be an important mode of recovery in tropical (Everham and Brokaw, 1996) and temperate forests (Schaetzl *et al*., 1989; Webb, 1999), but Whigham *et al.* (1999) questioned the importance of sprouting in tropical forests, on the basis that while many damaged stems produce new growth, in many forests few trees may effectively regain canopy positions in the long term due to the initiation of disease by the wind damage, and associated stem destabilisation. The ability of some of New Zealand's most widely distributed species to sprout indicates the potential importance of this recovery pathway. However, more detailed studies are needed to determine the persistence of sprouted stems in the long term, and their relative importance compared with recruitment and release.

Recruitment

Recruitment is defined in a variety of ways and is sometimes regarded as growth from young plants, regardless of whether they were present as seeds or seedlings prior to a disturbance (e.g. Brokaw and Walker, 1991). For the purposes of this review recruitment is defined as the establishment of new individuals from seed or spores whether present in a soil seed bank or dispersed to an area post disturbance (Marks, 1974; Whigham *et al.*, 1999; Burslem *et al*., 2000).

Internationally, recruitment is often regarded as being a minor regeneration pathway following wind damage, with the importance of recruitment highly dependant on

Table 7. Sprouting and recruitment of New Zealand forest species following wind damage. Species underlined occur in both lists, conifers marked with *.

	Sprouting	Recruitment
Potential canopy species		
	Beilschmiedia tawa [1]	*Beilschmiedia tawa* [1,4]
	Elaeocarpus dentatus [2]	*Elaeocarpus dentatus* [1,4]
	Metrosideros kermadecensis [3]	*Knightia excelsa* [1]
	Metrosideros robusta [2]	*Libocedrus bidwillii* [9,10,11] *
	Nothofagus menziesii [4]	*Nothofagus* spp. [2]
	Nothofagus solandri var. *cliffortioides* [5]	*Nothofagus fusca* [4,12,13]
	Nothofagus spp. [2]	*Nothofagus menziesii* [4,14]
	Phyllocladus alpinus [6] *	*Nothofagus solandri* var. *cliffortioides* [5, 13,15]
	Weinmannia racemosa [1, 2, 4, 6]	*Podocarpus hallii* [9] *
		Prumnopitys ferruginea [1,4] *
		Weinmannia racemosa [8, 14]
Short-lived gap species, often in the subcanopy		
	Coprosma spp. [1]	*Aristotelia serrata* [2]
	Melicytus ramiflorus [2]	*Ascarina lucida* [7]
	Myrsine salicina [2]	*Carpodetus serratus* [8]
	Pseudopanax arboreus [1]	*Fuchsia excorticata* [2]
	Pseudopanax crassifolius [1]	*Hedycarya arborea* [1]
	Schefflera digitata [1]	*Melicytus ramiflorus* [8]
		Myrsine salicina [1,4]
		Pseudowintera axillaris [1,4]
		Quintinia acutifolia [8]
Ground cover species capable of suppressing regeneration		
		Histiopteris incisa [7, 8]
		Hypolepis millefolium [7]
		Hypolepis sp. [8]
		Paesia scaberula [7,8]
Tree ferns		
		Cyathea smithii [7]
		Dicksonia squarrosa [7]

[1]Mason, 1950; [2]Thomson, 1936b; [3]Parkes, 1984; [4]Reid, 1948; [5]Martin and Ogden, 2005; [6]Ogden *et al*., 1991; [7]Adams and Norton, 1991; [8]Reif and Allen, 1988; [9]Wardle, 1978; [10]Veblen and Stewart, 1982 ; [11]Norton, 1983; [12]Foster, 1931; [13]Norton and Wilson, 1981; [14]Stewart, 1986; [15]Jane, 1986.

the species composition of the damaged forest, and the size of the canopy gaps formed (Everham and Brokaw, 1996; Webb, 1999; Whigham *et al*., 1999). However several studies, in both temperate and tropical forests, have clearly demonstrated that forest recovery following wind damage was dominated, or at least significantly contributed to, by the growth of new individuals (Foster, 1988; Burslem *et al*., 2000; Tanner and Bellingham, 2006). The importance of recruitment may be greater where winds cause high rates of mortality (Whigham *et al*., 1999).

In New Zealand wind damaged forests, the species recorded as recruiting are highly reflective of the locality and species compositions of the study sites (Table 7). *Nothofagus* were the most frequently recorded species, but this is to be expected as many studies were located in this forest type. Additionally, many of the records are derived from assessments of wind damage in southern North Island podocarp-broadleaf forest. No studies have yet investigated recruitment following wind damage in warm temperate forests.

Of the *Nothofagus* species, *N. fusca* (Foster, 1931; Norton and Wilson, 1981), *N. menziesii* (Reid, 1948), and *N. solandri* var. *cliffortioides* (Norton and Wilson, 1981; Jane, 1986; Martin and Ogden, 2005) are noted as recruiting abundantly in wind damaged areas. The absence of *N. solandri* var. *solandri* and *N. truncata* from this list is probably attributable to these species being absent from the study areas. Exposed mineral soil, brought to the surface by tree uprooting, is a substrate favourable to *Nothofagus* recruitment (Reid, 1948), but Stewart (1986) notes that following wind-throw in a

Nothofagus-broadleaf forest, all *Weinmannia racemosa* and the majority of *Nothofagus* had established on woody debris, such as logs, stumps, and root plates. Thus wind-throw creates a variety of microsites favourable to the recruitment of *Nothofagus* and *Weinmannia*. The ability of *Nothofagus* and *Weinmannia* to recruit and sprout following wind damage, results in these two genera having populations that are resilient to wind damage. In podocarp-broadleaf forest, some typically late-successional species may also be able to recruit successfully following severe wind damage, for example Mason (1950) and Reid (1948) observed the recruitment of *Beilschmiedia tawa* and *Elaeocarpus dentatus* in storm damaged areas in the Tararua Range. Both these species also sprout from fallen stems.

Recruitment in wind damaged forest rarely conforms to the characteristic secondary successions for a locality. Catastrophic wind, in contrast to disturbances such as fire, often results in low levels of mortality and thick leaf litter layers (Everham and Brokaw, 1996). This limits the establishment of early-successional species that are less able to compete with vegetation that survived the disturbance, and often require bared soil surfaces for germination. Greater dominance by early-successional species is expected if trees are predominantly felled by uprooting than by bole snap, as the upturning of root plates causes soil mixing and creates microsites suited for their establishment (Schaetzl *et al*., 1989). In areas damaged by the storm of 1936, the recruitment of late-successional species such as *Beilschmiedia tawa* and the relative abundance of *Nothofagus* germination on upturned soil, may be attributed to nature of wind disturbances, which often leave soils and the lowest vegetation layers relatively intact.

Shrub, liana and ground tier expansion

Mason (1950), in an assessment of growth 11 years after the 1936 storm, noted significant expansion of the liana species *Freycinetia baueriana*, *Metrosideros fulgens*, and *Rubus cissoides*. Fern species noted as more abundant in wind damaged areas included *Paesia scaberula* and *Hypolepis* spp. (Reif and Allen, 1988; Adams and Norton, 1991), *Histiopteris incisa* (Mason, 1950), *Dicksonia squarrosa* (Adams and Norton, 1991) and *Cyathea smithii* (Adams and Norton, 1991). No New Zealand studies follow the long term development of lowland forest following wind damage. Therefore the long-term effects of shrub, liana and ground tier expansion on tree growth following the 1936 storm are unknown.

The expansion of ground tier layers, resulting in the repression of woody vegetation growth, has been documented as occurring in other temperate and tropical regions (Everham and Brokaw, 1996; Whigham *et al*., 1999). Ferns, grasses, shrubs, herbs, and vines may all cause forest repression, but in most cases the proliferation of ground tier layers only delays forest development (Whigham *et al*., 1999). Therefore the expansion of shrub and ground tier layers immediately after a disturbance event can not be interpreted as the onset of repression, and longer term studies of wind damaged sites are needed to investigate its occurrence.

Release and suppression

New Zealand literature regarding the initiation of release or suppression after wind damage is sparse (Table 8), and a more general consideration of tree responses to various disturbance events is needed, to investigate the possible role of wind damage in causing changes in growth rates.

Release, defined as an increase in growth rate of plants due to the removal of competing vegetation (Everham & Brokaw, 1996; Whigham *et al*., 1999), is recognized as an important mode of forest recovery following wind damage in temperate (Webb, 1999) and tropical forests (Everham & Brokaw, 1996; Whigham *et al*., 1999). Wind damage often removes the canopy, leaving the understorey relatively unscathed. In New Zealand *Nothofagus*-dominated forests, the presence of advanced regeneration in the form of a 'seedling pool' is well established (Wardle, 1970; June, 1974; Jane, 1986; Ogden *et al*., 1996). Jane (1986) found that the majority of *Nothofagus solandri* var. *cliffortioides* regenerating following wind damage were present as small seedlings at the time of the disturbance event. The relative importance of release versus recruitment can therefore only be accurately determined by detailed monitoring following a disturbance event,

Table 8. Recorded release and suppression of some New Zealand forest species following wind damage.

Release	Suppression
Prumnopitys ferruginea [1,2]	*Libocedrus bidwillii* [4]
Nothofagus solandri var. *cliffortioides* [3]	*Nothofagus fusca* [5]
	Nothofagus menziesii [5]
	Nothofagus solandri var. *cliffortioides* [4]

[1]Reid, 1948; [2]Wardle, 2002; [3]Jane, 1986; [4]Martin and Ogden, 2005; [5]Hosking and Hutcheson, 1998.

as observations of small, released individuals might easily be mistaken for seedlings which germinated after the wind damage occurred. Release appears to be an important mode of canopy attainment for a diverse range of canopy species, for example *P. ferruginea* and *D. cupressinum* (Lusk and Smith, 1998), *A. australis* (Ogden *et al*., 1987), *E. dentatus* (Lusk and Ogden, 1992) and *Libocedrus bidwillii* (Ogden *et al*., 1993); indeed, canopy attainment for most species is dependant on disturbance creating space within the canopy. The release of an advanced 'seedling pool', a characteristic of New Zealand *Nothofagus* forests, has many parallels in other temperate (Webb, 1999) and tropical (Whigham *et al*., 1999) forests. In many cases, a dense, released understorey can preclude the recruitment of new individuals following gap formation, ensuring that release of individuals present prior to the disturbance is the dominant mode of recovery (Webb, 1999).

Wind damage can also result in suppression, defined as a decline in growth rate. Even species which are light-demanding and hence frequently released by canopy destruction can sometimes suffer suppression. This occurs through breakage of roots, loss of branches, or defoliation. Longer-term decline and mortality may be associated with increased susceptibility to disease (Everham and Brokaw, 1996). Severe winds can cause temporary or permanent growth declines according to damage severity and species. As previously discussed, species which sprout may regain canopy positions following uprooting. In contrast, species which do not sprout, for example *Libocedrus bidwilliii* (Martin and Ogden, 2005), are likely to have permanently decreased growth rates if badly damaged but not killed by a storm event. Thus wind damage may act to increase the proportion of species with sprouting ability in the canopy of a plant community.

The initiation of suppression by wind damage is not discussed in previous reviews which focus on the different modes of forest recovery rather than the reductions in growth rates that can be experienced by damaged trees. This is possibly attributable to the specialised dendrochronological techniques that are required to investigate decreases in radial growth rates. Investigating the long term effects of suppression, in terms of delayed mortality or overtopping by surrounding vegetation, also requires either long term monitoring or reconstruction of disturbance histories, which are rarely included in wind damage studies.

Initiation of forest dieback

Disturbance is widely regarded as a catalyst for forest dieback in New Zealand *Nothofagus*-dominated forests (Shaw, 1983b; Wardle and Allen, 1983; Ogden *et al*., 1993; Rogers and Leathwick, 1997; Vittoz *et al*., 2001,). Thus wind damage has the potential to initiate decline, which may eventually account for a greater proportion of the final damage than that caused immediately by the storm event. Hosking and Hutcheson (1998) investigated forest dieback initiated by Cyclone Bernie. Mortality of survivors peaked three to six years after the cyclone, and tree death was still occurring 10 years after the event, when less than 30% of the survivors were regarded as healthy. The link between the wind damage and dieback was suggested by the lack of dieback in the surrounding undamaged stands. *Platypus* spp. (pinhole borers), are regarded as a major cause of tree death after disturbance events in *Nothofagus* forest, as the larva depend on recently dead woody debris for development (Milligan, 1974). The effects of *Platypus* spp. and the pathogens for which they are vectors, are difficult to separate with regard to their roles in the initiation of forest dieback. Forest dieback following wind damage may be common, but is not a certainty; Jane (1986) found no evidence of subsequent tree death in damaged stands. Other authors regard sprouting or recruitment to be the major forest responses (Mason, 1950; Martin and Ogden, 2005). Whether wind damage primarily results in forest dieback or regeneration is likely to depend on the structure and species composition of the community. Ogden *et al*. (1993) described changes in forest composition in mixed-*Nothofagus*–conifer forest on Mount Ruapehu following dieback in the 1960s and Cyclone Bernie in 1982. *Nothofagus* was much more severely affected by the dieback event, but *Nothofagus* and conifers were almost equally affected by the cyclone, indicating the potential for disturbance events to mediate stand composition over long periods.

Discussion

Despite its widely recognized importance, there is poor spatial and species coverage of forest damage by wind in the New Zealand literature. Most studies are from central New Zealand *Nothofagus* forests, or eastern South Island exotic plantations. No detailed studies have yet been undertaken in the northern North Island, and few describe wind damage in lowland or coastal environments. Similar limitations are discussed in other reviews. Webb (1999) considered her review as limited by the "uneven geographic scope" of studies, and also noted the potential for results to be unrepresentative of former forest dynamics due to landscape fragmentation and a pervasive human influence.

The relationship between wind intensity and damage severity is unclear. Storms with wind speeds in excess of 110 km hr^{-1} have the potential to cause widespread and severe damage, but damage is often by gusts for which the wind speed is not reported. Everham and Brokaw (1996) recommend recording the following variables: maximum sustained wind;

maximum gusts; duration of the storm; total rainfall and the percentage of the average annual rainfall; and the distance between the study site and where these storm characteristics were measured. Adopting these measures of storm characteristics for future studies of wind damage will enable better comparisons to be made between storm intensity and damage severity.

To gain comparability between studies and aid the development of hypotheses regarding wind damage to forests, three further recommendations are made by Everham and Brokaw (1996): data needs to separate size classes, vegetation types, and damage types; studies need to either estimate species composition before the wind event or to investigate the species and abundance of trees unaffected by the event (to provide contextual information); and studies need to include average values for damage and mortality to aid comparison with other studies.

In New Zealand, forest damage assessments often focus on plantations of exotic trees, and the extent to which these events also affect indigenous forests, especially in remote locations, is largely unknown. Therefore, to investigate the true spatial extent and impacts of a storm, damage needs to be quantified for each of the forest types affected. Quantitative multi-species studies of damage which are common in the international literature (e.g. Glitzenstein and Harcombe, 1988; Zimmerman *et al*., 1994; Batista and Platt, 2003) are largely lacking for New Zealand indigenous forests. This is partly attributable to the predominance of studies in species-poor *Nothofagus* forests.

Topography is widely accepted as a key factor determining the pattern and severity of damage, but generalisations regarding the effect of different topographical positions are elusive (Everham and Brokaw, 1996; Webb, 1999); none of the New Zealand studies adequately separate the influence of topography from associated confounding variables.

Saturated soils increase vulnerability to wind damage. Soil type however strongly influences damage type more than damage severity. Trees growing on soils that provide firm or deep anchorage, such as rocky soils, frozen soils, or sand derived loams, are predisposed to wind damage by bole snap; whereas trees with restricted rooting depth, often due to an underlying consolidated layer or a high water table, tend to be uprooted (Everham and Brokaw, 1996).

Prior disturbance history may be a key component of forest vulnerability. Disturbances may cause immediate changes in vulnerability, for example wind damage resulting in an increase in canopy roughness, or result in a delayed increase in vulnerability, such as the initiation of rot by fire damage (Webb, 1989). Thus one disturbance can affect the nature and severity of disturbances several decades later, and wind damage can be regarded as "not a single event, but the summation of several disturbance processes interacting with tree demography at a particular point" (Matlack *et al*., 1993). Investigation of the effects of disturbance history on wind damage patterns requires either the study of areas with a well-documented site history, or longer-term studies that investigate the effects of multiple disturbances and the interactions between them.

Many studies from New Zealand found that large trees were particularly vulnerable to wind damage. Some authors suggested the operation of critical height thresholds, but these thresholds are likely to be correlated with other predisposing factors such as old age and increased incidence of stem rot. Studies also often rely on tree height alone for examining wind damage vulnerability, disregarding the potentially important variables of crown size and weight (Webb, 1999). Study of wind-throw in a diverse range of New Zealand forest types would be useful for determining if there are critical height thresholds which are species or site specific. Tree size is often confounded with age related factors. This review mirrors the findings of previous reviews; tree size is an important variable, but to differentiate the influence of size from other confounding factors is difficult.

It is impossible from the existing New Zealand literature to make generalizations even regarding vulnerability of angiosperms versus gymnosperms. Discerning differences between early and late successional species is also problematic; in New Zealand, classifying species according to successional types is difficult, and therefore so is the interpretation of vulnerability with regards to the early to late-successional continuum. Many of the methodologies were inappropriate for investigating the relative vulnerability of different species due either to a lack of controls or lack of contextual sampling of forest composition. However, international reviews do suggest that species have differential vulnerability that can sometimes be linked to differences in rooting structure, wood strength, and tree form (Everham and Brokaw, 1996; Webb, 1999). Classifying species as either resistant or susceptible to wind damage may be too simplistic an approach. There is likely to be a continuum of vulnerability between species and within species, determined by factors such as tree age and size, forest structure, and site conditions.

Sprouting, release and recruitment can all be important modes of forest recovery following wind damage in New Zealand forests, with the relative role of each influenced by the composition of the community disturbed and the spatial scale of the damage. Recruitment from seed is, akin to the findings of overseas studies, likely to be of greatest significance where mortality rates are high (Everham and Brokaw, 1996; Webb, 1999), and in *Nothofagus*-dominated forests when uprooting causes soil disturbance. However, the relative importance of recruitment versus other responses such as release and sprouting cannot be determined from the literature currently available.

Sprouting differs according to species, tree size and age, the exact nature of the damage, and site (Everham and Brokaw, 1996). The New Zealand literature suggests that, except for conifers which rarely sprout, the production of new stems is a common response to wind damage. However, no New Zealand studies have quantitatively compared sprouting from snapped versus uprooted stems, or monitored the long term growth and survival of sprouts.

Disturbances often result in the release of advanced growth. This makes distinguishing between recruited seedlings and small released seedlings difficult, especially if the vegetation has not been sampled prior to the disturbance event. Whigham *et al*. (1999) consider that the importance of release in tropical forests is currently underestimated, due to a lack of long term studies. The scarcity of long-term monitoring at sites of known wind damage age in New Zealand, and the potential confusion between release and recruitment, currently prevents the importance of release in New Zealand forests from being accurately assessed. There is a network of 984 permanent plots in New Zealand indigenous forests, many of which have data spanning 20+ years (Wiser *et al*., 2001); this resource provides the opportunity for the sampling of forests following wind disturbance, for which the pre-disturbance vegetation composition and recent history is known.

This review shares similar limitations and conclusions to previous international reviews. The different methodologies employed limit the degree to which studies can be validly compared, confounding factors are often inadequately accounted for or not considered, and many aspects of wind damage are difficult to understand without the perspective provided by long term studies. Adoption of the recommendations of Everham and Brokaw (1996) should see increased comparability for future studies of wind damage in New Zealand forests. Patterns of wind damage have many underlying, governing influences such as soil type and site exposure. Careful consideration of potentially confounding factors, at the early stages of research design, will enable studies to better explain the effects of wind. Most studies, both in New Zealand and overseas, investigate immediate or short term responses to wind damage. However, predictions of recovery paths made from such observations may not be valid. Only one New Zealand study involved long term monitoring (17 years) of forest response to wind damage (Harcombe *et al*., 1998). Further studies of this nature, in a range of forest types, are likely to provide many insights into wind damage and forest response.

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References

Adams, J.A.; Norton, D.A. 1991. Soil and vegetation characteristics of some tree windthrow features in a South Westland rimu forest. *Journal of The Royal Society of New Zealand 21:* 33-42.

Basher, R.E.; Xheng, X. 1995. Tropical cyclones in the Southwest Pacific: Spatial patterns and relationships to Southern Oscillation and sea surface temperature. *Journal of Climate 8:* 1249-1260.

Batista, W.B.; Platt, W.J. 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology 91:* 197-212.

Brenstrum, E. 1998. *The New Zealand Weather Book*. Craig Potton, Nelson, New Zealand.

Burslem, D.F.R.P.; Whitmore, T.C.; Brown, G.C. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *The Journal of Ecology 88:* 1063-1078.

Burt, S.D.; Mansfield, D.A. 1988. The great storm of 15-16 October 1987. *Weather 43:* 90-114.

Carter, P.C.S. 1989. Wind damage in Kinleith Forest - effects of Cyclone Bernie. *In:* Somerville, A.; Wakelin, S.J.; Whitehouse, L. (Editors) *Workshop on Wind damage in New Zealand exotic forests. FRI Bulletin 146*, pp. 17-19. Ministry of Forestry, Rotorua, N.Z.

Chandler, K.C. 1968. Climatic damage to the forests of the Tapanui District. *New Zealand Journal of Forestry 13:* 98-110.

Conway, M.J. 1959. Hurricane damage in Northland. *New Zealand Journal of Forestry 8:* 151-152.

Dawson, K.B. 1970. Storm damage to the vegetation of Kapiti Island, Easter 1968. *Bulletin of the Natural Sciences 1:* 34-44.

de Lange, W.P.; Gibb, J.G. 2000. Seasonal, interannual, and decadal variability of storm surges at Tauranga, New Zealand. *New Zealand Journal of Marine and Freshwater Research 34:* 419-34.

Doyle, T.W.; Gorham L.E. 1996. Detecting hurricane impact and recovery from tree rings. *In:* Dean, J.S.; Meko, D.M.; Swetnam, T.W (Editors). *Tree Rings, Environment and Humanity*, pp. 405-412. Radiocarbon, Tuscon, Arizona, U.S.A.

Everham, E.M. 1995. A comparison of methods for quantifying catastrophic wind damage to forests. *In:* Coutts, M.P.; Grace, J (Editors). *Wind and trees*, pp. 340-357. Cambridge University Press, Cambridge, U.K.

Everham, E.M.; Brokaw N.V.L. 1996. Forest damage and recovery from catastrophic wind. *The Botanical Review 62:* 113-185.

Finnigan, J.J.; Brunet, Y. 1995. Turbulent airflow in forests on flat and hilly terrain. *In:* Coutts, M.P.; Grace, J (Editors). *Wind and trees*, pp. 3-40. Cambridge University Press, Cambridge, U.K.

Fitzharris, B. 2001. Global energy and climate processes. *In:* Sturman A.; Sproken-Smith, R (Editors). *The Physical Environment: a New Zealand perspective*, pp. 62-75. Oxford University Press, Oxford, U.K.

Foster, D.R. 1988. Disturbance History, Community Organization and Vegetation Dynamics of Old-Growth Pisgah Forest, South-Western New Hampshire, U.S.A. *Journal of Ecology 76:* 105-134.

Foster, F.W. 1931. A stand of beech regeneration of known age. *Te Kura Ngahere 3:* 39-40.

Fowler, A.; Palmer, J.G.; Salinger, J.; Ogden, J. 2000. Dendroclimatic interpretation of tree-rings in *Agathis australis* (kauri): 2. Evidence of a significant relationship with ENSO. *Journal of The Royal Society of New Zealand 30:* 277-92.

Glitzenstein, J.S.; Harcombe, P.A. 1988. Effects of the December 1983 Tornado on Forest Vegetation of the Big Thicket, Southeast Texas, U.S.A. *Forest Ecology and Management 25:* 269-90.

Hosking, G.; Hutcheson, J. 1998. Wind-caused disturbance of a red/silver beech forest: ten years on. *New Zealand Journal of Forestry Science 28:* 325-334.

Hsu, S.A. 2002. The gust factor during hurricanes as measured by NDBC buoys. *Mariners Weather Log 46:* 12.

Irvine, R.E. 1970. The significance of windthrow for *Pinus radiata* management in the Nelson District. *New Zealand Journal of Forestry 15:* 57-68.

Jane, G.T. 1986. Wind damage as an ecological process in mountain beech forests of Canterbury, New Zealand. *New Zealand Journal of Ecology 9:* 25-39.

June, S.R. 1974 (unpublished). *The germination, growth and survival of red beech* (Nothofagus fusca) *seedlings in relation to forest regeneration*. MSc thesis, Massey University, Palmerston North, N.Z.

Littlejohn, R.N. 1984. Extreme winds and forest devastation resulting from Cyclone 'Bernie'. *Weather and Climate 4:* 47-52.

Lusk, C.; Ogden, J. 1992. Age structure and dynamics of a Podocarp-Broadleaf Forest in Tongariro National Park, New Zealand. *Journal of Ecology 80:* 379-393.

Lusk, C.H.; Smith B. 1998. Life history differences and tree species coexistence in an old-growth New Zealand rain forest. *Ecology 79:* 795-806.

Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs 44:* 73-88.

Martin, T.J.; Ogden, J. 2005. A blast from the past: A dendroecological reconstruction of forest windthrow, North Island, New Zealand. *In:* Calver, M.; Bigler-Cole, H.; Bolton, G.; Dargavel, J.; Gaynor, A. (Editors) *A forest conscienceness: 6th National Conference of the Australian Forest History Society Inc*, pp. 543-553. Millpress Science Publishers, Rotterdam, Netherlands.

Mason, R. 1950. Notes on regrowth in part of the Tararuas following the 1936 storm. *Wellington Botanical Society Bulletin 22:* 11-2.

Matlack, G.R.; Gleeson, S.K.; Good, R.E. 1993. Treefall in a mixed oak-pine coastal plain forest: immediate and historical causation. *Ecology 74:* 1559-66.

McCracken, I.J. 1979. Mountain climate in the Craigieburn Range, New Zealand. *In:* Benecke, U.; Davis, M.R. (Editors), *Mountain environments and subalpine tree growth*, pp. 41-59. New Zealand Forest Service, Christchurch, N.Z.

Milligan, R.H. 1974. Insects damaging beech (*Nothofagus*) forests. *Proceedings of the New Zealand Ecological Society 21:* 32-40.

Moore, J.; Quine, C.P. 2000. A comparison of the relative risk of wind damage to planted forests in Border Forest Park, Great Britain, and the Central North Island, New Zealand. *Forest Ecology and Management 135:* 345-53.

Nichol, E.R. 1997. *Common names of plants in New Zealand*. Manaaki Whenua Press, Lincoln, New Zealand.

Norton, D.A; Wilson, A.K. 1981. A permanent quadrat in a wind-thrown *Nothofagus fusca - N. solandri* forest, Arthurs Pass National Park. *Mauri Ora 9:* 97-103.

Ogden, J. 1988. Forest dynamics and stand-level dieback in New Zealand's *Nothofagus* forests. *Geojournal 17:* 225-230.

Ogden, J.; Fordham, R.A; Pilkington, S.; Serra, R.G. 1991. Forest gap formation and closure along an altitudinal gradient in Tongariro National Park, New Zealand. *Journal of Vegetation Science 2:* 165-172.

Ogden, J.; Lusk, C.H.; Steel, M.G. 1993. Episodic Mortality, Forest Decline and Diversity in a Dynamic Landscape: Tongariro National Park, New Zealand. *In:* Mueller-Dombois, D.; Huettl, R.F. (Editors), *Forest decline in the Atlantic and Pacific Region*, pp. 261-274. Springer-Verlag, Berlin, Germany.

Ogden, J.; Stewart, G.H.; Allen, R.B.; 1996. Ecology of New Zealand *Nothofagus* forests. *In:* Veblen, T.T.; Hill, R.S.; Read, J. (Editors), *The ecology and biogeography of Nothofagus forests*, pp. 25-82. Yale University Press, London, U.K.

Ogden, J.;Wardle, G.M.; Ahmed, M. 1987. Population dynamics of the emergent conifer *Agathis australis* (D.Don) Lindl. (kauri) in New Zealand II. Seedling population sizes and gap-phase regeneration. *New Zealand Journal of Botany 25:* 231-42.

Parkes, J.P. 1984. Feral goats on Raoul Island II. Diet and notes on the flora. *New Zealand Journal of Ecology 7:* 95-101.

Peterson, C.J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *The Science of the Total Environment 262:* 287-311.

Prior, K.W. 1959. Wind damage in exotic forests in Canterbury. *New Zealand Journal of Forestry 8:* 57-68.

Reid, J.S. 1948. Regeneration in indigenous forest after blowdown. *New Zealand Journal of Forestry 5:* 436-7.

Reif, A.; Allen, R.B. 1988. Plant communities of the steepland conifer-broadleaved hardwood forests of central Westland, South Island, New Zealand. *Phytocoenologia 16:* 145-224.

Revell, C.G.; Ward, G.F.A. 1983. Tropical Cyclone 'Bernie', 1-14 April 1982. *Weather and Climate 2:* 31-32.

Rogers, G.; Leathwick, J.R. 1997. Factors predisposing forests to canopy collapse in the southern Ruahine Range, New Zealand. *Biological Conservation 80:* 325-338.

Schaetzl, R.J.; Burns, S.F.; Johnson, D.L.; Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio 79:* 165-76

Shaw, W.B. 1983a. Tropical Cyclones: determinants of pattern and structure in New Zealand's indigenous forests. *Pacific Science 37:* 405-414.

Shaw, W.B. 1983b. The impact of tropical Cyclone Bernie on the forests of Urewera National Park, North Island, New Zealand. *New Zealand Journal of Ecology 6:* 155-156.

Sinclair, M.R. 2002. Extratropical transition of Southwest Pacific tropical cyclones. Part 1: Climatology and mean structure changes. *Monthly Weather Review 130:* 590-690.

Smale, M.C.; Burns, B.R.; Smale, P.N.; Whaley, P.T. 1997. Dynamics of upland podocarp/broadleaved forest on Mamaku Plateau, central North Island, New Zealand. *Journal of The Royal Society of New Zealand 27:* 513-32.

Somerville, A. 1995. Wind damage to New Zealand State plantation forests. *In:* Coutts, M.P.; Grace, J. *Wind and trees*, pp. 460-467. Cambridge University Press, Cambridge, U.K.

Steel, M.G. 1989 (unpublished). *Mountain beech forest on Mount Ruapehu: dynamics, disturbance and dieback*. PhD thesis, University of Auckland, Auckland, N.Z.

Stewart, G.H. 1986. Forest dynamics and disturbance in a beech/hardwood forest, Fiordland, New Zealand. *Vegetatio 68:* 115-126.

Stewart, G.H.; Rose, A.B.; Veblen, T.T. 1991. Forest development in canopy gaps in old-growth beech (*Nothofagus*) forests, New Zealand. *Journal of Vegetation Science 2:* 679-690.

Studholme, W.P. 1995. The experience of and management strategy adopted by the Selwyn Plantation Board, New Zealand. *In:* Coutts, M.P.; Grace, J. *Wind and trees*, pp. 468-476. Cambridge University Press, Cambridge, U.K.

Tanner, E.V.J.; Bellingham, P.J. 2006. Less diverse forest is more resistant to hurricane disturbance: evidence from montane rain forests in Jamaica. *Journal of Ecology 94:* 1003-1010.

Thomson, A.P. 1936a. An exceptional gale. *Te Kura Ngahere 4:* 32.

Thomson, A.P. 1936b. The recovery of an indigenous forest after wind-throw. *Te Kura Ngahere 4:* 33-36.

Ulanova, N.G. 2000. The effect of windthrow on forests at different spatial scales: a review. *Forest Ecology and Management 135:* 155-67.

Vittoz, P.; Stewart, G.H.; Duncan, R.P. 2001. Earthquake impacts in old-growth *Nothofagus* forests in New Zealand. *Journal of Vegetation Science 12:* 417-426.

Wardle, G.M.; Mark, A.F.; Baylis, G.T.S. 1973. Vegetation and landscape of the West Cape District, Fiordland, New Zealand. *New Zealand Journal of Botany 11:* 599-626.

Wardle, J.A. 1970. The ecology of *Nothofagus solandri* 4. Growth, and general discussion to parts 1 to 4. *New Zealand Journal of Botany 8:* 609-46

Wardle, J.A. 1984. *The New Zealand beeches: ecology, utilisation and management*. New Zealand Forest Service, Christchurch, N.Z. 447 pp.

Wardle, J.A.; Allen, R.B. 1983. Dieback in New Zealand *Nothofagus* forests. *Pacific Science 37:* 397-404.

Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge. 672 pp.

Webb, S.L. 1999. Disturbance by wind in temperate-zone forests. *In:* Walker, L.R. (Editor), *Ecosystems of the World 16: Ecosystems of disturbed ground. First Edition*, pp. 187-222. Elsevier Science B.V., Amsterdam, Netherlands.

Whigham, D.F.; Dickinson, M.B.; Brokaw, N.V.L. 1999. Background canopy gap and catastrophic wind disturbances in tropical forests. *In:* Walker, L.R. (Editor), *Ecosystems of the World 16: Ecosystems* *of disturbed ground. First Edition*, pp. 223-252. Elsevier Science B.V., Amsterdam, Netherlands.

Wilson, H.H. 1976. The effect of the gale of August 1975 on forestry in Canterbury. *New Zealand Journal of Forestry 21:* 133-40.

Wiser, S.K.; Bellingham, P.J.; Burrows, L.E. 2001. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *New Zealand Journal of Ecology 25(2):* 1-17.

Editorial Board member: David Coomes

Zimmerman, J.K.; Everham, E.M.; Waide, R.B.; Lodge, D.J.; Taylor, C.M.; Brokaw, N.V.L. 1994. Responses of tree species to hurricane winds in subtropical wet forests in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology 82:* 911-22

Zotov, V.D.; Elder, N.L.; Beddie, A.D.; Sainsbury, G.O.K.; Hodgson, E.A. 1938. An outline of the vegetation and flora of the Tararua Mountains. *Transactions and Proceedings of the Royal Society of New Zealand 68:* 259-324.