Salt-wind induced wave regeneration in coastal pine forests in New Zealand

D.J. Campbell

Abstract: Strong onshore winds and airborne sea salt can gradually defoliate trees at the exposed margin of temperate pine stands in New Zealand and induce a slowly moving front of dieback and regeneration. Overcrowded mature stands are vulnerable to crown abrasion: abrasion affects trees 20 m ahead of the dieback front; suppressed trees 12 m ahead die before the front reaches them. At the stand margin, trees die from abrasion and salt wind induced dieback. The dieback zone lets sunlight enter the stand; light-demanding pine seedlings establish, but a gradient of increasing litter depth from the dieback front and summer dryness restrict successful seedling establishment to a narrow zone that moves parallel with the dieback front and 11–13 m ahead of it. Further seedlings establish for 4–10 years before the juveniles form a closed canopy; competing vegetation is partly suppressed by infrequent cattle browsing. Regenerating juvenile maritime pine (*Pinus pinaster* Ait.), show a strict age-related gradation from the dieback front and indicate that wind and salt deposition have been constant for 30 years. Stands further from the sea, with lower stocking rates and other pine species, did not have a clear-cut regeneration zone, because there were no strong gradients of litter depth and light intensity.

Résumé : De forts vents du large et des embruns salins peuvent graduellement défolier les arbres de la bordure exposée des pinèdes en Nouvelle-Zélande et provoquer un front de dépérissement et de régénération qui se déplace lentement. Les peuplements mûrs d'une trop forte densité sont vulnérables à l'abrasion des cimes. Celle-ci affecte les arbres situés 20 m en avant du front, alors que les arbres supprimés, se trouvant 12 m en avant, meurent avant que le front de dépérissement les ait atteints. En bordure du peuplement, les arbres meurent à cause de l'abrasion et à cause du dépérissement provoqué par le vent chargé de sel. Dans la zone de dépérissement, la lumière pénètre dans le peuplement permettant l'établissement des semis du pin héliophile. Cependant, l'augmentation graduelle de l'épaisseur de la litière à partir du front et la sécheresse estivale limitent le succès de l'établissement des semis à une étroite bande qui se déplace parallèlement au front en le précédant de 11 à 13 m. De nouveaux semis s'installent pendant 4 à 10 ans avant que les jeunes sujets forment une canopée fermée. La végétation qui concurrence les semis est partiellement éliminée par le broutage occasionnel du bétail. À partir du front de dépérissement, la jeune régénération du pin maritime (*Pinus pinaster* Ait.) montre une gradation d'âge stricte, qui indique que le vent et la déposition du sel ont été constants durant 30 ans. Les peuplements éloignés de la mer, de faible densité relative et composés d'autres espèces de pin, n'avaient pas de zone de régénération clairement délimitée, car ils ne possédaient pas de gradients prononcés d'épaisseur de la litière et d'intensité lumineuse.

[Traduit par la Rédaction]

Introduction

Regeneration waves are slowly moving fronts of dieback and regeneration that form in subalpine fir (*Abies*) forests in central Japan and the northeastern United States (Oshima et al. 1958; Iwaki and Totsuka 1959; Sprugel 1976, 1985; Sprugel and Bormann 1981; Reiners and Lang 1979). Trees on the exposed side of a canopy gap are gradually killed by wind; more trees become exposed and they in turn lose vigour and die. The regenerating forest that establishes in the dieback zone is itself invaded after several decades by another dieback front.

Dieback of exposed trees in subalpine fir forests has been linked to rime ice buildup and foliage loss, damage to tree crowns by strong winds, and to stand structure including overcrowding of juvenile and adult stands, which leads to early growth stagnation and therefore, loss of stand vigour (Oshima et al. 1958; Marchand and Goulet 1985; Foster 1988; Kohyama and Fujita 1981; Kohyama 1988). Other suggested factors include wind effects during the growing season, damage to roots when trees rock, and extreme winter cold (Sprugel 1976, 1985; Harrington 1986; Marchand et al. 1986; Kai 1974; Kohyama 1988; Foster 1988; Waring 1987; Gerrish 1988).

Regeneration waves also occur in low-altitude fir forests on the coastal plain of Newfoundland where winters are cold, and "deposition of glaze and rime and ... sea-salt spray" contribute to crown deformation (Robertson 1987). "Wave-type" regeneration has been found in the extreme north of Japan in fir forests growing on coastal dunes "exposed to the constant sea winds from the west" (Kohyama 1988; Sato 1994).

In New Zealand, pine forests planted on sand dunes on the west coast of the North Island are exposed to the prevailing wind. The wind carries sea salt that stunts tree growth,

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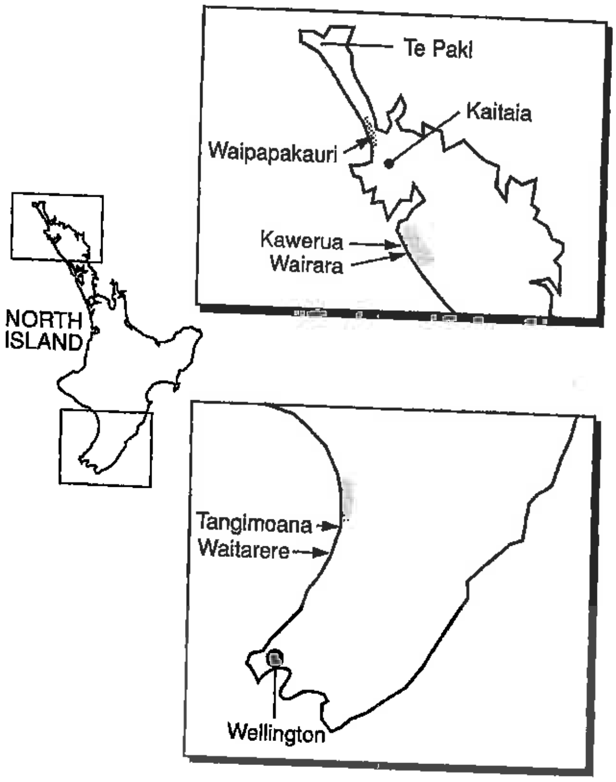
Fig. 1. Location map.



especially of sensitive species. Trees considered more resistant to salt, including densely planted maritime pine (*Pinus pinaster* Ait.) were planted to protect the seaward side of production forests.

Salt particles form when strong dry wind (>7 m·s^{-1} and <73% relative humidity) blows over the sea; the amount produced increases logarithmically with wind speed (Woodcock 1957; Junge 1963; Wu 1981). Smaller particles (0.1–10 μm) travel great distances as a salt aerosol (Boyce 1954; Junge 1963; Cassidy 1968, 1971; McCune 1991). Rain removes the atmospheric aerosol, but it forms again in <24 h (Cassidy 1968). During "dry" salt storms (<40% relative humidity), salt particles are driven into plants through open stomata, or through damaged or thin cuticle, especially of young leaves (Boyce 1954). The leaf tip and margin become necrotic and severely affected leaves are shed prematurely thus inhibiting the next year's growth (Moss 1940; Edlin 1943; Boyce 1954; Pyykkö 1977).

Mature *P. pinaster* stands at Waipapakauri and Kawerua (Fig. 1) have been dying along the seaward margin. Dieback at Waipapakauri appeared to be progressive, with pine seedlings establishing amongst dying and fallen trees, and appeared to fit features of a fir regeneration wave. Regeneration waves in fir forests are mainly associated with very cold climates. This study describes dieback and regeneration in temperate pine (*Pinus*) stands on coastal dunes. The objective was to determine (*i*) whether dieback and regeneration in pine stands is comparable with fir regeneration waves and (*ii*) whether published explanations for fir regeneration waves adequately explain dieback and regeneration in New Zealand.

Study sites

Waipapakauri

Waipapakauri (Fig. 1) has a mean annual temperature of 15.5°C; the prevailing southwest wind has a mean annual speed of 7.5 m·s^{-1} (Robertson 1960; Tomlinson 1976). *Pinus pinaster* was planted in 1941 at ca. 3 500 stems/ha on dunes 250 m from the sea. The unmanaged stand has thinned to 18–1900 stems/ha. The 15 m high trees have small crowns (width 2.1 ± 0.7m, (mean ± SD), depth 1.4 ± 0.84 m; $n = 7$)). A roadway separates the seaward side the stand from more recently planted *Cupressus macrocarpa* Hartweg. now 6 m tall (Fig. 2). Salt winds from 225°N shape tree crowns at the dieback front and stunt self-sown *P. pinaster* growing 100 m from the sea to <2 m tall.

Debris extends from 12 m ahead of the dieback front to naturally seeded 1 m high juveniles. Most standing dead trees have lost bark from the lower 1.5 m, and started to decay. Fallen trees have snapped at ground level and large-diameter trees have blown over when the deep taproot broke. Although not measured, there is a clear link between movement of the dieback front and shelter by seaward dunes. Ground near the dieback front is covered with bark and limbs but almost no needle litter; 5–10 m seaward of the dieback front fine debris has rotted, and 15–25 m from the dieback front only heartwood remains. The dieback zone has a sparse cover of grass, lotus (*Lotus pedunculatus* Cav.), catsear (*Hypochoeris radicata* L.), and scattered *Pseudopanax lessonii* ((DC.) C. Koch). Kikuyu grass (*Pennisetum clandestinum* Hochst. ex Chiov.) grows in gaps in the closed regeneration. Cattle have had occasional access to the forest and have lightly grazed grass in the regeneration zone. Although forage is scarce, few juvenile *P. pinaster* had been browsed, and a few ungrazed 1.5 m-tall grass tussocks (*Cortaderia* sp.) at the edge of the taller juvenile pines suggests that cattle are not confined for long.

Tangimoana and Waitarere

Forests on dunes 640 km south of Waipapakauri were searched for comparable dieback and regeneration. Mature stands 1.5 km from the coast at Tangimoana and Waitarere were exposed by a road to sea winds. Mean annual temperature at Tangimoana and Waitarere is 13°C; strong northwest, and west winds (mean annual wind speed 9.9–11 m·s^{-1}) frequently reach gale force during spring and early summer. Winds >17.8 m·s^{-1} blow 4–5 days per month in winter and for 6–8 days in other seasons (Esler 1978; Robertson 1960; Tomlinson 1976). At both sites wind-carried salt strongly shapes vegetation; salt-hardy radiata pine (*Pinus radiata* D. Don) trees growing on exposed ridges 50 km inland have been deformed into class C4 flag shapes (Noguchi 1979). Near the coast, newly planted *P. radiata* seedlings are sometimes so severely affected by wind-driven salt that most die (P. McCarthy, personal communication).

At Tangimoana, dieback and regeneration was found in bishop pine (*Pinus muricata* D. Don) planted ca. 1930 and thinned to 850 stems/ha. Initially a 35 m wide strip of *P. pinaster* and a few *P. radiata* had been planted on the seaward side, but most have died and been replaced by naturally seeded juveniles. The 18–20 m tall *P. muricata* have unbranched trunks and small crowns (ca. 2.5 m wide, 2 m deep) with wide abrasion gaps between them. Crowns of the *P. pinaster* are ca. 7 m wide and 4 m deep, whereas *P. radiata* trees are ca. 16 m wide and 6 m deep. Cattle have access to a sparse cover of grass in the forest, but pine seedlings were un-browsed. Trees at the dieback front are shaped by winds from 254°N.

Fig. 2. Cross section through *Pinus pinaster* dieback and regeneration at Waipapakauri. Prevailing wind and the dieback front travels from right to left. The stands at Tangimoana and Waitarere are similar except that they are further from the sea and *C. macrocarpa* is absent.

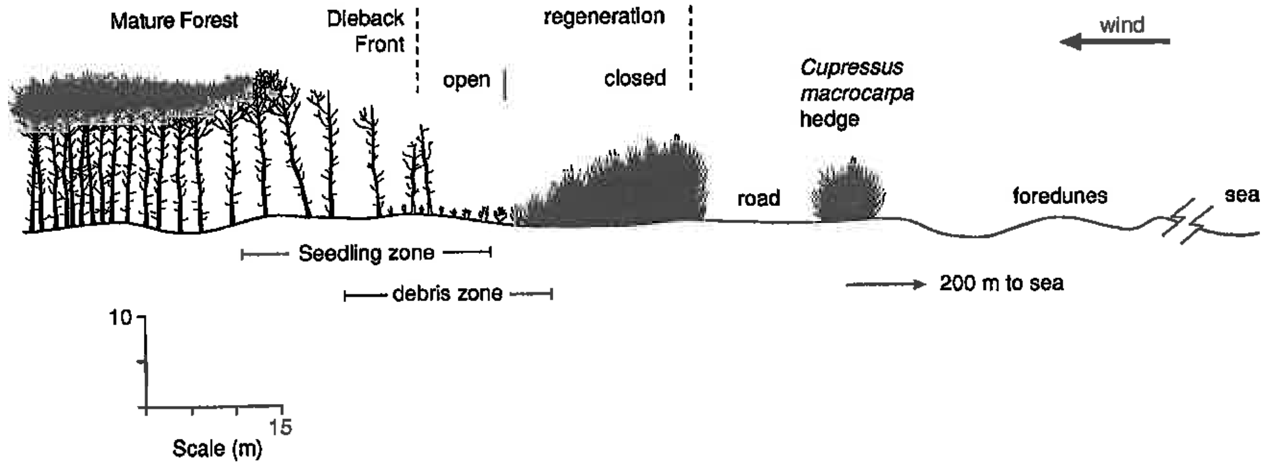
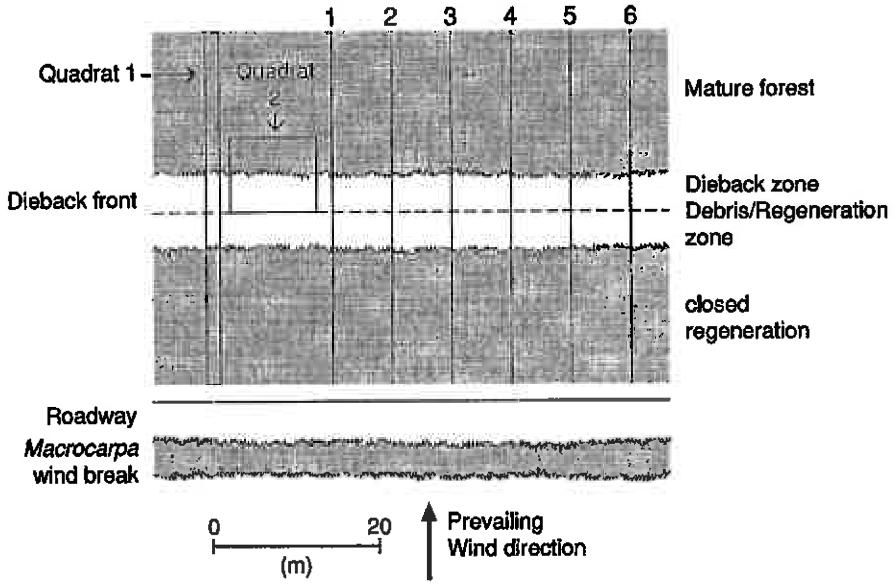


Fig. 3. Sample lines and quadrats at Waipapakauri in relation to mature forest, regenerating pines, and the dieback front.



Dieback and regeneration was found at Waitarere in *P. radiata* forest planted in 1962. Trees have been thinned to 38 trees/ha, are 35 m tall and have crowns 4 m wide by 7.5 m deep. Straying cattle have access.

Methods

Waipapakauri

Movement of the dieback front was determined from the shape of exposed tree crowns and a 70 m long baseline was established along the dieback front. From an arbitrary origin, a 3 m wide belt transect (quadrat 1) was run at right angles to the baseline into the forest for 30 m and into the juvenile pines for 30 m in the opposite direction (Fig. 3). The position was plotted of all mature and juvenile trees with ground-level stem diameter >5 cm, and measurements were made of height, stem circumference, crown depth and diameter, and densities of small seedlings. Tree crowns were photographed upwards, starting at the baseline, at 5-m intervals into the forest for 30 m, thereafter at 20 m intervals to 110 m. These photographs were used to measure the gap between four tree crowns at the dieback front and at 5 and 10 m into the forest. Quadrat 2 was located 5 m from the origin and was 12 × 15 m with the long axis on the baseline. The positions of dead standing trees, holes in the ground, and live trees were plotted, together with height and crown cover of live trees.

Six lines 10 m apart were run 30 m each side of the baseline at right angles to it; the first line was located 20 m from the origin. The seedling growing the furthest distance into the forest from the baseline was collected on each line, and within 1 m of the line, the nearest seedlings and juveniles were collected or sampled. If several plants were an equal distance from the baseline, representatives of

Table 1. Live and dead trees in relation to trunk size and position, dieback front, and exposure, Waipapakauri.

	Dead/total trees*		
Diameter (mm)	EO	DF	PS
>300	5/8	0/7	0/2
200–300	6/6	0/5	1/5
150–200	1/1	2/2	2/2

*EO, exposed outlier (isolated trees with greater than half the crown exposed); DF, dieback front (trees exposed to the wind on one side only); PS, partial shelter (trees sheltered by others <2 m from them).

all sizes were sampled. Seedlings <30 cm tall were collected, juveniles 30 cm tall to 10 cm diameter at ground level were sectioned 5 cm above ground, and increment cores were taken 20 cm aboveground from larger individuals.

Litter depth was measured using a 5 mm diameter probe to determine depth to mineral soil. Depth was measured at 10-m intervals, starting at the dieback front to 50 m into the forest, on 10 parallel lines 5 m apart along the baseline. The orientation of logs and wind-shaped crowns was measured with a compass to determine and the direction of strong winds and severe salt winds.

Tangimoana and Waitarere

At both Tangimoana and Waitarere a single line was run into the forest and regeneration, using the same methods as for the six lines at Waipapakauri. At Waitarere where the regeneration was less developed the transect extended into the juvenile trees for only 15 m. The gap between crowns was measured from photographs, and litter was measured as at Waipapakauri. Stand age was determined from cores, and the direction of salt winds was measured from shaped crowns.

Age determination and other methods

Increment cores that missed the tree centre were aligned on a cross section that had comparable rings so that rings of cross section and core coincided. The number of rings from the centre of the cross section to the innermost ring on the core was added to the minimum core age. All seedlings collected on quadrat 1 and the transect lines were sorted into size or age classes according to needle growth and shoot extension. Ten seedlings from each class were sectioned to determine when the first ring became clearly visible. For absolute ages, the years to the first ring was added to all ring counts. The first obvious growth ring formed at the fifth year, so 5 years have been added to ring-count ages derived from cross sections and cores. Absolute ages of core samples (extracted 20 cm aboveground) were adjusted by adding the age at core height. Core ages of juveniles on the line transects were adjusted by adding the age of a seedling at core height and subtracting its age at the time the dieback front reached it. This resulted in 1 year being added to core age.

Within the quadrats, cores were taken from the sheltered side of all live or recently dead trees (6 at the dieback front and 16 ahead of it), to measure radial increments, effects of exposure on ring width and the timing of dieback. Changes in radial growth over the last 10 years of trees growing near and ahead of the dieback front were determined from these cores, by comparing the last 5 years' growth with that of the previous 5 years' and expressing the difference as a percentage of the previous 5 years' growth. A growth decline was a 40% decrease in radial growth for at least two successive years. Increment cores from some dead trees could not be used because of decay.

Because growing leaves are more susceptible to atmospheric salt, the timing of needle growth in maritime pine was measured at Wellington. Ten branch-tip needles were measured fortnightly from 1 September 1995 to mid-April 1996. The frequency of salt-generating storms (<73% RH for >8 h), in relation to needle growth, was determined by analysing hourly RH data from Kaitaia merged with hourly wind direction and speed from Te Paki for the same period. The only available data with the above parameters were June 1982 – July 1983, but as regeneration (and thus dieback) is similar each year, any year's data should be representative.

Results

Waipapakauri

Dieback

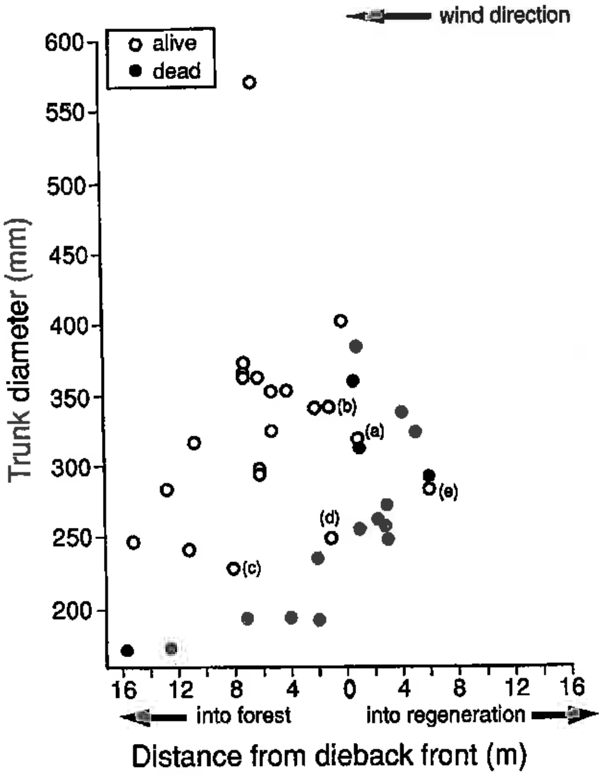
Dieback affected all trees on the seaward margin of the stand; some crowns had only a few live twigs on the sheltered side. Each year about 35 salt storms (>7 $m \cdot s^{-1}$, RH <73% for >8 h) can stunt plant growth or induce premature needle loss. Needles of *P. pinaster* grow continuously from October to April, coinciding with a rise in storm frequency from October (four) to February (nine) and a drop in April (three).

In the forest interior the gap between tree crowns was less than 4 m. As the dieback front approaches, exposure and wind sway increases, abrading adjacent crowns. The gap starts to increase 20 m ahead of the dieback front, averaging 7 m at the dieback front. Abrasion ahead of the dieback front usually is accompanied by a decline in radial growth. Growth of seven trees at the dieback front decreased 46 ± 21% over the last 5 years compared with the previous five. Trees 5 m ahead of the front had their growth reduced by 38.9 ± 17.6%, and several trees 8 m ahead had not yet been affected. Growth changes were very variable, as some trees initially grew better after neighbours died, but heightened exposure induced a progressive decline. Radial growth of two outlier trees that initially survived passage of the dieback front increased by 67 and 32%. However, their growth during the previous 5 years had been less than the preceding five, and the final year's growth had dropped to only 20% of the year before. Five other outlier trees had had their growth suppressed by 64 ± 6.8%.

All trees in quadrant 2 (Table 1) <200 mm diameter at breast height (DBH) had died, whereas 12 of 17 trees >300 mm were still alive, even though 10 were at the dieback front or persisted as outliers. Fewer trees were in the 150–200 mm DBH size class, because many small trees die when the dieback front approaches within 12 m. The six 200–300 mm diameter outlier trees died after the front had passed, yet only one tree of this size had died just ahead of, or at, the dieback front. Few trees are able to withstand exposure for more than 4 years; usually only large trees survive the passage of a front (Fig. 4, Table 1). Growth of an outlier tree 13 m behind the dieback front with a 5 m wide crown and 589 mm DBH bole, had decreased by 53% over the last 5 years. Of the six separately identified trees on the windward side of the dieback front (Fig. 4) trees *a* and *c* were sheltered behind another dying tree, trees *b* and *d* were at the dieback front and dying, and the smallest diameter outlier (tree *e*) had a 70% reduction in radial growth.

Rate of movement of the dieback front was determined from the oldest juveniles on each line in relation to their distance from the dieback front. The mean dieback rate for all lines was 1.6 ± 0.2 $m \cdot year^{-1}$, and it has been regular for >30

Fig. 4. Trunk diameter of live (○) and dead (●) trees plotted in relation to distance from the dieback front, Waipapakauri. Trees *a* and *c* were partly sheltered by another dying tree; trees *b* and *d* were dying; and radial growth of the smallest diameter outlier (tree *e*) had declined by 70%.



years. Several exposed outliers are on or near line six, and local variations in dieback rate have arisen because vigorous trees have sheltered those behind them. The dieback front was 52.9 m from the oldest juveniles, showing it has been moving through the forest for 33 years. As the trees are 54 years old, dieback must have started 21 years ago.

Regeneration

Seedlings establish from 13–15 m ahead (leeward) of the dieback front to 12–15 m behind it. Onshore winds carry seed towards the forest interior, and most first-year seedlings are found in a narrow zone 11–13 m (max >20 m) ahead of the dieback front. Dead first-year seedlings 4–8 m ahead of the dieback front suggests that the 4–5 cm deep litter must dry out in summer. Litter was deepest (9 ± 1 cm) under trees 50 m into the stand and depth declined steadily to 1 ± 1 cm under dying trees at the dieback front.

Seedlings continue to establish in the moving dieback zone for up to 10 years before rapidly growing juveniles form a closed stand (Figs. 2 and 5*a*). Densities of seedling and juvenile pines on quadrat 1 increased from 15 000 / ha at 8–16 m ahead of the dieback front to 28 750 / ha between the front and 8 m behind it; numbers then declined steadily to 6250/ha between 16 and 24 m behind. Recently germinated seedlings in the debris zone have to compete with older, faster growing seedlings. For example, a 2-year-old *P. pinaster* seedling has grown to only 200 cm after another 5 years, whereas an 8-year-old juvenile grows to 1 m in the same time, and those over 1.5 m tall add more than 1 m each year.

Juvenile age varies predictably with distance from the dieback front (Figs. 5*b*–5*h*), indicating that seedlings that establish first can exclude or suppress later arrivals. In Figs. 5*c*, 5*g*, and 5*h*, seedlings ca. 15 m behind the dieback front disappear from older stands.

Tangimoana

On the seaward margin of the stand, dying or dead *P. muricata* and small-diameter *P. pinaster* trees occupy a 40–50 m wide zone. *Pinus muricata* trees up to 327 mm DBH had died at the dieback front, whereas 30 m ahead, trees only 273 mm DBH were still alive. Large-diameter *P. pinaster* trees, dead on the exposed side, remain after the front had passed. Trees die standing, and fallen trees show no sign of root wrench. Dieback rate, determined from the six oldest juveniles, was 1.5 ± 0.1 m·year^{-1}. Dieback has been moving through the forest for less time than at Waipapakauri.

Intercrown gaps were 8–11 m throughout the forest, and the gaps were not wider at the exposed forest edge. Litter depth was 1 ± 0.5 cm throughout the forest. Seedlings established >30 m ahead of the dieback front, and there was no clear regeneration zone (Fig. 6*a*). Compared with Waipapakauri, the relationship between regeneration age and dieback was less distinct, and seedlings of widely different age were along most of the transect (Fig. 6*a*).

Juveniles 14–15 years old were growing 5–15 m behind the dieback front, together with 2-year-old seedlings, and younger juveniles had died when older trees were 15 years old.

Waitarere

Because *P. radiata* is more resistant to salt and the managed trees are more vigorous, the dieback zone was less distinct. The dieback rate, calculated from the oldest six stems, was 0.4 ± 0.3 m·year^{-1}). Litter depth throughout the forest was 1 ± 0.5 cm. Seedling pines were >50 m ahead of the dieback front together with a sparse cover of grass.

Discussion

Does dieback and regeneration in these pine forests fit the concept of wave regeneration described by Sprugel (1976, 1985), Foster (1988), and Kohyama (1988)? In fir forests, dieback and regeneration migrate through the stands at a relatively constant rate, trees die standing, and canopy tree seedlings establish or are released as the front passes. All these features are present at Waipapakauri (Figs. 2 and 5) and, to a lesser extent, at Tangimoana and Waitarere.

Dieback

Which dieback factors affect these pine stands? Extreme winter cold and rime ice cannot be factors, because the climate is temperate at all sites. Damage to shallow root systems caused by trees rocking in gusting winds is not a factor as the trees are deeply rooted in sand. Some or all stands are affected by overcrowding, wind damage to tree crowns,

Fig. 5. Ages of seedlings and juveniles in relation to distance from the dieback front, Waipapakauri: (*a*) all lines combined; (*b*) quadrat 1; (*c*–*h*) lines 1–6, respectively.

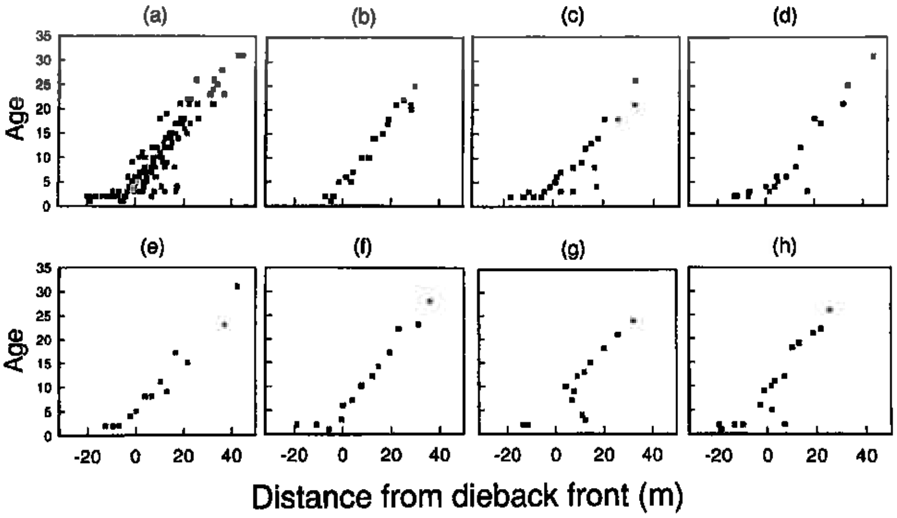
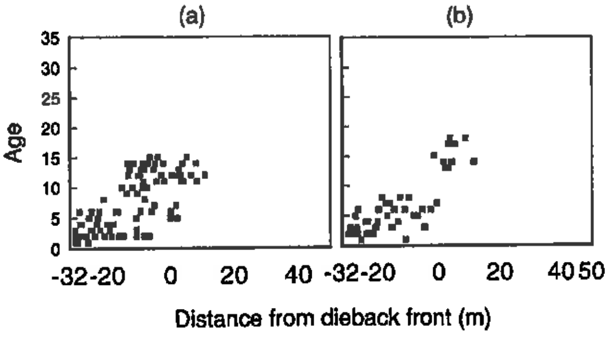


Fig. 6. Ages of seedlings and juveniles in relation to the distance from the dieback front: (*a*) Tangimoana; (*b*) Waitarere.



exposure to sea winds, deposition of sea salt, and wind effects during the growing season.

Because trees were planted densely at Waipapakauri, overcrowding and competition has resulted in trees with slender trunks and small crowns. Trees at the stand margin sway in strong winds; crown abrasion produces a gradient of decreasing foliage loss extending up to 15–20 m into the forest from the exposed margin. The "pipe model" of tree growth closely links stem length, crown size, and carbon balance (Shinozaki et al. 1964*a*, 1964*b*). It predicts that tall trees with small crowns are vulnerable to stress, and those that are senescent or "prematurely senescent," experiencing little growth for extended periods, are most likely to die (Sprugel 1984, 1985; Mäkelä 1986; Gerrish 1988).

Overcrowding also affected the unthinned stand at Tangimoana but not the managed Waitarere stand. *Pinus muricata* trees at Tangimoana are tall, their trunks are slender, and crown abrasion extends well into the stand. Compared with Waipapakauri the abrasion gaps between crowns are larger, because the taller trees sway more in stronger winds. The Waitarere stand has been thinned to 38 stems/ha, and the intercrown gap is similar to that at Tangimoana; although the trunks are thicker, the trees are both more widely spaced and taller (35 m compared with 18–20 m).

Furthermore, exposure to wind-carried salt is greatest at the exposed margin, and the effect decreases from the stand margin. The combined effects of crown abrasion and foliage loss induced by salt kills trees at the exposed margin, and the dieback front slowly moves through the stand. During a typical growing season, 30 or more salt-producing storms lasting for >8 h intensify the stress gradient. Storm frequency is only a guide to salt production, because on windy days, particles are produced whenever RH is <73%. Together, exposure, crown abrasion, and foliage loss reduce tree growth; small-diameter, subcanopy trees, stressed beyond their tolerance, die before the dieback front reaches them (Fig. 4).

Dieback rates at Waipapakauri vary from 1.2 to 1.9 m·year^{-1}. Dieback rates at Tangimoana were similar to those at Waipapakauri, but the dieback rate at Waitarere was much less because the trees were larger, more salt tolerant, and were not overcrowded. In part, the rate is determined by exposure and is less when trees are partially sheltered. Often, large trees do not die when the dieback front reaches them but remain as isolated trees and succumb from exposure several years later. The time taken for these vigorous trees to die depends on crown size and the amount of residual foliage on the sheltered side. Crown size and tree height are both in part governed by initial stocking density, because at wider spacing, some trees grow faster and larger than their neighbours.

Moloney (1986) reported similar effects of exposure on trees of different vigour from fir stands, where old canopy trees growing in less exposed sites survived the passage of a dieback front.

Regeneration

In contrast to firs, which are shade tolerant and stagnate until released by the advancing wave front, pine seedlings are light demanding and establish and survive only in relatively strong light. The dieback front in all pine stands was on the western side, which lets sunlight into the stand and, although improving the light environment, makes the litter drier. In Japan, dieback fronts are orientated so that sun enters the mature stand suggesting that, in fir stands, direct sunlight is important in the formation of regeneration waves (Kai 1974; Iwaki and Totsuka 1959; Kohyama 1988).

Summer dryness and some cattle grazing exclude competing species from the regeneration zone. Cattle are absent from dieback and regeneration areas in *P. pinaster* forests planted in the 1950s at Kawerua and Wairara. At Kawerua a 30 cm thick layer of kikuyu grass prevents pine seedlings from establishing, whereas at Wairara seedlings are excluded by tussock grass (*Cortaderia* sp.).

Pine seed is carried into the stand by prevailing onshore winds and can germinate 20 m ahead of the dieback front, but seedlings there must contend with litter that falls from vigorous trees above as well as that which is blown into the stand by wind. Seedlings can establish successfully 11–13 m ahead of the dieback front, but those that establish 20 m ahead die from summer drought if their roots fail to penetrate the thicker litter layer. Occasional seedlings that establish and survive 20 m ahead of the advancing front, gain from 1 to 3 year's competitive advantage before others establish, and this advantage is permanent. "Late" arrivals that germinate near already-established seedlings are handicapped by lower relative growth rates, and usually remain smaller or die early. Suppressed juveniles usually do not become part of the canopy but survive for 15–25 years, often growing taller but hardly increasing in girth. Some persist into mature stands as small-diameter, understorey trees and die as the front approaches.

Wave-regenerating fir forests are distinguished by the formation of several dieback fronts that follow one another, because both the mature and regenerating stands are overcrowded. Seedling densities at Waipapakauri are much lower than the 168 000 / ha found in some fir forests (Kohyama and Fujita 1981), but juvenile densities are higher than the current stocking rate of trees in the mature stand, suggesting that overcrowding will persist in the regenerating stand. At Waipapakauri, dieback began 21 years after the forest was planted. The oldest juveniles are now 33 years old, indicating that the development of a second dieback front has been suppressed by the *Cupressus macrocarpa* windbreak.

Forests at Tangimoana and Waitarere do not show the same clear-cut zones of regeneration (Fig. 6). Larger abrasion gaps have formed at Tangimoana, more light and less litter reaches the forest floor, and a scatter of grass and pine seedlings establishes well ahead of the dieback front (Fig. 6*a*). As smaller individuals die from self-thinning, the gradient of mixed-age juveniles should become less fuzzy. At Waitarere, grass and herbs grow on the forest floor, litter depth is constant, and seedlings establish up to 50 m ahead of the dieback front. There is no strong gradient of litter depth and light intensity extending ahead of the dieback front in either of these stands.

What factors drive regeneration waves?

The pine and fir forests grow in very windy sites, but temperatures, soils, and behaviour of trees are very different. Similarities and differences can isolate factors that drive regeneration waves. For regeneration waves to develop, the following combination of features appears to be essential:

1. (1) A unidirectional stress caused by persistent strong winds. Strong winds induce severe crown abrasion on the exposed side of a canopy gap or a stand. Dieback is caused by additional directional stress (sea salt or rime ice and root damage).
2. (2) Stand dominance by a tree species that is vulnerable to unidirectional stress. When high densities of seedlings establish at the dieback front, competing species are excluded, resulting in persistence of single-species dominance; other competitors are suppressed especially during episodes of drought or browsing.
3. (3) Regeneration that establishes (or is released) in a narrow zone that moves ahead of the dieback front; the narrow zone is created by a gradient of increasing litterfall ahead of the dieback front and summer dryness.
4. (4) Overcrowding of mature stands containing trees with tall trunks and small crowns.

Stands with a strongly developed age structure form when the juveniles establish in high numbers in a narrow zone that moves ahead of the dieback front. These stands have zones parallel with the dieback front of almost even-aged trees that will be all equally vulnerable when a dieback front approaches. Once the dieback starts it continues regardless of the age or status of the trees, providing that the unidirectional stress persists. As successive cycles pass through the stands and they become more zoned with respect to age, the dieback becomes increasingly synchronised. Propagation of a dieback front through such structured stands reinforces the strict gradation of ages with respect to the direction of wind stress.

Unlike the fir forests, the New Zealand pine forests do not show multiple regeneration waves. This may in part, result from differences in regeneration behaviour. Firs, in contrast to pines, are mast seeders, and the resulting severe overcrowding of seedlings and saplings excludes competing tree species and, thus, perpetuates near-pure stands of the canopy species. This amplifies the vulnerability of the mature stands and the synchrony of dieback and regeneration on a landscape scale.

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