Vegetation Mortality in the Kaimai Ranges, North Island, New Zealand[1]

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ABSTRACT: Areas of vegetation mortality have been recognized in the upland forests of the Kaimai Ranges, North Island, New Zealand. The mortality is not confined to any particular vegetation type, but occurs above a critical altitude that differs at different points along the ranges. The mortality is episodic and has occurred at intervals over a period of several hundred years, with severe droughts implicated as the causative factor. The numerous mortality events have resulted in forests of many age classes where trees do not reach potential maturity. The coincidence between the occurrence of cloud and the mortality is suggested to make the forests drought-sensitive through poorly developed root systems caused by prolonged soil waterlogging.

VEGETATION MORTALITY HAS BEEN EVIDENT in the Kaimai Ranges, North Island, New Zealand, for at least 40 yr, but it was only reported after a period of severe erosion triggered by an increased storm frequency (Dale and James 1977). Initially, it was suggested that introduced animals were responsible for both the vegetation mortality and the erosion, but in the ensuing investigations this was largely refuted and other causes sought (Jane and Green 1983a, 1983b).

The Kaimai Ranges are located in the northern North Island, range in altitude from 100 m to 950 m, and form three distinct prominences, Te Aroha, Te Rere, and Te Hunga, in which study areas were established (Figure 1). Lowland temperatures average 17°C in summer, 7°C in winter, and maxima rarely exceed 30°C in lowland areas or 20°C at upland sites. Rainfall ranges from 1500 mm in the foothills to the west to over 3000 mm on the southern prominences. Fog occurs on over 200 days a year and often persists for much of the day (Jane and Green 1983a). The average cloud base is at about 150 m below the ridge crest and differs in altitude among study areas. Upland soils are waterlogged for much of the year and rarely fall below field capacity (Jane and Green 1983a). Basement rock throughout the study areas is andesite or dacite overlain by fine-textured tephra up to 1 m deep. Soils in upland areas (derived from andesitic lava and breccia) are stony clays less than 1 m deep and low in bases and phosphates; these are further reduced in fertility by the presence of allophane.

VEGETATION

An altitudinal gradation in forest composition is marked by two ecotones. At the lower ecotone, near 300 m altitude, lowland *Beilschmiedia tawa/Dysoxylum spectabile* forest is replaced abruptly by *B. tawa* forest, in which *Dacrydium cupressinum* occurs as a scattered emergent and *Podocarpus ferrugineus* is common. At 600–700 m, there is a broad ecotone in which *B. tawa* disappears and *Ixerba brexioides* predominates. At 720 m, *Nothofagus menziesii* appears abruptly and rapidly increases in prominence to dominate the upland forest zone. In the upland zone, seral stands dominated by *Quintinia acutifolia* and *I. brexioides* are common and often cap the crest of the range.
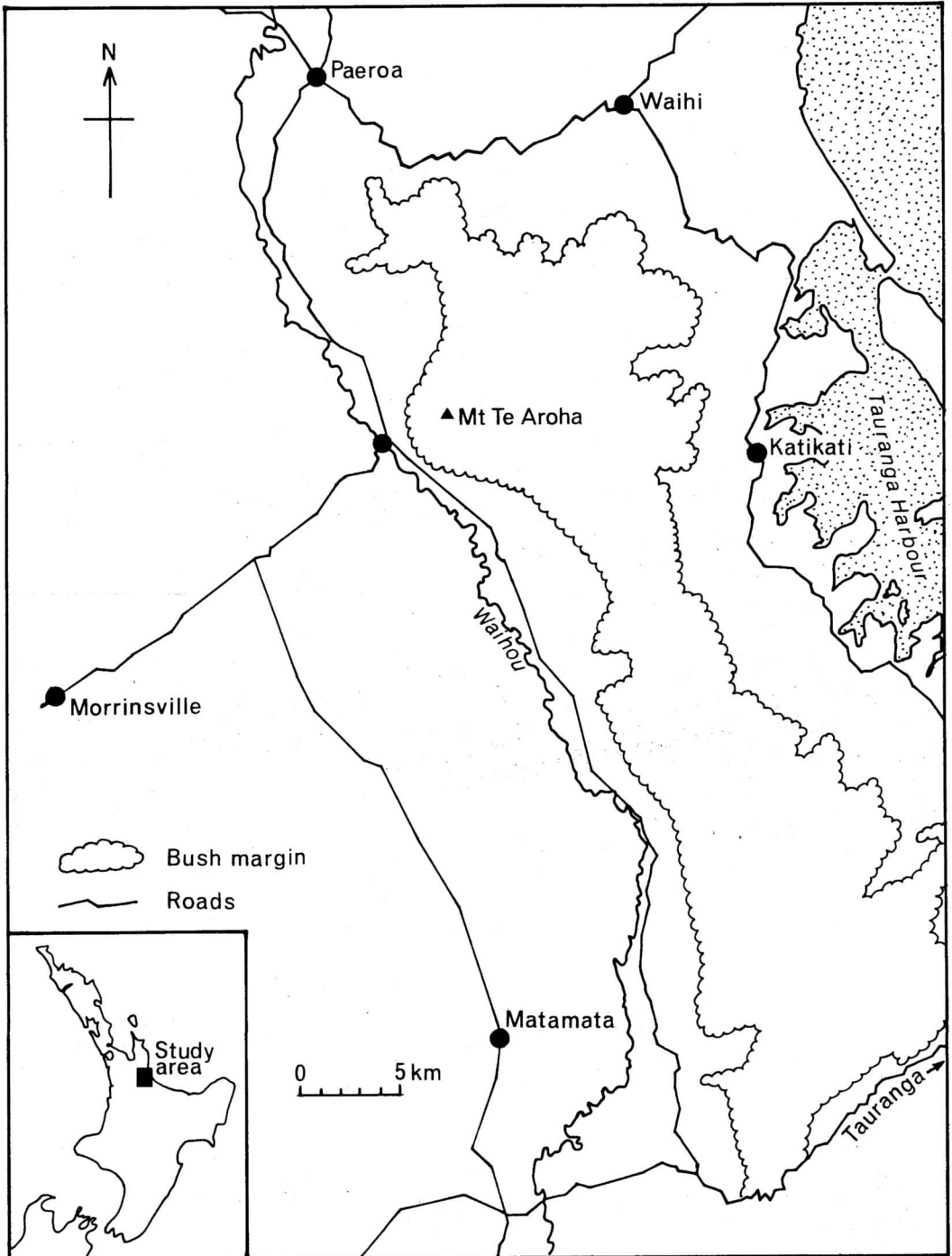
FIGURE 1. Location of the study areas in the Kaimai Ranges, North Island, New Zealand.
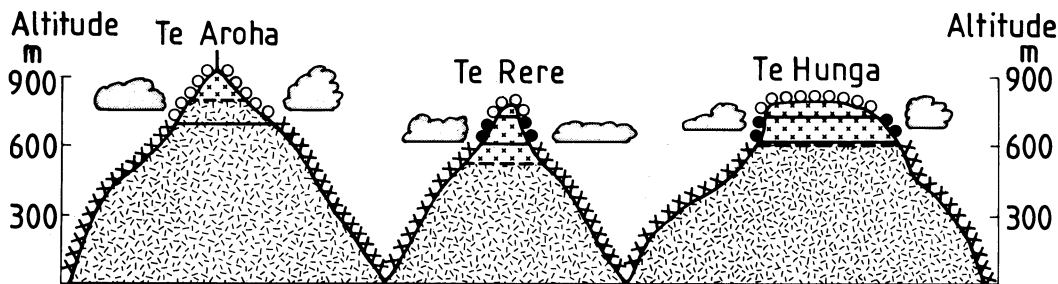
FIGURE 2. Schematic profile of the three peaks on the Kaimai Ranges showing vegetation distribution, vegetation vigor, and relative fog levels. Large Xs indicate *Beilschmiedia tawa* forests, solid dots indicate *Ixerba brexioides* forests, and open circles indicate *Nothofagus menziesii* forests; forest type boundaries are marked by solid lines, lower altitude boundaries of vegetation mortality are marked by dashed lines; healthy forest areas are indicated by short, straight lines, unhealthy forest areas are indicated by small xs; average cloud levels are indicated by the bases of the clouds.

VEGETATION MORTALITY

Location

Mortality occurs above 550 m altitude and on each prominence has a lower limit that corresponds closely with the predominant cloud base (Figure 2). In the cloud zone all forest types are affected, including *Beilschmiedia tawa*, *Ixerba brexioides*, and *Nothofagus menziesii* forest zones. There is a strong link between mortality and topography. Mortality may be severe in gully heads and absent in the lee of prominences. The severity of the damage ranges from complete mortality of canopy species to a light mosaic of killed trees. On individual trees, damage may be evident as leader dieback and general illthrift —stunting, yellow foliage, and reduced leaf size. Several age classes can be distinguished by vegetation height, and the mortality appears to be episodic (Jane and Green 1983a). Recent mortality can be reliably dated to droughts in 1972 and 1946 by comparison of aerial photographs and from observations of local inhabitants. Tree ring structure clearly expresses the intensity of these two summer droughts and suggests a number of earlier dates for similar episodes in 1656, 1804, 1861, and 1914. Forest age class structure also indicates periods of recruitment at these times. Many species do not survive for more than a portion of their potential life-spans, and seral species are killed in minor droughts so they do not reach their potential stature.

Causes

The distinct topographic and altitudinal bounds and dendroclimatic data suggest a strong direct drought effect. This is difficult to reconcile with the apparently abundant annual rainfall and in particular the close link with the cloud zone. One proposal was that since the habitat was largely waterlogged, root systems would be restricted, and the plants would be unable to respond adequately to water stress.

WATER POTENTIAL

Throughout the summer of 1981–1982, water potential and stomatal aperture were monitored at a number of localities inside and outside the fog zone (Jane and Green 1983c). Within the fog zone, dawn water potentials remained high and, when overnight fog was present, were close to full turgor. Midday values were about −1.5 MPa and generally compare with values obtained from plants of streamsides and wet habitats (Jane and Green 1983c). Afternoon recovery was normally evident in all species except *Quintinia acutifolia*, which was the least healthy of species studied. Plants at 700 m (below the fog zone) had lower dawn potentials, especially late in the season, but midday values were close to those obtained at higher altitudes. At no time was there evidence from plant water potentials for severe water limitation in any of the species.

TABLE 1

CUTICULAR CONDUCTANCES AND RATES OF STOMATAL CLOSURE

SPECIES	CUTICULAR CONDUCTANCES, OCTOBER	INTRINSIC RATES OF STOMATAL CLOSURE	RWD AT WILTING POINT
Tawari (*Ixerba brexioides*)	0.0034	0.014	6.2
Kamahi (*Weinmannia racemosa*)	0.0051	0.058	8.9
Quintinia (*Quintinia acutifolia*)	0.0052	0.150	7.0
Toro (*Myrsine salicina*)	0.0044	0.150	6.5
Silver beech (*Nothofagus menziesii*)	0.0041	0.044	Not evident
Miro (*Podocarpus ferrugineus*)	0.0025	0.264	Not evident
Five finger (*Pseudopanax colensoi*)	No data	0.020	2.2
Red beech (*Nothofagus fusca*)	0.0049	0.044	11.3
Hard beech (*Nothofagus truncata*)	0.0032	0.031	17.4

NOTE: Cuticular conductances measured at 20°C, 78% rh. Three replicates were taken of each species.

STOMATAL CONDUCTANCES

Stomatal conductances in the seral species were higher than in the canopy species, the latter having values similar to those found in hardwood trees. Diurnal patterns of conductance changed as the season progressed. Early in the season seral plants showed earlier, more rapid, morning opening than *Ixerba brexioides*, which is apparently restricted to the fog zone. All species showed gradual afternoon closure (Jane and Green 1983c). Later in the season, closure often began before midday. On two occasions closure occurred rapidly following fog clearance at midday. Water potential at stomatal closure was near usual midday values and well below the turgor loss point determined by pressure–volume techniques (Jane and Green 1983d). The high stomatal sensitivity was suggested to be due to restricted root development caused by soil waterlogging.

PLANT MORPHOLOGY

The physiological characteristics were reinforced by studies on plant habit, leaf characteristics, and leaf responses to drying under controlled conditions. Drying rates of beech species of limited distribution in the cloud forests and of seral plants were considerably higher than those of species common in the cloud forests (Table 1). Rates of stomatal closure and cuticular conductances show a similar pattern, with tawari (*Ixerba brexioides*), in particular, showing low values. In general, stomatal numbers were high compared to published values for evergreen shrubs and trees.

Nothofagus fusca and *N. truncata*, the beeches more common outside the cloud forests, have a very open canopy with high atmospheric coupling and high transpiration rates even after stomatal closure. Also, their thin leaves provide poor buffering capacity against rapid changes in water stress, suggesting a requirement for a good coupling with soil water. Plants from the cloud forests show many xeromorphic features. Scanning electron microscope (SEM) examinations of leaf surfaces showed very smooth cuticles with stomata enclosed below a cuticular antechamber in the canopy species and an abundance of waxes and rough cuticles in the seral species. Canopy species appear to differ in their capacity to retain intercepted precipitation in their canopies. *Nothofagus menziesii* retains large amounts of water in the canopy, a feature that would tend to ameliorate soil waterlogging and also lower transpiration losses after fog clearance. *Ixerba brexioides* retains much less water in the canopy but is tolerant of soil flooding and has thick leaves to buffer water losses. Both species have tight, smooth canopies in the cloud zone which would tend to minimize atmospheric coupling.

CONCLUSIONS

Dendrochronology studies and the resulting age-class analysis demonstrates that severe mortality events have occurred at intervals during the past 400 yr. Severe mortalities affecting all species have occurred every 100–150 yr; and lesser events that have affected plants, particularly seral species, or more sensitive sites have occurred at shorter intervals. Correlation with climate records in this century and dendrochronological climate estimations suggest droughts to be the major contributing factor. This is an unusual result in view of the high rainfall and fog occurrence in the area. Physiological studies indicate that the plants in the cloud forest are sensitive to even slight water stress and that the classic xeromorphological features of these forests are probably an adaptation to water stress. It is suggested that the almost continuous soil waterlogging in the area leads to poor root system development, in particular to very shallow root systems, and that a consequence of this is extreme sensitivity to even minor droughts.

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