

A REVIEW OF VEGETATION DEVELOPMENT FOLLOWING RECENT (<450 YEARS) VOLCANIC DISTURBANCE IN NORTH ISLAND, NEW ZEALAND

Summary: Volcanic activity has damaged or destroyed at least 20,000 ha of indigenous vegetation in the North Island in the last 450 years. The primary and secondary successions initiated are discussed and considered in relation to some recently proposed models of succession. Most of the variation relates to the scale and intensity of disturbance, and the type and heterogeneity of the substrate emplaced. Where disturbance has been extensive and severe, elements of slow 'classical' successions, from lichens and mosses to flowering plants, and facilitation by nitrogen-fixers such as *Coriaria* spp., are evident. In contrast, minor disturbance results in vegetative regrowth or regeneration of surviving species. Heterogeneity of substrate enables many taxonomic plant groups to establish more or less concurrently. Partial disturbance successions are not easily categorised and may contain elements of several successional models. The resource-ratio hypothesis of succession can be used to explain the general pattern of the volcanic successions outlined. Insufficient information, of the type suggested necessary by recent authors, is available to make detailed accurate predictions in respect of future volcanically-initiated successions. Recent volcanism has had a major influence on species distribution and vegetation patterns in the North Island.

Keywords: Succession; volcanic disturbance; vegetation; flora; New Zealand.

Introduction

This paper reviews vegetation development following disturbance by recent (<450 years) volcanic activity in the North Island, and discusses the applicability of various models of plant succession. Eruptions from major volcanic vents have occurred on seven volcanoes (Cole and Nairn, 1975): Rangitoto Island, White Island (Whakaari), Mt Tarawera, Mt Ngauruhoe, Mt Tongariro, Mt Ruapehu and Mt Taranaki (Mt Egmont) (Fig. 1). A range of vegetation disturbance from minor damage to complete destruction has occurred, spanning altitudes from sea level to more than 2000 m. Disturbance is here used in the sense of Sousa (1984), that is, a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.

Succession and successional models are considered first, followed by a select history of volcanic disturbance and vegetation development of locations which have been studied by the author. In the third section, an ecological interpretation of the successions outlined is provided. Fourth, the successional models described earlier are applied to some examples of vegetation development following volcanic disturbance. Concluding comments concern the chances of predicting successional trends after volcanic disturbance.

Models of succession

For the purposes of this review succession is considered a directional change with time in species composition and vegetation physiognomy of a single site where climate remains effectively constant (Finegan, 1984). Primary succession is the community formation process that begins on substrates that have never before supported vegetation whereas secondary succession occurs where residual soil and plants survive a disturbance. However, the distinction between the two is not always clear (Miles, 1979).

Clements (1916) restricted the concept of succession to changes resulting from biological reaction causing replacement of one plant community by another until, within a given climatic region, a climax was established. This came to be known as facilitation and relay floristics (Miles, 1979). Facilitation is also synonymous with autogenic change (Miles, 1979), that is, environmental changes occurring during succession as a consequence of the presence of plants, as opposed to allogenic change, which is caused by factors external to the vegetation.

Clements' model of succession was rejected by many researchers as inapplicable or not wholly applicable to observed vegetation change. Egler (1954) showed that an important factor in old field vegetation development was initial floristic composition. In contrast to the relay floristics

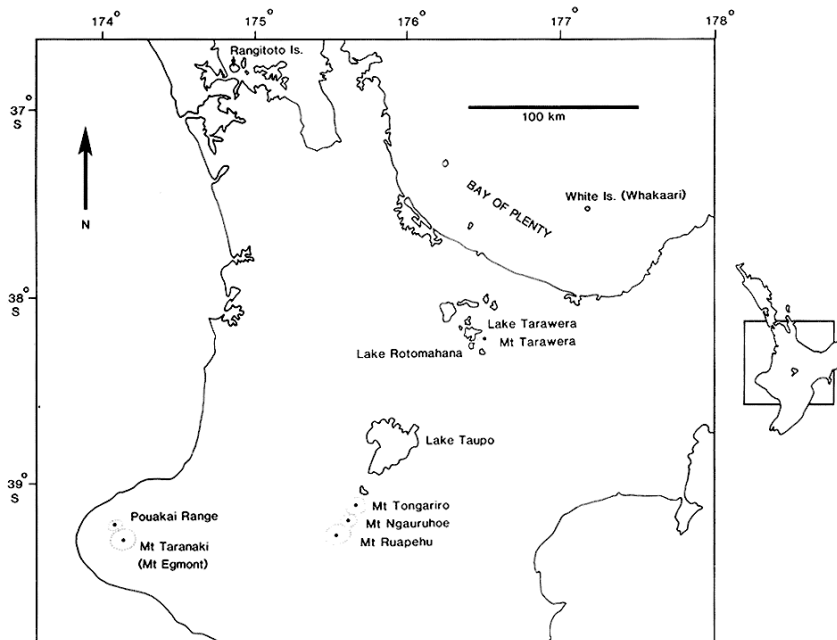


Figure 1: North Island showing localities mentioned in text.

emphasised by Clements, seed banks provide all the species destined to predominate at the start of the succession. In the early stages, the later dominants are small and inconspicuous. One succeeding group after another dominates the physiognomy, often weakening or killing preceding dominants.

Connell and Slatyer (1977) classified successional theories and outlined three alternative models of mechanisms that bring about successional change after a perturbation, assuming no further changes in the abiotic environment. In the 'facilitation' (relay floristics) model, the early-succession species modify the environment so that it is more suitable for later succession species to invade and grow to maturity. This sequence continues until the resident species no longer modifies the site in ways that facilitate the invasion and growth of different species. In the tolerance model, the modifications wrought on the environment by earlier colonists neither increase nor reduce the rates of recruitment and growth to maturity of later colonists. Species that appear later are simply those that arrived either at the very beginning or later and then grew slowly. The sequence of species is determined solely by their life history characteristics and tolerance of environmental factors (e.g., shade tolerance). The inhibition model holds that once earlier colonists secure space and/or resources they inhibit invasion

of subsequent colonists or suppress the growth of those already present. The latter invade or grow only when the dominating residents are damaged or killed, thus releasing resources.

Connell and Slatyer (1977) suggested there was evidence for the first model mainly in relation to primary successions, that there was little evidence presently available to support the tolerance model, and a considerable body of evidence supporting the inhibition model. More recent work (e.g., Hils and Vankat, 1982) has suggested that the tolerance model was only disfavoured because the right kinds of experiments had never been undertaken. The major dichotomy between the alternative models of succession occurs between relay floristics and initial floristic composition. Up to this point all the models agree that certain species will usually appear first because they have evolved 'colonising' characteristics but they differ in the mechanisms which determine how new species appear later in the sequence.

Finegan (1984) noted that the different models of succession were not mutually exclusive. He considered that neither the reductionist (e.g., initial floristic composition) nor holistic (e.g., facilitation) theories of succession have produced models which explain field observations and that a synthetic approach should be sought. Thus facilitation, tolerance, inhibition and allogeneses are

interdependent mechanisms and may affect the same individual successively or simultaneously during its life cycle. Further, the relative importance of various mechanisms is likely to vary widely between environments and attempts to classify succession on the basis of a single underlying mechanism only obscure understanding and inhibit progress.

Tilman's (1985) attempt at an alternative simple theory of succession focussed on resource changes during succession. According to his resource-ratio hypothesis, succession results from a gradient through time in the relative availabilities of limiting resources, in particular the inverse relationship between soil nutrient status and light available at the soil surface. Each species is a superior competitor at different points along the temporal gradient. In addition, succession should be directional or repeatable only to the extent that the resource supply trajectory is repeatable or directional.

Johnstone (1986) in reviewing invasion success pointed out that time was not a cause of succession, as inferred by many studies. Rather, succession should be seen as the expression of an interaction of species in an assemblage as a result of invasion, maintenance and decline. These processes are stochastic in the sense that the causes for the probability is system dependent, and because of the dynamic interaction of processes, inherently difficult to predict.

Pickett, Collins and Armesto (1987) clarified and expanded Connell and Slatyer's models by elaborating the mechanisms of succession involved in each. Facilitation was seen as operating through enhanced invasion, amelioration of environmental stress or increase in resource availability. Tolerance was shown to be able to be interpreted in two ways, active and passive. An example of active tolerance is the ability of an organism to endure low resource levels. An example of passive tolerance is contrasting life histories (e.g., life span leading to replacement of short-lived faster growing species by longer-lived slow growing species). Inhibition was also shown to be complex, grading into tolerance depending on whether the interaction is seen from the viewpoint of the incumbent or the challenger. In attempting to generalise about the mechanisms of replacement, Pickett *et al.* (1987) noted that the models were only useful when restricted to describing particular replacements of species in a succession.

Select history of volcanic disturbance and vegetation development

Six areas are described as summarised in Table 1. Vegetation and substrate type names follow the

naming system of Atkinson (1985) but underlining to indicate cover classes of the leading dominants is not used. Species names follow Allan (1961), Moore and Edgar (1970), Allison and Child (1971), Galloway (1985) and Connor and Edgar (1987).

White Island

White Island, a 238 ha andesite cone in the Bay of Plenty, has been in a state of continuous solfataric activity, with intermittent small steam and tephra eruptions since 1826 when the first recorded landing was made by Europeans (Nairn and Wood, 1986). Between December 1976 and December 1981 the largest and longest eruptive episode on the island in historic times occurred (Houghton *et al.*, 1983), killing large areas of *Metrosideros excelsa* forests (B.J. Scott, pers. comm.). Prior to this there are reports of only minor vegetation damage, for example, loss of leaves by *Metrosideros* followed by rapid recovery (parham, 1973).

The extant vegetation on the island comprises a simple forest and scrub type entirely dominated by *Metrosideros excelsa*, and herb fields and grasslands associated with gannetries in which the dominant species are *Disphyma australe* subsp. *australe*, *Einadia trigonos* subsp. *trigonos*, and *Poa anceps* subsp. *anceps*.

A survey in 1986 (Clarkson, Clarkson and Smale 1989) showed that the extent of the *Metrosideros* forest and scrub (c. 48 ha) had been reduced by more than one half by the recent eruptions. Only c. 5% of the *Metrosideros* trees in the area badly affected by the eruptions survived, the result of resprouting from epicormic buds (Fig. 2). A few carried seed capsules, evidently formed during the December 1985 flowering season but no seedling or sapling *Metrosideros* were noted in the vicinity. At a site where all the *Metrosideros* trees were dead, a single individual of the fern *Histiopteris incisa* had apparently survived. The actual cause of death of the *Metrosideros* trees and shrubs was difficult to determine so long after the eruptions. However, as no evidence of blast or burn was seen, and ultimate branches remained intact on the majority of individuals, the most likely causes were toxic fumes, wet ash coating leaves and interfering with vital processes, and 'acid rain'. Fumes were identified by earlier workers (Oliver, 1915; Hamilton, 1959) as the most likely factor controlling the distribution and extent of *Metrosideros* forest and scrub. The vascular flora in the last 50 years has numbered at most 13 species (Oliver, 1915; Hamilton, 1959; Wilcox, 1967) but a recent survey (Clarkson *et al.*, 1989) recorded only 7 species. I have found no published records of bryophytes, lichens or terrestrial algae. Species lost from the eruption-affected area were

Table 1: Summary of selected vegetation successions following recent volcanic disturbance.

Location	Bioclimatic zone	Main present day vegetation types discussed	Succession P vs S	Timespan	Volcanic Deposits	Rates of change and/or recovery.
White Is	coastal	<i>Metrosideros excelsa</i> forest & scrub <i>Disphyma australe</i> , <i>Einadia trigonos</i> , and <i>Poa anceps</i> herb fields & grasslands	P > S	10-20 yrs	AT	F
Rangitoto Is	coastal	<i>Metrosideros excelsa</i> forest	P > S	10-20 yrs	AT	F
		<i>Leptospermum scoparium</i> - <i>Olearia furfuracea</i> scrub [<i>Stereocaulon vesuvianum</i>] + [<i>Racomitrium lanuginosum</i>] lavafields	P > S	>200 yrs	BAL + BT	F
Mt Tarawera	lowland	<i>Beilschmiedia tawa</i> forest	P	>200 yrs	BAL	S
		<i>Weinmannia racemosa</i> forest	S	103 yrs	RM	F
Mt Tarawera	montane	<i>Meliclytus ramiflorus</i> forest	P > S	103 yrs	BT + RM	F
		<i>Coriaria arborea</i> scrub grass-herb-lichen plant aggregations <i>Muehlenbeckia axillaries</i> - <i>Campylopus clavatus</i> plant aggregations	P	103 yrs	BT	M
Mt Tongariro	montane	<i>Racomitrium lanuginosum</i> mossfield	P	103 yrs	BT	S
		<i>Phyllocladus alpinus</i> / <i>Leptospermum scoparium</i> scrub	P	103 yrs	BT + RB	S
Mt Ngauruhoe	montane & subalpine	<i>Racomitrium lanuginosum</i> mossfield	P	c.450 yrs	AAL	M
		<i>Rytidosperma setifolium</i> - <i>Gaultheria colensoi</i> - <i>Dracophyllum recurvum</i> gravelfield	P	c.450 yrs	AAL	S
Mt Taranaki	lowland	<i>Stereocaulon vesuvianum</i> - <i>Racomitrium lanuginosum</i> boulderfield	P	129 yrs	AAL + AT	S
		[<i>Campylopus clavatus</i>] gravel & stonefields	P	35 yrs	AAL	S
		[<i>Raoulia albosericca</i>] gravel & boulderfields	P	35 yrs	AAL	S
			P	14 yrs	AAD	S
Mt Taranaki	lowland	<i>Metrosideros robusta</i> - <i>Weinmannia racemosa</i> forest	P > S	c.450 yrs	MD	M
		<i>Dacrydium cupressinum</i> - <i>Metrosideros robusta</i> / <i>Meliclytus ramiflorus</i> - <i>Weinmannia racemosa</i> forest	S	c.330 yrs	AT	F
		<i>Leptospermum scoparium</i> / <i>Baumea rubiginosa</i> sedgeland	P	c.450 yrs	MD	S
	subalpine	<i>Weinmannia racemosa</i> forest	S > P	c.330 yrs	AT	M
		<i>Brachyglottis elaeagnifolia</i> scrub	P	c.450 yrs	MD	S
		<i>Libocedrus bidwillii</i> / <i>Brachyglottis elaeagnifolia</i> scrub grass-herb-moss plant aggregations	P > S	c.330 yrs	AT	S
	P	c.450 yrs	MD	S		

* i.e., expected time to return to vegetation type predicted for the bioclimatic zone, in the absence of further disturbance.

P	= primary succession	RM	= Rotomahana mud (weakly altered rhyolitic pumice and lake sediment)	F	= fast (several centuries)
S	= secondary succession	MD	= Maero debris flows (andesitic)	M	= medium (several centuries to many centuries)
AT	= andesitic tephra	RB	= rhyolitic boulders	S	= slow (many centuries to one thousand years or more)
AAL	= andesitic aa lava				
BT	= basaltic tephra				
BAL	= basaltic aa lava				
AAD	= andesitic avalanche deposits				

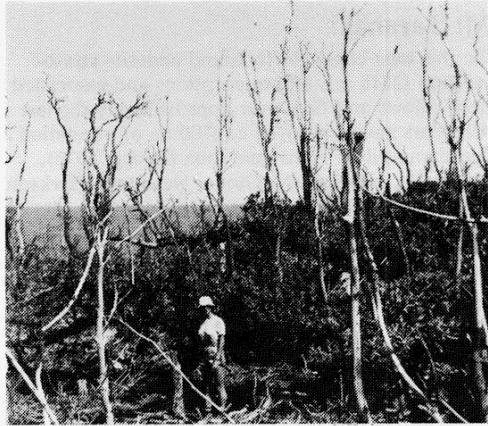


Figure 2: *Metrosideros excelsa* at old campsite Ohauora, White Island showing dead crowns and recovery by epicormic resprouts (1986).

mainly dicotyledonous herbs associated with gannetries, and burial by tephra was probably the main cause.

Mt Tarawera

Mt Tarawera, a series of coalescing low rhyolite domes and an associated crater lake (Lake Rotomahana) erupted in 1886, initiating primary successions over c. 10 km² and secondary successions over a further c. 20 km². Eye witness accounts of the eruptions and subsequent 100 years of vegetation change are available (Thomas, 1888; Aston, 1915; Turner, 1928; Burke, 1964; Nicholls, 1963; Dickinson, 1980; Timmins, 1983; Clarkson and Clarkson, 1983).

Rates and patterns of vegetation change have been variable. At some of the most inhospitable sites on the peaks, such as those comprising large rhyolite boulders with a matrix of scoria, lichens and mosses have established but not flowering plants. On the unstable ash and lapilli slopes in the vicinity of Ruawahia trig (1111 m) plant aggregations, dominated by *Muehlenbeckia axillaris* and *Campylopus clavatus* and assumed to have established within 50 years of the eruption, in a 15 year period (1964-1979) doubled from 2.5 m² to 4.5 m², and taxa increased from 13 to 19 (Clarkson and Clarkson, 1983). At other high altitude sites, life forms ranging from mosses to ferns and flowering plants were all present within 27 years of the eruption but in different microsites e.g., rock crevices, tephra flats, hollows (Aston, 1915). At a crater site ('Crater 7') the total vascular flora increased from 63 to 74 in fifteen years (1964-1979), with 28 taxa having established and 17 being lost (Clarkson and Clarkson, 1983). A

Racomitrium lanuginosum mossfield adjacent to the crater doubled in extent over the same period (Clarkson and Clarkson, 1983). On the extensive tephra flats of Plateau dome plant aggregations dominated mainly by grasses, herbs, mosses, lichens and small shrubs with up to 35 taxa, including several hybrids, over the last 25 years coalesced into continuous mats of vegetation (Fig.3).

In the last 10 years taller shrubs, especially *Coriaria arborea*, which fixes nitrogen through symbiosis with an actinomycete endophyte (*Frankia*) (Silvester, 1978), have entered these aggregations and plants have now coalesced to form continuous scrub. During this transition up to 50 taxa were present in some large aggregations but with the development of continuous scrub and the consequent loss of light-demanding taxa the number dropped to as few as 10. Change has been most rapid along a front just beyond the present forest edge. In 70 years bare surfaces progressed to grass-herb-lichen ring growths (Burke, 1964). Subsequently *Coriaria* scrub has developed in 15 years (1964-1979) (Clarkson and Clarkson, 1983). Seedlings and saplings of the forest trees *Weinmannia racemosa* and *Griselinia littoralis* had established in this scrub type before 1979. Unusually severe winter frosts in 1982 caused some *Coriaria* to die back, releasing some saplings of *Weinmannia* and *Griselinia* the following year. The sequence described above was considerably contracted in time closer to the interface between a primary surface and sites where forest survived the eruption, low *Weinmannia* or *Kunzea ericoides* forest having been in place more than 50 years.



Figure 3: Plant aggregations, comprising mainly mosses, lichens and grasses with shrubs of *Dracophyllum subulatum*, on Plateau dome (944 m a.s.l.), Mt Tarawera; *Conaria arborea* shrubs are beginning to invade (1979).

One pocket of forest within 1.5 km of the nearest crater has trees of six different canopy species which survived the eruption. However, it is surrounded by stands of *Weinmannia* into which there is little or no spread of the other potential canopy dominants.

Nearly all taxa present on dome tops have probably arrived from sources within the Rotorua Lakes District, through propagules dispersed by wind or birds from a range of unforested sites such as 'frost flats', mire margins or rock outcrops, or from vegetation disturbed at an earlier time. Likely exceptions include *Helichrysum* sp. unnamed ('H. alpinum' of Cockayne, 1928), *Raoulia* sp. unnamed (aff. *R. australis*), *Cassinia vauvilliersii*, *Epilobium glabellum* and *E. melanocaulon*, all with wind dispersed seed and otherwise known only from localities more than 50 km away.

Where Rotomahana mud was thickly deposited on slopes, as in parts of Lake Tarawera Scenic Reserve, successions have led to *Melicytus ramiflorus* dominance and *Weinmannia* is either absent or rare. Where forest was only partly damaged, trees such as *Weinmannia* and *Beilschmiedia tawa* resprouted from epicormic buds and some even flowered within a year of the eruption (Aston, 1915). Outside the forests the fern *Pteridium esculentum* penetrated wherever the Rotomahana mud was less than 0.6 m thick (Nicholls, 1963). Remnants of *Beilschmiedia*-dominant forest, covering 10-30 ha, representing many survivors of the Tarawera eruption, have a native vascular flora of 60-80 taxa, similar in number to stands unaffected by the eruption. However, in the volcanically-disturbed forest, *Litsea calicaris*, *Knightia excelsa* and *Weinmannia* are more common in the canopy, *Metrosideros robusta* and *Dacrydium cupressinum* less so, and tree height and basal area are significantly lower.

The relatively even-aged *Weinmannia* forests which developed on the southern slopes of Mt Tarawera after the eruption have the potential for cohort senescence and die back. Assuming a lifespan of c. 300 years (Beveridge, 1973), dieback could be expected to occur about 2200 AD. Perhaps then, potential canopy species, represented now by saplings and seedlings will have their opportunity to reach the canopy. Thus at higher altitude there may be a return of *Podocarpus hallii* *Weinmannia* forest which existed before the eruption, as evidenced by the many dead *Podocarpus* spars. And at lower altitude, *Nestegis lanceolata*, *Beilschmiedia* and *Litsea* should benefit but there is only limited indication yet that *Dacrydium* or other podocarps might become prominent (Burke, 1974).

Mt Taranaki

On this west coast North Island andesite strato-volcano (2518 m), tephra eruptions and associated debris flows and fires over approximately the last 450 years have destroyed c. 6700 ha of vegetation and damaged an equivalent area (Druce, 1976).

Pollen analysis (McGlone, Neall and Clarkson, 1988) suggests that areas of upper montane forest completely destroyed or badly damaged by the Burrell eruptions of 1655 AD (Druce, 1966) have shown a succession from shrubs, including *Coriaria arborea*, to *Kunzea* and *Fuchsia excorticata*, and then to *Weinmannia* forest. However, *Libocedrus bidwillii* has not, as yet, regained lost ground, being found as scattered survivors over a low canopy of broadleaved shrubs such as *Brachyglottis elaeagnifolia* (Fig. 4). The treeline and upper altitudinal limits of tree species are generally lower on Mt Taranaki than on the adjacent, less-affected Pouakai Range (Clarkson, 1981). Upper montane forest stands today are still characterised by the extreme dominance of *Weinmannia* and a vascular flora of c. 40 taxa (probably fewer than in the transitional stages some 100-150 years ago). In the lowland forest zone, where damage was less severe, many *Weinmannia* resprouted from epicormic buds and gained dominance within 50 years of the eruption except in the sector between Waingongoro River and Kaupokonui Stream. Here the combination of minor damage and a dressing of very fine ash, raised soil nutrients to a level that enabled *Melicytus* to become very prominent (Druce, 1964). A topographic pattern of *Melicytus* dominance on flat to moderate slopes, where ash is retained or accumulated, and *Weinmannia* on steeper slopes, where it has been lost, remains to this day (Clarkson, 1981).



Figure 4: Pre-Burrell eruption *Libocedrus bidwillii* emergent over broadleaved scrub beside Stratford Mountain Road (1035 m a.s.l.), Mt Taranaki (1990).

On the debris fans formed by Maero debris flows following the Newall eruptions of c. 1550 AD (Druce, 1966), the forest upper limit is depressed by 300 m. A lowered upper limit of the forest tree *Beilschmiedia* also occurs. On the lower portion of these fans *Metrosideros*, which established terrestrially along with more slender *Weinmannia*, make up the bulk of the forest. *Kunzea* is prominent on sites affected by even more recent (c. 100 yr) Kahui flows. Above the forest limit the debris fans have been colonised by moss fields of *Racomitrium lanuginosum* and *R. ptycophyllum*. In these mossfields, circular aggregations of the rhizomatous shrubs *Coriaria pteridoides* and *C. plumosa*, which have nitrogen-fixing symbionts, along with *Chionochloa mbra* and up to 15 subalpine or alpine grass and herb taxa have established (Fig. 5) (Clarkson, 1986). Similar aggregations of shrub species also occur at lower altitude on these debris fans; there are places where these have coalesced to produce a continuous scrub. Elsewhere 100 year old 'crops' of *Brachyglottis elaeagnifolia* occur with no obvious evidence of aggregation. On moderately sloping portions of the fans, where drainage is impeded, simple mire types comprising mainly the shrub *Leptospermum scoparium* and the sedge *Baumea mbiginosa* have developed.



Figure 5: *Chionochloa rubra* (centre) and *Coriaria pteridoides* and/or *Coriaria plumosa* (margins) aggregations in a matrix of *Racomitrium lanuginosum* mossfield on the western slopes (1066 m a.s.l.) of Mt Taranaki (1982).

Rangitoto Island

On Rangitoto Island, a basalt shield volcano, lava flows and cone building tephra eruptions provided some 20 km² of primary surface for plants to colonise. According to Robertson (1986), the volcano appears to have been active between 850 AD and 1800 AD with a maximum lava flow

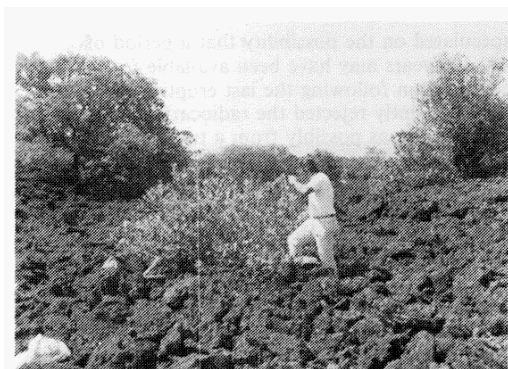


Figure 6: *Metrosideros excelsa* aggregations on Rangitoto Island basalt aa lava (1990).

activity around 1300 AD. However, Clark (1989) suggests that it is unlikely any eruption occurred after 1500 AD. The primary surface is mainly crusty (aa) basaltic lava but the summit consists of scoria cones. The last lava flows were followed by an emission of ash which filled most of the crevices and shallow hollows (Millener, 1979).

Millener (1953; 1979) and Atkinson (1960) have described the vegetation in detail. On the most inhospitable sites only lichens, mosses (including *R. lanuginosum*) and blue-green algae are present and forest is not expected to develop for hundreds, probably thousands, of years. On the other lava fields this sequence is being bypassed by the progressive establishment of aggregations of higher vegetation, usually centered around the prime rock coloniser, *Metrosideros excelsa* (Fig. 6). In places these have coalesced to form continuous forest. In the more scrubby open growth, *Leptospermum scoparium*, *Styphelia fasciculata*, *Hebe stricta* var. *stricta*, *Olearia furfuracea* and *Coriaria arborea* are prominent. On the scoria cones, *Leptospermum* and *Olearia* are most abundant and the presence of emergent *Metrosideros excelsa* and *Knightia excelsa* indicates the early stages of forest development.

The indigenous vascular flora of the island exceeds 210 taxa (R.O. Gardner, 1987, unpublished species list) and of great interest is the range and abundance of *Metrosideros excelsa* x *M. robusta* hybrids (Cooper, 1954).

Millener (1979) claimed that, as the oldest trees he aged were <200 years and a radiocarbon date of wood buried beneath the lava gave 225 years BP \pm 110, the development of *Metrosideros excelsa* forest was initially rapid. The first trees established in the ash accumulations and quickly spread over the island last century, slowing down as favourable habitats became fewer. However, Atkinson (1960)

speculated on the possibility that a period of 450-500 years may have been available for plant colonisation following the last eruption and Clark (1989) recently rejected the radiocarbon date cited by Millener, as possibly from a tree-root post-dating the lava. Further research on the vegetation is required to resolve what Atkinson termed the problem of Rangitoto.

In forest on much older basaltic lava blocks on the eastern flank of Mt Eden, *Metrosideros excelsa* shares dominance with *Vitex lucens*, *Litsea calicaris*, *Dysoxylum spectabile*, *Alectryon excelsus* and *Myoporum laetum* (Millener, 1979) and this might indicate future trends.

Mt Ngauruhoe and Mt Tongariro

Lava flows, pyroclastic flows and debris flows from Mt Ngauruhoe (Fig. 7) and Mt Tongariro, andesite central North Island cones reaching 2291 m and 1968 m respectively, have overwhelmed some 12 km² of vegetation between c. 1550 AD and the present day.

Prehistoric lava flows in the Mangatepopo Valley support mainly *Dracophyllum recurvum*-*Rytidosperma setifolium*/*Campylopus clavatus* shrubland with up to 50 taxa present overall.



Figure 7: Mt Ngauruhoe showing prehistoric lava flows (foreground), 1949-54 lava flows (middleground) and 1975 pyroclastic flows on upper slopes (1987).

The c. 450 year old Te Mari flow (Topping, 1974) on the northern slopes of Tongariro extends from 1400 m to 800 m a.s.l. Adjacent unaffected vegetation is, in ascending order, *Podocarpus hallii* forest, *Phyllocladus alpinus* / *Leptospermum scoparium* scrub and *Chionochloa rubra*/*Dracophyllum recurvum* tussockland (Atkinson, 1981). The lower one-third of the flow has returned to tall *P. alpinus*/L. *scoparium* scrub containing the probable future forest dominant *P. hallii* (Atkinson, 1981) while the upper two-thirds supports only sparse vegetation dominated by

Racomitrium lanuginosum although with more than 30 other taxa present (I.A.E. Atkinson and C.C. Ogle in Uhe, 1972).

At 1675 m, Ngauruhoe lava flows erupted in 1870 support a floristically poor (c. 30 taxa) vegetation with 25-39/0 cover, the main species being *Rytidosperma setifolium*, *Gaultheria colensoi* and *D. recurvum*. The grasses, herbs and shrubs grow mainly in ash or gravel overlying the lava with mosses and lichens present on the lava boulders. There has been no detectable change in cover or composition since Uhe (1972) sampled these flows in 1966.

Flows erupted in 1949 and 1954 (Gregg, 1960) and extending in a westerly and northwesterly direction from 2070 m to 1324 m a.s.l., are floristically poorer with 4 to 11 taxa, depending on altitude and the proportions of boulders, stones, gravel and ash present. The most extensive surface, comprising boulder-sized lava blocks, has the poorest type, *Stereocaulon vesuvianum*-*Racomitrium lanuginosum* boulderfield, which has cover values exceeding 50%. Sites with higher proportions of gravel, stones and ash, that accumulated after the lava was emplaced, are mainly [*Campylopus clavatus*] gravel or stonefields. Although supporting more species, including *Rytidosperma setifolium* and *Raoulia albosericea*, cover does not exceed 33%. In 1966 Uhe (1972) noted only *R. lanuginosum* and *S. vesuvianum* on the 1954 lava blocks so there has been a significant increase in the number of species and cover of vegetation in the intervening 21 years but rates of change are still extremely slow.

From the outset the pyroclastic flows of 1975 (Nairn and Self, 1978) comprised a greater mixture of different sized particles, and subsequent debris flows have continued to add to this. They can be classified mainly as [*Raoulia albosericea*] gravel or boulderfields and have 6-10 taxa. The faster rate and concurrent establishment of different taxonomic groups, highlights the importance of the nature of the ejecta for plant colonisation and establishment.

Only on the lower portion of the Te Mari flow has there been sequential replacement of one species group by another. In contrast, on the other flows, although species have established either at different times or concurrently, albeit on different microsites, there has been a gradual accumulation of species.

Interpretation

Plant successions on volcanic substrates are extremely variable both in terms of rates of change and the sequence of species establishing. Allowing for bioclimatic zonal differences, the variability is

explicable in terms of a gradient of scale and severity of disturbance, and of suitability of the substrate emplaced for plant establishment and growth. On relatively homogeneous, excessively drained or exposed habitats, resulting from disturbance so severe that no plants or dormant propagules survive, the slow 'classical' succession beginning with lichens and mosses is evident.

Where the severity is as great but there is less uniformity in the surface emplaced, with different microsites available, especially ash accumulations, all taxonomic groups of plants establish more or less concurrently. Most of the 'soils' available following extensive severe disturbance are deficient in nutrients, particularly phosphorus and nitrogen, and have very low water-holding capacity (Uhe, 1972).

Nitrogen-fixers, including lichens and *Coriaria* spp. may significantly alter soils or other aspects of the environment, making it more suitable for later successional species to invade or grow to maturity. Plant aggregations that later coalesce into continuous cover are usually a feature of these successions. The species involved are generally shade-intolerant, tolerant of low nutrient levels or possess efficient nutrient uptake systems through mycorrhizal associations (Uhe, 1972). They also tend to be short lived and have propagules that are readily dispersed by wind or birds. Dispersal is mainly from nearby open sites or vegetation recovering from earlier eruptions. The creation of open habitat (*sensu* Grant, 1981) allows abundant overlap of taxonomically related species, which rarely or never occurs in later successional stages. Thus hybrids and hybrid swarms are relatively common. On soils low in nitrogen but with sufficient phosphorus and bases to allow *Coriaria* spp. to establish and grow vigorously (Vucetich and Wells, 1982), succession rates are faster, e.g., Rotomahana mud and Burrell tephra, than on soils where *Coriaria* spp. establishment is delayed, e.g., Tarawera lapilli.

Where vegetation is severely damaged but new surfaces are discontinuous or where new material forms a thin veneer, recovery can involve establishment of species ranging from those characteristic of primary successions to those from existing 'mature' vegetation. Seed banks, short-distance dispersal, sapling release and vegetative regrowth may all be involved. Decay of plants killed by the disturbance may provide an initial nutrient source to early colonisers and, depending on rooting depths, tephra depths and penetrability, buried soils may or may not be available. Several of the tall forest trees have attributes which enable them to recover from damage rapidly or reoccupy bared ground quickly. *Weinmannia* and

Metrosideros produce abundant, light, wind-dispersed seed from an early age, and can coppice after damage. *Bellschmidia* also coppices but has more limited seed dispersal and is less competitive on thick tephra. *Litsea* and *Meliclytus* are apparently intermediate in their ability to cope with volcanic disturbance, with the latter requiring a relatively fertile substrate.

Finally, in situations where damage is only slight, little change may occur in the composition or structure of the vegetation. Frequently a small canopy gap or margin may be closed by vegetative expansion or release of an existing juvenile.

Application of successional models

The examples of vegetation succession outlined illustrate many elements of successional models or theories described earlier. At one extreme some primary successions, for example, on the dome tops of Tarawera, have elements of facilitation, autogenic change, and relay floristics. Changes in the composition of plant aggregations seem to involve a range of models including facilitation and inhibition but the replacement is not deterministic. That is, when dieback occurred of plants within the Tarawera Plateau dome aggregations, the resulting space could be occupied by either new species or species already present. Alternatively, new species established even in the absence of dieback of parts of the plant aggregation.

The tolerance model is applicable when considering early establishment of plant aggregations as the species are able to tolerate low substrate resource levels and full exposure to light. The facilitation model is applicable where the aggregations modify the substrate in any way which enables new species to colonise. For example, through stabilisation of tephra on slopes or trapping of 'fines', improving the water holding capacity of the substrate or increasing the nitrogen status of soils.

The development of *Coriaria* scrub increases the nitrogen status of the soils and changes the microclimate and light characteristics of the 'soil' surface. The rapid change in the flora which results from *Coriaria* dominance and shading out of the plant aggregations is consistent with relay floristics. Seedlings of forest trees *Weinmannia* and *Griselinia* establish preferentially beneath the *Coriaria* (facilitation); the change from *Coriaria* scrub to *Weinmannia-Griselinia* forest however arises in several ways. The checking of *Coriaria* caused by frosting and the subsequent release of saplings of *Weinmannia* and *Griselinia* fits the inhibition model. When *Weinmannia* or *Griselinia* overtop healthy *Coriaria* they are able to do so because they can, as seedlings or saplings, tolerate the

degree of shading characteristic of a *Coriaria* canopy. When *Weinmannia* or *Griselinia* overtop a naturally senescent *Coriaria* canopy the inhibition model is applicable.

Successions with partial disturbance are especially difficult to fit into successional models. On Mt Tarawera and Mt Taranaki where forest canopies were partly killed, neither relay floristics nor initial floristics encompass the resulting mosaic vegetation pattern. Some existing canopy trees recovered, some undergrowth species were released and other species colonised the sites. Separating examples of tolerance and inhibition seems almost impossible in some instances. On Mt Tarawera and Mt Taranaki most canopies dominated by *Kunzea* seem to offer little resistance to invasion by *Weinmannia*. In contrast, *Beilschmiedia* seedlings are both suppressed by, and tolerant of, the lower light levels under the earlier established *Weinmannia* canopy. In successions on the lava flows of Rangitoto Island and Mt Ngauruhoe, allogenic change through the accumulation of ash or lapilli after the lava is emplaced significantly affects the composition and rate of species invasion. On White Island the very depauperate flora, including the single pioneer tree species *Metrosideros excelsa*, ensures that the relay floristics model cannot apply at all over the period studied. *Metrosideros* becomes dominant early by recovery from the disturbance, or later by colonisation of the new surface. This succession could be considered as an example of the tolerance model but the term 'direct succession' as used by Whittaker and Levin (1977) appears more appropriate.

In short, these examples support Finegan's (1984) conclusion that facilitation, tolerance, inhibition and allogenesis are interdependent mechanisms in succession and may affect the same individual successively or simultaneously during its life cycle. They also highlight the need to consider specific replacements rather than whole pathways as outlined by Pickett *et al.* (1987).

The recently proposed resource-ratio hypothesis of succession (Tilman, 1985) can be used to explain the general pattern of the successions described without the need to categorise them. As outlined earlier, succession results from a gradient through time of the relative availabilities of limiting resources, in particular the inverse relationship between soil nutrient status and irradiance levels at the soil surface. Different scales or severities of volcanic disturbance initiate different resource supply trajectories and each species is a superior competitor at different points along such temporal gradients. As predicted by the hypothesis, the same qualitative separation and

ordering of species along spatial resource gradients is apparent. However, Tilman recognises but does not incorporate into his scheme other important processes that could be involved such as species-specific herbivory, differential colonisation abilities and temperature-dependent growth. Chance factors may also intervene. Nevertheless, the model it stands provides a simple way of organising much variable information about vegetation change following volcanic disturbance.

Following the recommendations of the authors cited, prediction of volcanic disturbance successions will require knowledge of resource supply trajectories, the potential flora, the life histories and attributes of the major species, and quantification of the probabilities of the process of invasion, maintenance and decline. Generalised predictions for relatively short time frames can be made at present but detailed predictions are not possible. No experimentation or manipulation has been carried out to test which are the most significant contributing processes or conditions causing succession, or to differentiate between successional models.

Concluding comments

For the volcanic sites studied, the return period for volcanic disturbance varies from less than once to more than ten times per 500 years, that is, less than the life span of many late successional tree species of the central North Island. Thus, species dominant elsewhere in the same region which are characteristically absent or severely reduced are those of late successional vegetation, example of which have been given earlier. Although area for area, volcanically disturbed vegetation may have a larger flora because of the vegetation mosaics present, when particular plant communities on different volcanoes are compared they may be significantly depauperate or sometimes entirely absent. Thus, the *Metrosideros* forest on White Island has only a fragment of the flora of the same type on Rangitoto Island, which in turn is floristically poorer than the type on Hauturu (Little Barrier Island) (see Hamilton and Atkinson, 1961). The *Chionochloa* tussockland and herb field zones on Mt Taranaki lack many species (Druce, 1974) and these types are all but absent from equivalent altitudes on Mt Ngauruhoe.

On White Island and Mt Ngauruhoe, at least, the disturbance regime could be viewed as producing a shifting-mosaic steady-state (*sensu* Sousa, 1984). The patchy and asynchronous nature of the disturbance results in a continuously changing mosaic of patches of different sizes and ages which average to an equilibrium pattern when one considers the mean dynamics of an area

containing such patches. Fleming's (1963) tentative identifications of fossil *Metrosideros*, *Histiopteris* and *Phormium* suggest *Metrosideros* forests have been waxing and waning on White Island for many centuries. In contrast, *Weinmannia* abundance in Mt Taranaki forests apparently coincides only with recent eruptions (McGlone *et al.*, 1988).

Many genera and species are common to the volcanic successions outlined but there is no exclusive volcanic succession flora; the same attributes ensure success in the face of other types of disturbance, especially fire. Indeed, the range and abundance of many of the same species was considerably expanded in periods of Polynesian and later European burning (McGlone, 1983) and fire sometimes is caused by volcanic disturbance (Cooper, 1949; Druce, 1976). Recent volcanic disturbance has shaped most species distributional and abundance patterns in a large portion of the North Island. Other consequences are the frequent occurrence of hybrids and possibly the low number of regionally endemic species.'

Too little is known about many aspects of the processes directly and indirectly controlling succession. Long term quantitative studies of vegetation change and quantitative characterisation of associated disturbance events will be needed to enter the realm of detailed prediction (Miles, 1979; Sousa, 1984). Prediction will be probabilistic rather than deterministic or mechanistic (Egler, 1942; Johnstone, 1986). Long term monitoring will also be necessary to detect the rare event (for example, the frosting of *Coriaria* oil Mt Tarawera) which may shape vegetation pattern for decades or centuries (Miles, 1987).

Experimental and manipulative studies are now needed to test which are the most significant processes or conditions causing succession and to differentiate between successional models.

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