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HEATH LAND VEGETATION OF THE SPIRITS BAY AREA, FAR NORTHERN NEW ZEALAND

Summary: The heath land vegetation of northern New Zealand is usually regarded as a "derived" vegetation type resulting from forest destruction during the Maori and European periods of settlement. Plant species cover-abundance data from sample quadrats in the Far North are analysed using Detrended Correspondence Analysis (DCA) and Two-way Indicator Species Analysis (TWINSPAN) and are then correlated with soil nutrient data. Variations in species composition of heaths appear to be related primarily to soil type. Age since last fire is also important but was not examined in detail in this study. Heaths on volcanic soils were commonly dominated by *Kunzea ericoides* and will follow a succession to forest in the absence of recurrent fire. Heaths on podzolised earths and sands were characterised by low nutrient status and dominance of *Leptospermum scoparium* and a number of cyperaceous species. Slow growth rates, probably due to nutrient limitation and seasonal waterlogging of soils, in combination with occasional fires are likely to maintain a heathland vegetation type.

Keywords: heathland; gumland; scrubland; soil nutrients; seasonal waterlogging; conservation; fire; Spirits Bay; New Zealand.

Introduction

Specht (1979a) defines heathland as being characterised by: 1) its evergreen sclerophyllous nature, 2) the presence, but not necessarily dominance, of the plant families Epacridaceae and/or Ericaceae, and 3) its ecological restriction to soils very low in plant nutrients. He further notes that, in the Australian context, the families Myrtaceae, Proteaceae and Rhamnaceae are often prominent. Recurrent fire is important in determining floristic composition of heath lands and most species may be expected to possess adaptations which enhance either survival or reproduction after fire (Specht, 1981). Such adaptations include serotiny (the storage of seed within woody fruits on the plant for several to many years), and vegetative resprouting from protected buds either above or below ground (Bell, Hopkins and Pate, 1984).

Burrows *et al*. (1979) review the ecological literature on heath lands in New Zealand. They recognise a number of heath types on peat and gley soils in both the North and South Islands. However, the heathlands of far northern New Zealand have received little attention (Rumball and Esler, 1975). Here, heaths occur on podzol and gley-podzol (gumland) soils, many of which may have supported kauri *(Agathis australis* Salisb.) forest until a few hundreds, or thousands, of years ago (Mason, 1952; Wheeler, 1963; Rumball and Esler, 1975; Burrows *et al.,* 1979). This is indicated by the presence of fossil kauri gum within the soil profile.

The areal extent of such communities has almost certainly increased over the last 200-800 years as a result of forest clearance associated with the presence of *Homo sapiens* (McGlone, 1983). The resultant heaths have, in some places, been maintained through regular burning, and in others cleared for farming and forestry. It is unclear whether any of the far northern heaths represent plant communities which arose prior to the arrival of man in New Zealand.

Conservation of representative areas of heathland in northern New Zealand is likely to depend upon several factors:
1. The identification of rare or restricted species, habitats and community types.
2. The ability to maintain heathland community properties through the managed use of fire, while at the same time ensuring protection from fire for surrounding land uses.
3. Scientific evidence which suggests that heathland vegetation is other than an induced vegetation type resulting from fire during the Maori and European period of settlement in New Zealand. And, acceptance by both the public, and government agencies, that heathlands have conservation merits in addition to assumed naturalness. This includes aesthetic, recreational and educational uses. Certainly, much of the reserved European heathland is of the induced type (Gimingham, 1979).

This paper describes the heathlands and associated soils at a number of sites in northernmost New Zealand. It concentrates on the Spirits Bay area (Fig. 1), and comparison of heaths here with spot samples from similar vegetation elsewhere in the far north. While primarily descriptive, several questions of a more general nature are raised:
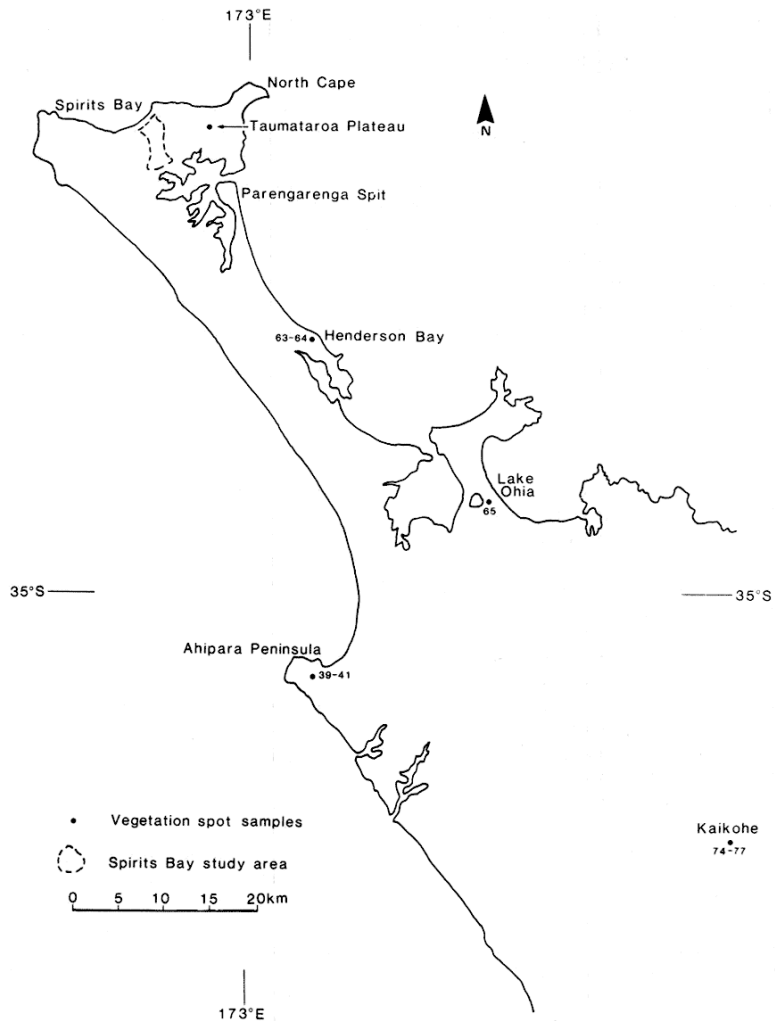
Figure 1; *Location of the Spirits Bay study area, and other sites, in far northern New Zealand where heath vegetation was sampled. Numbers refer to vegetation quadrats as described in the text.*

1. To what extent are the heaths "natural", in the sense of being self-perpetuating in the absence of human interference?
2. To what extent are they a function of low fertility soils?
3. What is the extent of floristic relationship with eastern Australian heathlands?

Methods

A random-sited systematic sample design (Orloci, 1978) was used to establish the position of sample quadrats. From a random starting point on each accessible road, track or stream channel, quadrats were located at regular intervals along the route and
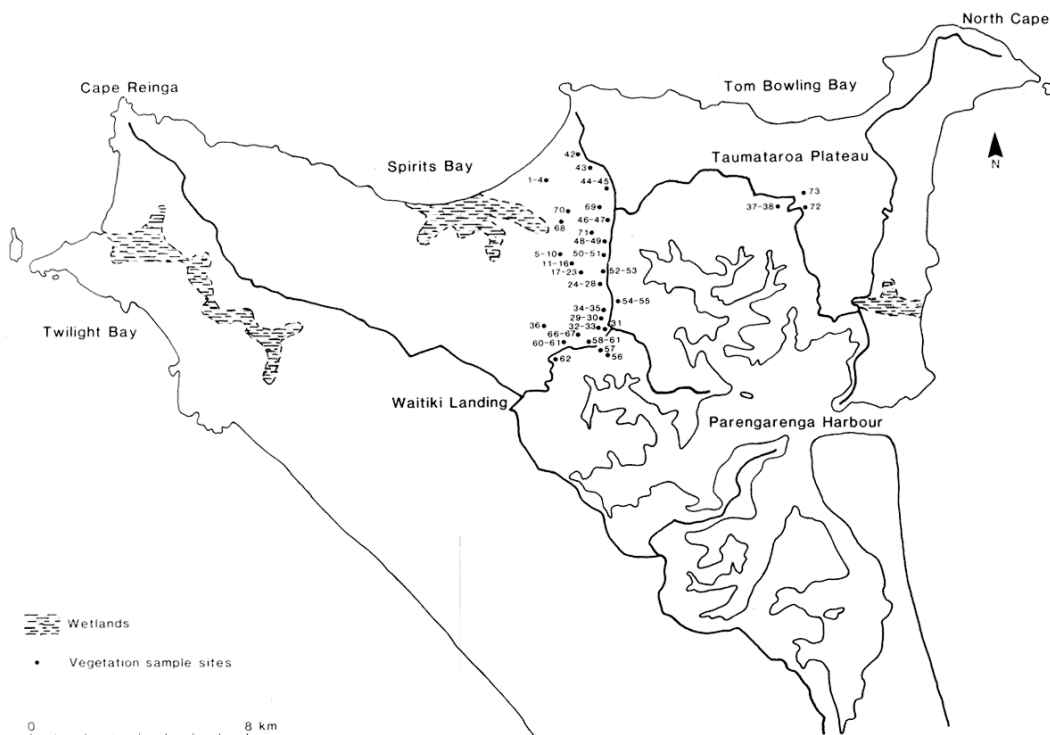
Figure 2: *Location of vegetation quadrats within the Spirits Bay area, and at Taumataroa Plateau, far northern New Zealand.*

50 m in from any disturbance. Sixty-five 4 m² vegetation quadrats were located within the Spirits Bay area (Fig. 2), and a further eight quadrats provided spot data on heaths elsewhere in the region (Fig. 1). Data for four additional sites were derived from the study of heathland near Kaikohe by Rumball and Esler (1975). Thus, there was a total of seventy-seven vegetation samples.

The Braun-Blanquet cover-abundance scale was used to assign a semi-quantitative value to all species within each quadrat (Mueller-Dombois and Ellenberg, 1974). This method is fast and tends to rank species according to their above-ground biomass. Cover and abundance classes are broad, so that errors in value determination are only likely for border cases and will not exceed one class. In the present study two workers scored each quadrat independently and differences in cover-abundance estimates were rare. Height (m) of the tallest plant in each quadrat was measured.

A single, A, horizon soil sample (0-5 cm depth, 15 x 15 cm area) was collected from the centre of each vegetation quadrat. Samples were dried at 105∞C for 24 hours and analysed for exchangeable Ca^{2+}, Na^+, Mg^{2+}, and K^+ using the ammonium acetate leaching (pH=7.0) technique of Allen et al. (1974). Soil hydrogen ion concentration was measured for the ammonium acetate soil extracts using an acetic acid titration. This allowed subsequent determination of total exchangeable bases (TEB), cation exchange capacity (CEC) and percent base saturation (%BS).

Soil particle size distribution was determined for a subset of seven samples using sieve and pipette analysis (Carver, 1971). Loss on ignition (LOI), an approximate measure of soil organic matter content, was determined by igniting 10 g of oven dry soil in a muffle furnace for 30 min at 650∞C, and available phosphorus was measured colorimetrically using the molybdenum blue method (Allen et al., 1974).

Vegetation data were analysed using Detrended Correspondence Analysis (DCA) and Two-way Indicator Species Analysis (TWINSPAN; Hill, 1979; Hill and Gauch, 1980). Both methods provide solutions for sites (quadrats) and species.

Loadings on the first two axes of the DCA solution were correlated with independent vegetation and soil data using Spearman's rank correlation. Significance of difference between nutrient properties of soils by soil series was tested using Analysis of Variance, and the Duncan and Waller tests of difference between means (SAS Institute Inc., 1985).

Nomenclature for most angiosperms and gymnosperms follows Allan (1961), Moore and Edgar (1970) and Webb, Sykes and Garnock-Jones (1988). Pteridophyte names follow Brownsey, Given and Lovis (1985). Nomenclature changes relating to native plants are reviewed by Connor and Edgar (1987), many of which are followed.

Results

Vegetation analysis

A total of 52 species was recorded in the 77 vegetation quadrats. Of these, 40% are endemic to New Zealand, compared with 80% for the native New Zealand flora as a whole (Given, 1981), 50% occur in both New Zealand and Australia, and 10% are adventives (Appendix I). The timing of fieldwork in late summer may have precluded the sampling of some orchid and ephemeral grass species. The families Epacridaceae, Myrtaceae and Rhamnaceae are all present. There are no endemic members of the Proteaceae in the heaths studied, and only two in the whole of the New Zealand flora. However, the family is represented by two abundant adventive *Hakea* species.

The distributions of both quadrats and species on the first two axes of the DCA are presented in Figs. 3 and 4 respectively. Eigenvalues decline consistently over the first four axes (0.331, 0.240,0.158,0.110) suggesting that most of the variation in species composition is described by axes I and II. Interpretation is concentrated upon these.

Quadrats with low loadings on the first DCA axis are largely confined to the centre of the Spirits Bay area and occur on podzolised yellow-brown earths of the Hurewai (HW) series (Sutherland *et al.,* 1979). These soils, derived from Tertiary siltstones and mudstones, are strongly leached and poor in nutrients.
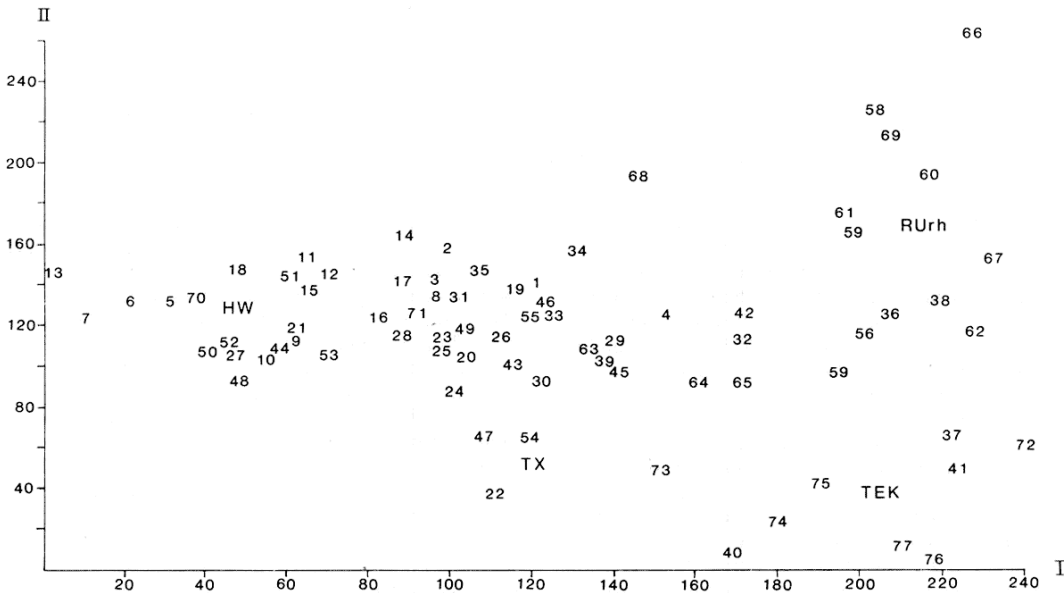

Figure 3: *Position of quadrats on the first two axes of the ordination using Detrended Correspondence Analysis (DCA). Dominant soil series associated with approximate groupings of vegetation quadrats are indicated. Axes are scaled in s.d. units x 100.*
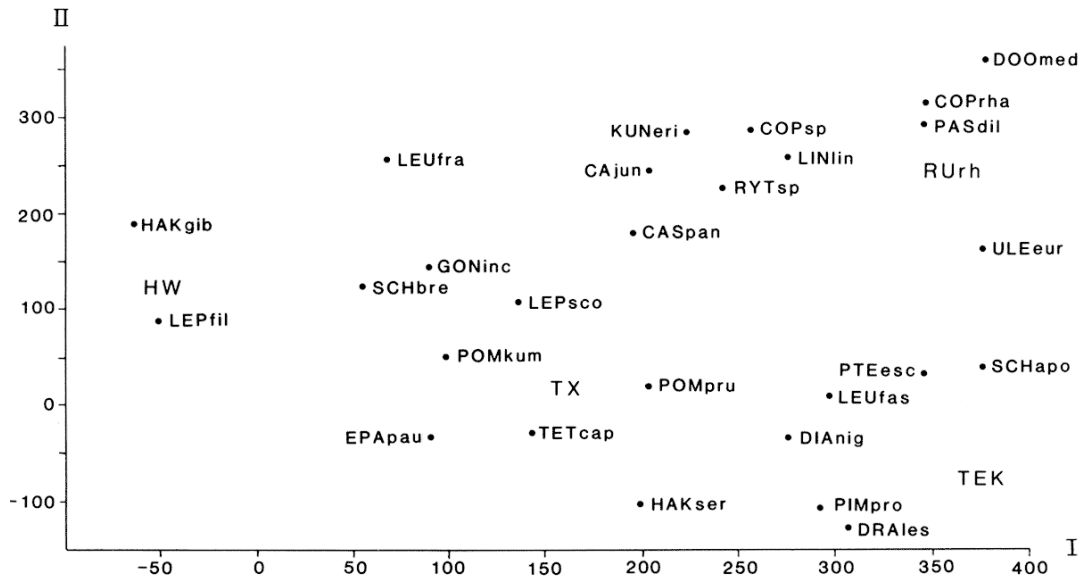
Figure 4: *Position of species on the first two axes of the ordination using DCA. Dominant soil series are indicated as in Fig. 3. Only species present in more than 2 quadrats are shown.*

Although some species are common to nearly all quadrats (e.g. *Leptospermum scoparium* (manuka), *Schoenus brevifolius* and *Pomaderris kumeraho),* these quadrats are also characterised by the dominance of *Lepidosperma filiforme* and/or *Hakea gibbosa.* *Epacris pauciflora* and *Leucopogon fraseri* are occasionally present.

Quadrats with intermediate loadings on axis I are also largely from the Spirits Bay area, but include vegetation on soils of both the Hurewai and Te Hapua (TX) series. Te Hapua series soils are similar to those of the Hurewai series but more strongly leached (J.E. Cox, pers. comm.). In addition to the common species noted above, *Cassytha paniculata, Kunzea ericoides* and *Hakea sericea* are locally abundant.

Quadrats with high loadings on the first axis are also more widely distributed along the second axis of the DCA. This separates quadrats on brown granular clays of the Rangiuru (RurH) series from quadrats on Te Kopuru (TEK) sands. Heaths on Rangiuru series soils have high loadings on the second axis. They are generally tall (>1.5 m) and are dominated by *Kunzea ericoides* (kanuka) rather than *Leptospermum scoparium. Coprosma spathulata, Cyathodes juniperina* and the ferns *Doodia media* and *Lindsaea*

linearis are often present beneath a low canopy of kanuka. The adventive *Ulex europaeus* (gorse) and *Paspalum dilatatum* are abundant close to roads and tracks.

Heaths on Te Kopuru sands (podzolised Pleistocene sands with a well-developed organic B horizon) have low loadings on the second axis. They are low heaths (<1.3 m) characterised by *Dracophyllum lessonianum, Pteridium esculentum* (bracken) and *Leptospermum scoparium. Epacris pauciflora, Dianella nigra* and *Leucopogon fasciculatus* are other frequent species. These quadrats are all located outside the Spirits Bay area, and include heaths from Taumataroa Plateau, Ahipara Plateau and Kaikohe (Figs. 1and 2).

Heath samples close to the coast at Henderson Bay, Lake Ohia and Spirits Bay (quadrats 4,42, 63-65) are all strongly dominated by *Leptospermum scoparium.*

Results of TWINSPAN mirror those described for the DCA (Fig. 5; Appendix I). The first division separates quadrats rich in *Schoen us brevifolius, Lepidosperma filiforme* and *Hakea gibbosa* from those supporting *Pteridium esculentum* and *Leucopogon fasciculatus.* While the former species
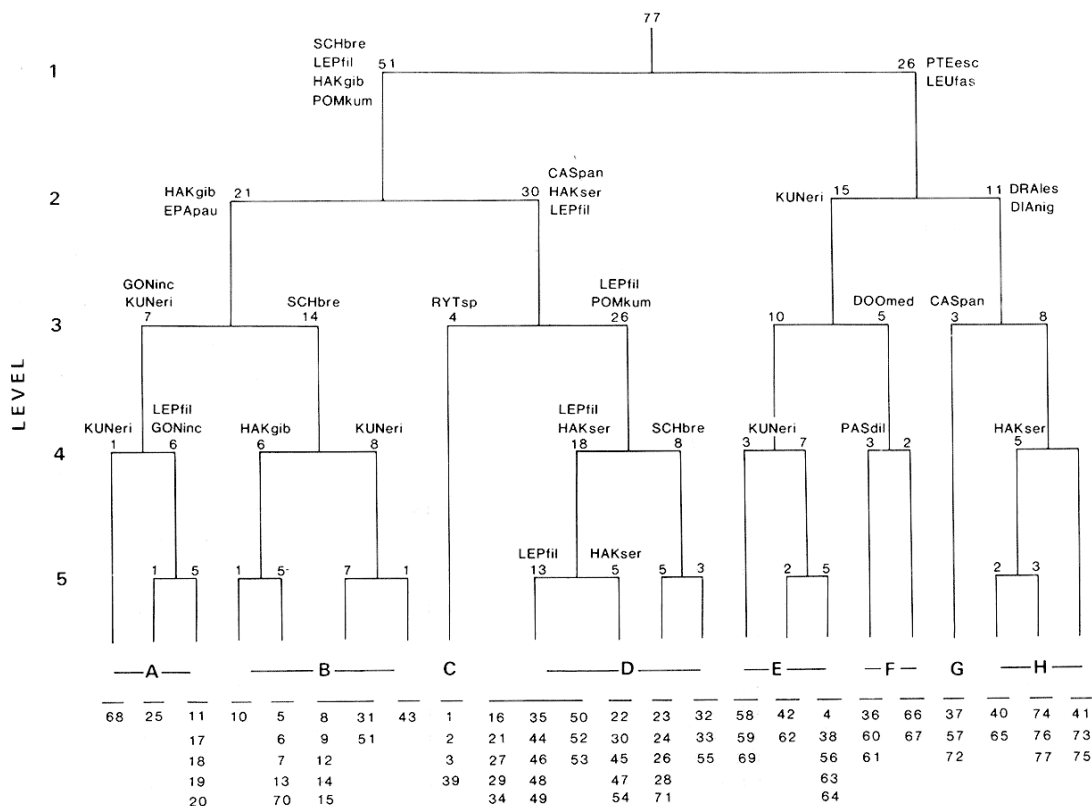
Figure 5: *Classification of quadrats using Two-way Indicator Species Analysis. Numbers on the dendrogram show the numerical division of quadrats at each level, while species are identified with the group of quadrats with which they are positively associated. Groupings A - H represent the classification of quadrats to level 4, the lowest level discussed in the text.*

tend to be restricted to soils derived from Tertiary siltsone and mudstone parent materials within the Spirits Bay area, the latter species occur both on volcanic soils (Rangiuru series) and gumland soils (Te Kopuru series, Wharekohe series) over a wider geographic area.

Divisions at level two separate the Spirits Bay heath lands into those on Hurewai sandy loams supporting *Hakea gibbosa* and *Epacris pauciflora* (groups A and B), and those mostly on Te Hapua fine sandy loams where *Hakea sericea* and *Cassytha paniculata* are more common (groups C and D). Gumland heath (groups G and H) is distinguished from heaths on volcanic soils (Rangiuru clays) by the presence of *Leptospermum scoparium, Dracophyllum lessonianum* and *Dianella nigra*. Vegetation on the Rangiuru clays is dominated by *Kunzea ericoides*. Understorey species such as *Coprosma spathulata* and *Doodia media* are found in the taller (older?) quadrats dominated by *Kunzea ericoides* (group F). These quadrats are divided from lower (younger?) vegetation at level three (group E).

Further divisions of note in the TWINSPAN are the separation of sites containing *Rytidosperma* sp. which are all close to the coast (group Q, and the separation of the taller *Kunzea ericoides* quadrats (group A) from low heaths containing *Schoenus brevifolius* (group B).

Correlation of vegetation and soil variables

Both height of vegetation and species richness are significantly correlated with quadrat loadings on axis 1 of the DCA (Table 1. Thus, along with changing species composition, there is a tendency for vegetation to increase in height from about 0.7 m to >2.0 m, and for species number to increase. This trend corresponds with a change in soil type from podzolised yellow-brown earths of the Hurewai and Te Hapua series, to brown granular clays of the Rangiuru series. However, heaths on Te Kopuru sands, which also have high loadings on axis 1 are typically low and do not conform to the trend for height. It appears that patterns for these two variables are more closely linked to discontinuities associated with soil type, and perhaps age since last fire, than with any continuous variation in soil properties along axis 1 of the DCA.

Soil samples were grouped by soil type following the soils map of Sutherland *et al.* (1979) and field checks of soil boundaries. Means of nutrient properties, and significance of difference between soil types for selected nutrients, are given in Table 2. All soils are low in available cations. Te Kopuru sands (TEK) show the lowest overall nutrient status, with extremely low CEC (<10 100 g^{-1}) and low %BS.

Soils of the Hurewai (HW) and Te Hapua (TX) series have almost identical values for CEC ($\approx$10 me 100g^{-1}) and have a slightly higher %BS than Te Kopuru soils. Soils of the Rangiuru series (RurH) have considerably higher nutrient levels, CEC and %BS than any of the above soil types. This may be a function of their higher clay and organic matter content (Table 3), and higher mineral content of the basalt parent material from which they are derived. Phosphorus concentration in the A horizon was much greater for a tall (older) heath sample (quadrat 36) on Rangiuru clay than for a low (young) heath sample (quadrat 32) on the same soil type. Several small remnant patches of forest occur in gully heads on Rangiuru clays in the Spirits Bay area. A single soil sample from one such remnant showed markedly higher nutrient levels than occur for any of the heathland soils.

The hill series samples of the Hurewai sandy loam (HWH), quadrats 1-4 near the coast at Spirits Bay, have nutrient concentrations similar to those of Rangiuru series soils. This may result both from wind-blown sand from the coastal dunes, and wind-blown additions of nutrients of marine origin.

There was no significant difference between Hurewai and Te Hapua series soils for any of the nutrients tested (exchangeable Ca^{2+}, Mg^{2+}, K$^+$, H$^+$).

Table 1 *Spearman's rank correlation of soil and vegetation variables with DCA axes 1 and 2 (n = 64: significance of r: *<0.05, **<0.01, ***<0.001). Height is of tallest plant in each quadrat, and species richness is total number of species per quadrat.*

	Height (m)	Species Richness	Exchangeable Mg^{2+}	Ca^{2+}	K$^+$	H$^+$	TEB	CEC	% BS
Axis 1	0.35 **	0.44 ***	0.39 **	0.50 ***	0.37 **	0.31 *	0.44 ***	0.51 ***	0.30 *
Axis 2				0.48 ***			0.28 *	0.28 *	
Height						0.36 **			
Richness			0.29 *	0.32 *			0.31 *	0.36 **	

Table 2: *Mean nutrient concentrations by soil series, and significance of difference between series for selected soil properties (Duncan and Waller tests, p<0.05). Values followed by the same letter are not significantly different.*

Soil series	(n)	milli-equivalents 100 g^{-1} Ca^{2+}	Mg^{2+}	K$^+$	CEC	%BS
HWH	4	3.79 A	5.92 A	0.67A	16.59	66.60
HW	28	1.22 B	2.06 B	0.24B	10.34	39.40
TX	13	1.18 B	2.32 B	0.23B	10.01	39.90
TEK	7	0.57 B	0.55 C	0.09C	6.49	26.20
RurH	12	2.68 C	4.34 D			

Table 3: *Particle size distribution, percent loss on ignition (% LOI) and available phosphorus concentration (ppm) For selected soil samples.*

Quadrat	Soil series	% Sand	% Silt	% Clay	%LOI	P
2	HWH	17.84	58.21	23.95	8.7	20
7	HW	35.54	51.03	13.43	6.2	20
22	HW	30.10	44.25	25.65	7.9	20
27	TX	25.49	54.78	19.73	9.5	10
38	TEK	93.42	5.57	1.01	5.2	20
32	RurH	27.61	43.43	28.96	22.3	20
36	RurH	19.42	51.83	28.75	25.3	210

Rangiuru series soils showed significant differences from all other series for all of these nutrients (Table 2), while Te Kopuru series soils were significantly different from all others for both Mg^{2+} and K^+ but not Ca^{2+} and H^+ .

The marked differences in nutrient concentrations, height and species composition between heaths of the Rangiuru clays and Te Kopuru sands, despite similar loadings high on axis 1 of the DCA, makes a simple environmental interpretation of this axis impossible. The TWINSPAN groupings of sites, primarily by soil type and height of vegetation, appear to provide a more useful framework for interpreting the vegetation-environment relationships in this case.

Discussion

The question of long term stability of heathlands poses many problems. Stability here refers to the maintenance of a stable floristic and structural composition from one generation to the next in the absence of human interference. There is little doubt that fire frequency has increased during the Maori and European periods in New Zealand. This has led to expansion of areas of heath-like vegetation on soils capable of supporting forest. It is necessary to differentiate between such areas, where succession to forest may proceed if human interference is eliminated, and areas where a heathland vegetation will be maintained under a "natural" disturbance regime.

The dominant species found in heaths on Rangiuru clays (high loadings on both axes of DCA, and TWINSPAN groups E and F) include species common in regenerating forest; e.g. *Kunzea ericoides, Pteridium esculentum, Cyathodes juniperina, Coprosma rhamnoides, Coprosma spathulata, Myrsine australis, Cordyline australis* and *Knightia excelsa*. It seems that vegetation on these soils will follow a succession to forest. The soils are well drained and have a higher nutrient status than other soils analysed in this study. In addition, vegetation height was greatest here (Table 1). This suggests a faster growth rate if mean vegetation age is similar to that for sites on other soil types. Remnant patches of forest are all located on these volcanic soils. However, the volcanic areas are more hilly than the sandstone and mudstone areas, so survival of forest in moist, fire-protected gully-heads is more likely. Palynological evidence from the Paranoa wetland, which drains the Spirits Bay catchment, indicates a greater extent of forest near the swamp until at least the last few thousand years (Dodson, Enright and McLean, 1988). Such cover would certainly have existed on the volcanic soils, and probably also in valley bottoms on other soil types because of increased moisture and nutrient availability. Nevertheless, the frequency of charcoal particles, and pollen of *Leptospermum scoparium/Kunzea ericoides,* and to a lesser extent Epacridaceae, suggests that at least small areas of heathland may have existed here for thousands of years.

Heathlands on soils of the Hurewai series at Spirits Bay (low loadings on DCA axis I, and TWINSPAN groups A and B) are distinctive both floristically and structurally. *Schoenus brevifolius* and *Lepidosperma filiforme,* along with woody shrubs such as *Epacris pauciflora* and *Leptospermum scoparium,* represent a rare species combination (Fig. 6). Furthermore, this tussock-shrubland is a vegetation structure not found in other northern heathlands. Soils of the Hurewai series are moderately to poorly drained (Sutherland *et al.,* 1979). They have a sandy A horizon (30-35% sand), but a massive, columnar B horizon impedes drainage and leads to waterlogging for at least the winter months. Waterlogging alternates with very dry soil conditions during summer. Together with a low nutrient status these conditions are likely to result in a slow growth rate which makes succession to forest unlikely even with a relatively long interval between fires (Specht, 1979b; Groves, 1979).

Figure 6: *Heathland on podzolised yellow-brown earths of the Hurewai series showing* Epacris pauciflora *(white flowers) and* Schoenus brevifolius *(foreground),* Leptospermum scoparium *(centre) and* Hakea gibbosa *(centre right). Several large tussocks of* Lepidosperma filiforme *are partly visible (middle background).*

The Te Hapua series soils are similar to those of the Hurewai series but are, supposedly, more strongly leached (Sutherland *et al.,* 1979). No differences in mean nutrient concentrations were apparent in this study. However, heathland species composition did differ, mainly through the additional presence of *Hakea sericea* and *Cassytha paniculata* in some sites (moderate loadings on DCA axis I, and TWINSPAN group D).

Fire in the Spirits Bay area has declined in frequency since 1966 when land management was transferred to the crown. Two fires are recorded for parts of the area sampled here; February 1973 (quadrats 1-4), and April 1976 (at least quadrats 46-49, 71; Crane, pers. comm.). The low stature of the vegetation, and dominance of cyperaceous species < 1.0 m tall at some sites after more than 10 years confirms that growth rates are slow.

Heathlands on Te Kopuru sands are also distinctive (high loadings on DCA axis I, low loadings on axis II, and TWINSPAN groups G and H). These are the so-called gumlands of Taumataroa (quadrats 37, 38, 72, 73) and Ahipara Plateau (quadrats 40, 41).

These soils are extremely nutrient deficient, and have a well-developed organic B horizon which impedes drainage so that vegetation grows in seasonally waterlogged conditions. *Epacris pauciflora, Dracophyllum lessonianum, Leptospermum scoparium, Pteridium esculentum, Schoenus apogon* and *Lepidosperma laterale* are common. This assemblage does not have the tussock-shrubland structure found in heaths containing *Lepidosperma filiforme*. The soil parent material is a fine white sand of late Pliocene to mid-Pleistocene age which occurs at points > 100 m a.s.l. at both Taumataroa and Ahipara. The limits placed on plant growth by soil conditions, and occasional fires, make it unlikely that succession to forest will occur on these sites. However, a remnant of kauri forest on podzolised sands is recorded by Clunie and Wardle (1983) for a steep gully at Ahipara, and kauri ricker stands are found on sandy podzols at Waipoua (Enright, unpubl.). Radiocarbon ages for remnant stumps and peg roots from the Ahipara Plateau suggest that forest disappeared from at least part of this area before man arrived in New Zealand (NZ6839: 930±54 years B.P.;

Table 4: *Comparison of species richness for heaths on different soil series within the study area, and with similar heaths in eastern Australia. Note: New Zealand figures include pteridophytes but probably exclude some orchid and ephemeral grass species due to the timing of sampling in late summer. Australian figures are for angiosperm species only.*Abbreviations refer to soil series as described in the text.*

Locality	Vegetation type	Species richness 4 m^{-2}	Source
New Zealand	Heath on HW, TX*	5.20 ± 2.03 (n=38 quadrats)	This study
	Heath on RurH	8.93 ± 2.13 (n=12 quadrats)	This study
	Heath on TEK	9.00 ± 1.83 (n= 7 quadrats)	This study
Australia	Dry Heath	24.8 (n=7 studies)	Specht (1979b)
	Wet Heath	15.4 (n=4 studies)	Specht (1979b)

NZ6396: 1955± 60 years B.P.; NZ6394: 26900±850 years B.P.; NZ6395: >34400 years B.P.).

The replacement of some kauri forest areas by heath on strongly podzolised, nutrient-poor soils could have resulted from rare fire events prior to the arrival of man in New Zealand. The podzolising action of the kauri forest itself, might also modify soil nutrient and drainage characteristics such that continued forest growth is impossible (Rumball and Esler, 1975; Beever 1988). In some areas, e.g. Lake Ohia (quadrat 65), changing sea-level has contributed to waterlogging of the soil profile.

All heathland soils examined here (excluding soils of the Rangiuru series) are extremely low in nutrients, and concentrations are similar to those described for representative heathland soils in Australia (Groves, 1979). Low nutrient status, seasonal waterlogging and occasional fire precludes development of tall, woody vegetation. However, the heathland flora of northern New Zealand is not well developed. Species numbers are low relative to heathlands of eastern Australia (Table 4). Wet heaths in Australia contain fewer species than dry heaths, but species richness is still considerably higher than that found in this study.

Given (1981: p.65) notes that "one of the odd features of the more northern parts of New Zealand is the occurrence of scrubland species which appear to be recent arrivals from Australia. . . and which have probably spread by long distance disperal of seeds." Among these species are a number of ferns and orchids which have spores or very light seeds, as well as several rare varieties of *Pomaderris phylicifolia*. Other species held in common with Australia include *Leptospermum scoparium, Kunzea ericoides, Lepidosperma filiforme, Lepidosperma laterale, Schoen us brevifolius* and *Schoenus apogon*. All genera regularly found in these heathlands are also found in eastern Australia.

Certain families common in Australian heaths are poorly represented in New Zealand. This is particularly true of the Proteaceae. Other families typical of southern hemisphere heaths (e.g. Myrtaceae, Epacridaceae, Rhamnaceae) are represented by only a few species.

Some species from the northern heaths appear well adapted to cope with low nutrient soils, fire and waterlogging. Members of the genera *Schoenus, Lepidosperma* and *Baumea* within these heaths can resprout from underground rhizomes after fire, as can the ferns *Lindsaea linearis* and *Pteridium esculentum*. The native shrub *Leptospermum scoparium* is both tolerant of waterlogging (Cook, Mark and Shore, 1980), and has woody fruits which release seeds after fire (serotinous). Beever (1988) suggests that seeds of some species may also survive fire in the soil seed bank (e.g. *Pomaderris kumeraho)*. However, many others probably depend on wind disperal from adjacent unburned areas.

The low number of resprouter and serotinous species in the New Zealand heathland flora may make such communities susceptible to invasion by fire-adapted adventives where increases in fire frequency occur. Regular burning of heaths at Spirits Bay prior to the 1960s probably facilitated the rapid spread of both *Hakea* species. These species are fire sensitive. Plants are killed by fire but have a large canopy-stored seed bank which is released upon death. Fruit production for *Hakea sericea* in Australia begins at age 4-6 years (Gill, 1984). The species is a pest in South Africa where seed production appears higher than in Australia, perhaps due to the absence of insect predators. Neser (1984) has identified a number of Australian host-specific insects which may be capable of controlling *Hakea sericea* population growth in South African heathlands. Unchecked by predators, or other management strategies, both *Hakea* species are likely to increase in abundance in northern New Zealand heaths after every fire.

The distribution and abundance of adventives follows a clear pattern associated with soil type. *Hakea gibbosa* and *Hakea sericea* are common on the sandstone soils but rarely occur together (2 co-

occurrences out of 41 quadrats containing *Hakea*). *Hakea gibbosa* is abundant on soils of the Hurewai series and is absent from volcanic soils of the Rangiuru series. *Hakea sericea* is most common on Te Hapua soils, but also occurs in young vegetation on Rangiuru clay. *Oxylobium lanceolatum* (an Australian legume) was noted along roadsides on Te Hapua soils at Spirits Bay. *Ulex europaeus, Paspalum dilatatum* and *Psoralea pinnata* (a South African legume) are largely restricted to the volcanic soils and are most common close to roads and tracks.

Some genera characteristic of the northern heaths are known to have existed in New Zealand since the early to mid-Tertiary (e.g. *Dracophyllum, Leptospermum;* Fleming, 1977). However, they are common components of forest and wetland communities and their presence cannot be taken as evidence for the existence of heathlands at that time. A number of factors lead to the conclusion that heath lands in northernmost New Zealand are more recent in origin (perhaps mid to late Quaternary) and probably covered only small areas prior to the arrival of man:

1. Many elements of the heath land flora are held in common with Australia at either species or sub-species level.
2. Percentage endemism is much lower than the New Zealand average (Given, 1981).
3. Communities have low species richness compared with similar wet heaths in eastern Australia (Specht, 1979b).
4. Only a small number of the heathland species appear well adapted to cope with recurrent fire (Beever, 1988).
5. Many of the species are found in other community types, especially regenerating forest.

Nevertheless, heathlands on podzolised sands and sedimentary parent materials in the far north have a distinctive structure and species composition within the New Zealand context. They probably predate the arrival of man, although having expanded considerably over the last few hundreds of years. Heathlands as described here, should be distinguished from regenerating bush such as that which occurs on richer soils (e.g. the Rangiuru clays) and are characterised by the presence of a variety of woody secondary species and faster growth rates. Studies of heathland vegetation dynamics are needed to explore further the relationships between soil properties, fire, and floristic and structural composition of such communities in northern New Zealand.

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Appendix I: *Species list of plants in sample quadrats, and affiliation (% Frequency) with quadrat groupings from TWINSPAN (Fig. 5, level 3). Two grass species were unidentified.*
*Key to status codes: * = native to Australia, e=endemic to N.Z., n = native to N.Z., a = adventive to N.Z.*

	Status	A	B	C	D	E	F	G	H
Adiantum hispidulum	n*						20		
Axonopus affinus	a			25					
Baumea juncea	n*					10			
Cassinia leptophylla	e					10			
Cassytha paniculata	n*			25	48	40		100	
Coprosma rhamnoides	e					20	40		
Coprosma spathulata	e					20			
Cordyline australis	e					10			
Cyathodes juniperina	n*				10	10			
Dianella nigra	e	14			10		20	67	88
Dichondra repens	n						20		
Doodia media ssp. *australis*	n						100		
Dracophyllum lessonianum	e				10			67	75
Drosera peltata ssp. *auriculata*	n				3	10			
Epacris pauciflora	e	29	29						50
Gleichenia dicarpa	n*								13
Gnaphalium audax ssp. *audax*	e				3				
Gonocarpus incanus	e	57		75	31	10		33	
Hakea gibbosa	a*	86	100	75	17				
Hakea sericea	a*				28	10		33	63
Haloragis erecta	e				3	10			
Hypericum humifusum	a						20		
Kunzea ericoides	n*	86	43		45	60	80	67	13
Leontodon taraxacoides	a			25					
Lepidosperma australe	e					10			
Lepidosperma filiforme	n*	57	50		72				
Lepidosperma laterale	n*				3				
Leptospermum scoparium	n*	86	100	100	100	90	100	100	100
Leucopogon fasciculatus	e	29			3	60		33	63
Leucopogon fraseri	e	43							
Lindsaea linearis	n*					10		33	
Lobelia anceps	n*				3				
Lycopodium laterale	n*				3				13
Microlaena stipoides	n*						20		
Morelotia affinus	e	14							
Muehlenbeckia australis	e				6				
Myrsine australis	e				6				
Oxylobium lanceolatum	a*		7						
Paspalum dilatatum	a					30	60		
Pimelea prostrata	e				3				13
Pomaderris kumeraho	e	86	71		69	20		33	38
Pomaderris phylicifolia var. *ericifolia*	n*				6	10			
Pomaderris prunifolia var. *edgerleyi*	e		50		3			33	13
Pteridium esculentum	n*				6	50	80	100	63
Rytidosperma sp.	e or n or a			100	17	60	40	33	13
Schoenus apogon	n*						20	33	
Schoenus brevifolius	n*	57	100	25	93	50	20		63
Tetraria capillaris	n*	14			10				38
Thelymitra longifolia	n*			25					
Ulex europaeus	a					10	40		13