Geothermal Vegetation Dynamics

Part I: Map of the geothermal vegetation of the Te Kopia Scenic Reserve

Part II: Plant species organisation along major environmental gradients

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Bruce Burns and John Leathwick

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Part I Map of the geothermal vegetation of the Te Kopia Scenic Reserve

1. Introduction

The distinctive environmental conditions associated with geothermal sites allow unusual assemblages of plants to become established. These may include disjuncts normally found in warmer climates (e.g., tropical ferns) and combinations of plants from surrounding communities capable of surviving under high-stress conditions of soil mineralisation and temperature. Several threatened plants (e.g., *Calochilus* spp.) are also characteristic components of this special habitat. Development of geothermal fields, weed invasion, and fertiliser drift have already had an impact on existing geothermal fields or are potential threats, yet little detailed research on the composition, structure and dynamics of this vegetation has been undertaken in New Zealand. The study, of which this map is a port, will provide baseline data from possibly the least disturbed field (Te Kopia Scenic Reserve) and examine vegetation composition, structure, and dynamics in relation to soil temperature, pH and soil chemistry. Such understanding, coupled with the development of appropriate monitoring methodologies, will enhance our ability to predict the nature and rate of vegetation change which might follow disturbances such as draw-off from a geothermal field. These are fundamental requirements for the effective management of DoC administered geothermal reserves and will provide a sound basis for advocacy where development or use of a field is being considered. Sampling for and preparation of a vegetation map of geothermal vegetation in the Te Kopia Scenic Reserve is the first phase of this study.

The Te Kopia Scenic Reserve is a 1408 ha protected natural area on the Paeroa Range south of Rotorua and within the Atiamuri Ecological District (Wassilieff & Timmins 1984). Geothermal features and vegetation occur over approximately 95 ha of this reserve and are located on a scarp and at the base of the Paeroa Fault. The geothermal vegetation is notable as (a) it contains several rare plant species, and (b) adventive weeds (e.g., pines), which are problems in many other geothermal reserves, are still at low densities. The reserve contains large colonies of the rare fern *Dicranopteris linearis,* and the rare orchids *Calochilus paludosus* and *C. robertsonii* are well-represented (Clarkson 1984; Humphries and Ecroyd 1990).

2. Objective

- To map the geothermal vegetation of Te Kopia Scenic Reserve.

3. Methods

Study area boundaries were chosen to include all geothermal vegetation using enlargements of the most recent (1991) colour aerial photos (scale = 1: 3300). Parallel E-W transects were systematically located over this study area every 200 m, and the vegetation composition and structure described on plots spaced every 50-100 m along these transects, giving a total of 56 plots. At each plot, vegetative cover by tier was recorded for all vascular plants and bryophytes in quadrats varying between 9 and 25 m^2 in area. Small samples of plants (particularly bryophytes) were sometimes taken for verifying identification. At each plot, environmental and site data were collected, and at every second plot a soil sample was taken for later analysis. A quantitative gradient analysis based on these data will be presented in Part 11.

Quadrat data were classified into groups using the classification program TWINSPAN. The characteristics of these plot groups were summarised to form the vegetation unit descriptions which accompany the map. Vegetation unit names were derived using the criteria of Atkinson (1985). The quadrat locations were identified on the aerial photos, and vegetation unit boundaries established by extrapolation and interpretation. A planimetrically accurate base map was generated by digitising roads, streams, fences and spot heights off a DOSLI 1:25,000 compilation sheet for NZMS 260 U17 using the GIS (geographic information system) TERRASOFT. Aerial photos were registered to this baseline data using a set of clearly identifiable registration points, and the vegetation unit boundaries were digitised to form the final map.

4. Results

Two views of the vegetation are presented. First, a horizontal view of the area was developed at a scale of 1 : 7700 (Figure 1). Second, this map was then draped over a computer-generated digital terrain model (DTM) of the study area to more clearly show the relationships between distribution of vegetation units and the landscape (Fig.2). Seven vegetation types, identified from the TWINSPAN classification, are delineated on these maps. These are described in detail below:

1. Prostrate kanuka / *Campylopus* spp. moss-shrubland occurs around the most geothermally active sites with a mean soil temperature at 15 cm depth of 54 °C. Vegetation consists of a sparse, low (30 cm - 1 m) canopy of prostrate *Kunzea ericoides var. microflora* with a few stunted *Leucopogon fasciculatus* and *Dracophyllum subulatum*. Groundcover is dominated by mosses, mostly *Campylopus* spp. (*C. clavatus*, *C. introflexus* and the endemic geothermal moss *C. holomitrium*) and *Dicranoloma* spp.; liverworts, particularly *Lepidozia glaucophylla*; and the lichens, *Cladonia capitellata* and *Cladia leptoclada*. The

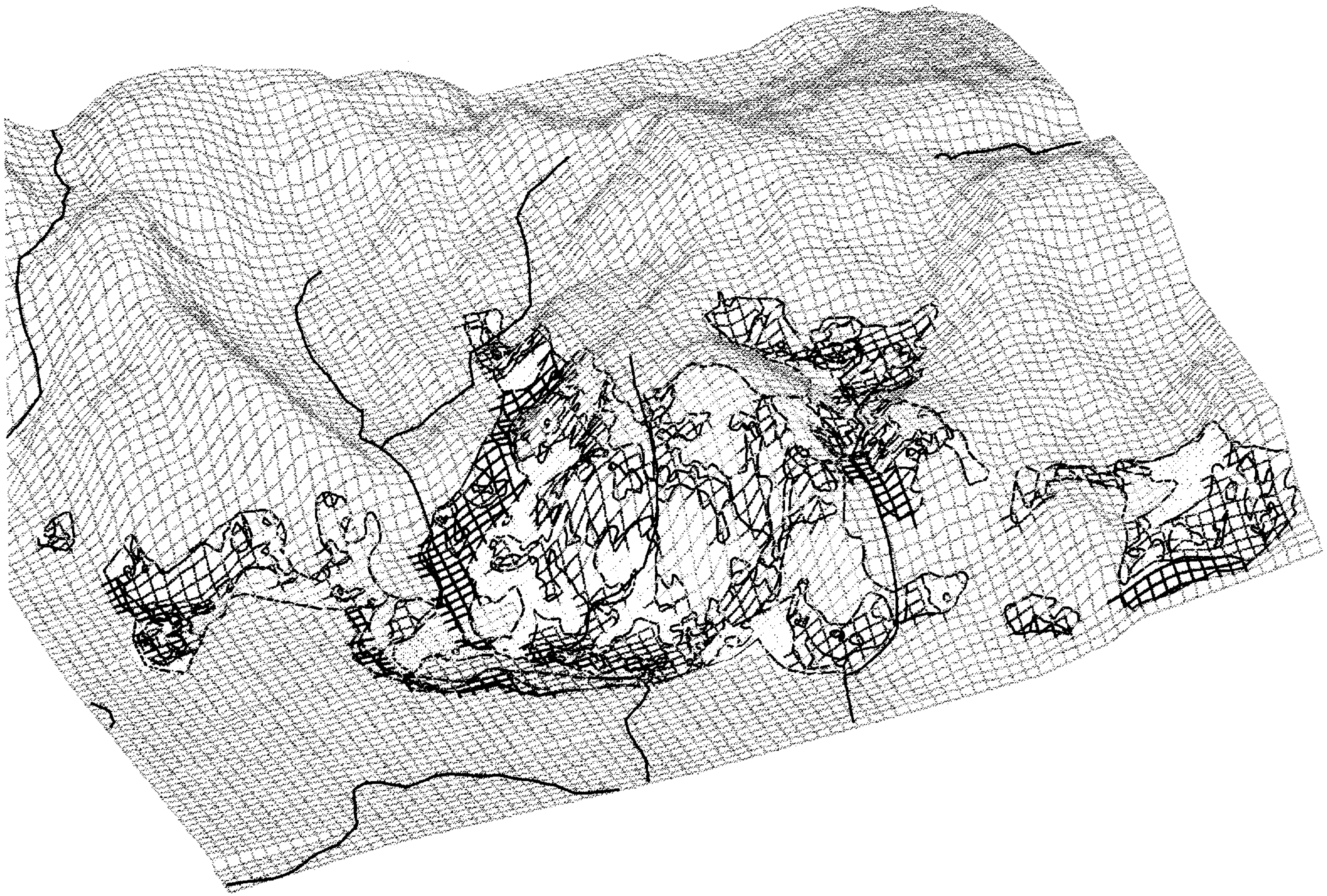


FIGURE 2 ORTHOGANAL PLOT OF STUDY AREA WITH VEGETATION MAP UNITS, LEGEND AS ON MAP.

fern ally *Lycopodium cernuum* is also a common component of the groundcover. Some open patches of bare earth are characteristic of this type.

2. Prostrate kanuka - mingimingi shrubland occurs on slightly cooler ground than the previous type (mean soil temperature at 15 cm = 35 °C). A dense 1 m tall canopy is dominated by an equal mix of prostrate *Kunzea ericoides* var. *microflora* and *Leucopogon fasciculatus*. The ferns *Histiopteris incisa* and *Dicranopteris linearis* are an occasional component, with the groundcover a dense mat of liverworts comprising *Lepidozia glaucophylla*, *Kurzia* spp. and *Chiloscyphus* spp. Infrequent tufts of *Dianella nigra* also occur as groundcover. This and the previous type are mapped together as they form a complex mosaic around geothermal hotspots and could not be accurately separated at the scale of the map.

3. (Pine) / mingimingi - manuka scrub is one of the most common vegetation units of the area and is apparently the most prone to invasion by *Pinus radiata*. Forty percent of plots classified within this unit contained pine as an emergent or as fallen trees. Soil temperatures here are still elevated, with an average of 26 °C at 15 cm depth. The 2-4 m tall canopy is largely dominated by *Leucopogon fasciculatus*, *Leptospermum scoparium*, and a few *Weinmannia racemosa*. A 1-2 m tall subcanopy consists of these species, as well as *Cyathodes juniperina*, *Dracophyllum subulatum*, *Dicranopteris fnearis* and *Pteridium esculentum*. Groundcover is dominated by *Dianella nigra* and a moss and liverwort mat.

Common species of this bryophyte mat are *Lepidozia glaucophylla*, *Kurzia* spp., *Chiloscyphus* spp., *Dicranoloma* spp., and *Leucobryum candidum*. The ferns *Schizaea dichotoma*, usually found in more northern localities, and *Schizaea* sp. (cf. *fistulosa*) are found growing in this mat.

4. Manuka - kamahi/ *Cyathodes juniperina* scrub has only slightly elevated soil temperatures with a mean of 19 °C at 15 cm depth. The 4-6 m canopy is dominated by *Weinmannia racemosa*, *Pseudopanax arboreus*, *Leptospermum scoparium* and *Leucopagon fasciculatus* and occasional *Knightia excelsa*. *Cyathodes juniperina* dominates a subcanopy, with *Pteridium esculentum*, *Coprosma lucida*, and *Gautheria antipoda* also present. The groundcover tier is comprised of *Dianella nigra*, *Lycopodium deuterodensum*, *Lycopodium volubile*, *Morelotia affinis* and scattered *Phymatosorus diversifolium*. Bryophytes are less common than in the three previous types described, and are on average 17% of the ground cover. Common ground mosses here are *Ptychomnion aciculare*, *Thuidium furfurosum*, *Hypnum cupressiforme* **and** *Dicranoloma* sp.

5. Kamahi - fivefinger forest was distinguished on the edges of the study area on zones that are probably little influenced by geothermal activity. Mean soil temperature at 15 cm depth was 17 °C, which was also the mean soil surface temperature. This is the main forest association on this portion of the Paeroa Range and generally surrounds the study area to the east. It probably represents forest regeneration after fires that occurred at least several decades ago. The 6-16 m tall canopy consists of dense *Weinmannia racemosa* and *Pseudopanax arboreus* with a sparse subcanopy of *Geniostoma rupestre*, *Dicksonia squarrosa*, *Pteridium esculentum*, *Leucopogon fasciculatus* and *Gaultheria antipoda*. A dense groundcover is dominated by *Gleichenia microphylla*, *Gahnia setifolia*, *Schoenus tendo*, *Dianella nigra*, and *Blechnum* sp. 1 (Brownsey and Smith-Dodsworth 1989), with *Pyrrosia eleagnifolia* as a common epiphyte.

6. Bracken - baumea fern-reedland occurs in a wetland formed in the base of an old explosion crater. Here, the water is free-standing, permanent and generally about 50 cm deep, although deeper channels exist. The soils are not heated above normal, with a mean 15cm depth soil temperature of 17°C. Scattered *Phormium tenax*, *Cortaderia spp.* and *Leptospermum scoparium* are emergent over a dense, almost impenetrable, sward of *Pteridium esculentum* and *Baumea rubiginosa*. Other less abundant but still common species are *Gleichenia dwarpa*, *Baumea tenax*, *Hypolepis distans*, *Blechnum minus* and *Blechnum sp. 1.*

7. Manuka - (makomako)/Hypolepis *ambigua* fernland forms the vegetation on an alluvial fan that occurs where a stream from the main range enters the explosion crater. The fan sits over geothermal activity, as evidenced by variable soil temperatures, which have a mean of 26°C at 15 cm depth. The vegetation consists of a woodland of *Leptospermum scoparium* and *Aristotelia serrata* over a dense 1 m high fernland of *Hypolepis ambigua* and *Histiopteris incisa*. Dense patches of *Carex geminata* also occur. Other common species are *Muehlenbeckia australis*, *Dicksonia squarrosa* and *Baumea teretifolia*.

5. Conclusions

Marked differences in vegetation composition and physiognomy at Te Kopia enabled distinct boundaries to be identified easily on the aerial photos. Consistent relationships between vegetation units 1-5 generally form a gradient from vegetation on the hottest soils closest to geothermal features to that on the coolest soils farthest away. A further vegetation unit is found on an alluvial fan geothermally heated from below, and the final unit identified occurs in a large explosion crater that has infilled to form a wetland.

6. Acknowledgements

We wish to thank Bronwyn Rogers who greatly assisted with GIS map production.

Part II. Plant Species Organisation Along Major Environmental Gradients

Abstract

Geothermally active areas provide unique, stressed environments characterised by unusual vegetation assemblages and rare plant species of high conservation value. However, these previously research-neglected ecosystems are vulnerable to modification resulting from such impacts as energy extraction and weed invasion (e.g., of *Pinus radiata*). To improve understanding of these ecosystems, we investigated how geothermal vegetation composition and structure changed with environmental variation at Te Kopia Scenic Reserve, Atiamuri Ecological District, using ordination and regression techniques.

A gradient in soil temperature, which is also correlated with a large number of soil parameters, is most strongly correlated with variation in vegetation composition and structure. Species are differentially sensitive to temperature change, with a few showing strong relationships between their abundance on a site and temperature. Changes in their distributions may be useful as indicators of change in the underlying geothermal conditions. Canopy height and species richness decreased along the increasing temperature gradient, and groundcover changed from dominance by leaf litter to dominance by large mats of bryophytes. These changes in vegetation composition and structure with environment provide an important and feasible basis on which to design a monitoring system using key vegetation boundaries or plant indicator species.

1. Introduction

The composition and structure of geothermal vegetation in relation to environmental factors such as soil temperature and chemistry were investigated at Te Kopia Scenic Reserve near Rotorua by Native Plants and Animals Division, Landcare Research New Zealand Ltd, Hamilton for Science and Research Division, Department of Conservation, Wellington.

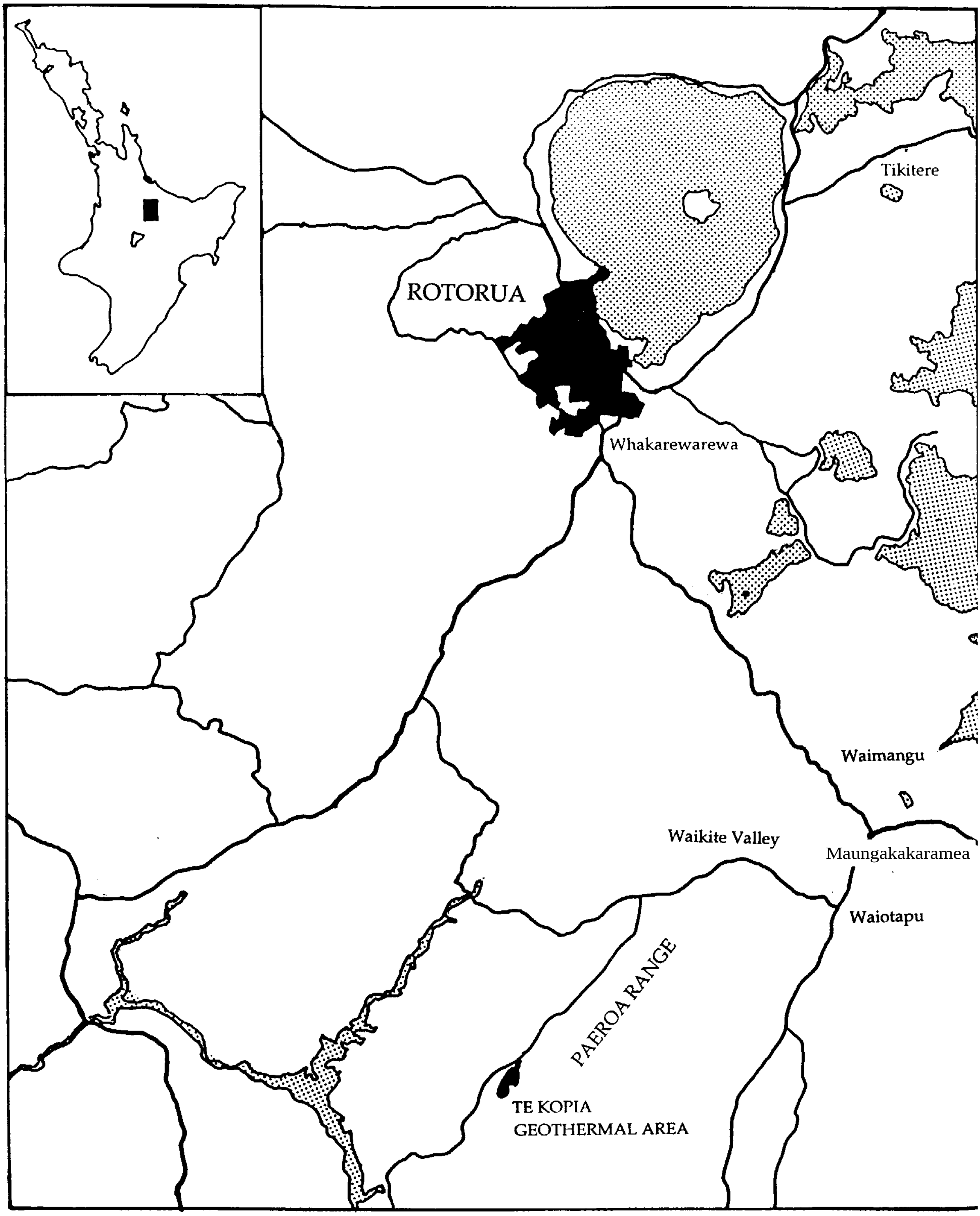
2. Background

Geothermally active areas provide unique, stressed environments characterised by unusual vegetation assemblages. In the Bay of Plenty - Rotorua active zone, plant species of geothermal areas are generally of three types: (1) stress-tolerant species that are also found in surrounding communities (e.g., manuka, mingimingi); (2) geographically disjunct fern or orchid species normally found in warmer climates and with light seeds or spores capable of long-distance dispersal (e.g., *Schizaea dichotoma*, *Dicranopteris linearis*, *Calochilus* spp.); and (3) a few species or varieties which appear to be endemic to New Zealand geothermal areas (e.g., prostrate kanuka, *Christella* sp. (unnamed), *Nephrolepis* sp. (unnamed), and *Campylopus holomitrium*). These distributional and taxonomic anomalies impart high conservation values to geothermal vegetation. However, development of geothermal fields for energy extraction, weed invasion, and fertiliser drift have already had an impact on the vegetation of existing geothermal fields or are potential threats. A recent assessment suggests that geothermal activity is the renewable resource best able to provide large amounts of new energy cheaply (Dench 1993). Therefore, further development of geothermal areas for energy extraction is likely. If vegetation/environment relationships and vegetation dynamics along the dominant gradients are better understood, managers will be able to either better predict the nature and rate of vegetation change resulting from development, or use vegetation change to monitor changes in the surface expression of geothermal activity following such development. Previous research on the composition, structure, and dynamics of this vegetation in New Zealand is restricted to one preliminary study (Given 1980).

This study provides baseline data from possibly the least disturbed geothermal field of the central North Isand (Te Kopia Scenic Reserve, Fig. 3), examining vegetation composition, structure, and dynamics in relation to soil temperature, pH, and chemistry. Here, we report on completion of the second objective of a three-part project - an analysis of geothermal vegetation along major environmental gradients. Objective 1 saw the completion of a map of the geothermal vegetation of the Te Kopia area (see Part I). Objective 3 will report on the development of a vegetation monitoring system based in part on the results presented here, in order to detect changes resulting from the effects of draw-off from geothermal fields. This third objective will be funded by Environment Waikato, although it is agreed that the results will also be made available to the Department of Conservation.

The Te Kopia Scenic Reserve (Fig. 3) is a 1408 ha protected natural area on the Paeroa Range south of Rotorua and within the Atiamuri Ecological District (Wassilieff & Timmins 1984). Geothermal features and vegetation occur over approximately 95 ha of this reserve, and are located on the scarp and at the base of the Paeroa Fault. The geothermal vegetation is notable as (a) it contains several rare plant species, and (b) adventive weeds (e.g., pines), which are a problem in many other geothermal reserves, are still at low densities. The reserve contains large colonies of the rare fern *Dicranopteris Iinearis,* and the

FIGURE 3 LOCATION OF STUDY AREA AND OTHER LOCALITIES MENTIONED IN THE TEXT. ALSO SHOWN ARE MAJOR LAKES (STIPPLED), ROADS, AND THE LOCATION OF OTHER NEARBY GEOTHERMAL AREAS.



rare orchids *Calocbilus paludosus* and C. *robertsonii* are well represented (Clarkson 1984; Humphries & Ecroyd 1990).

The geothermal environment is characterised by steep gradients in temperature and soil chemistry, providing unique opportunities to study the effects of stress on organisms and communities and how species are organised along such gradients. Plant community patterns in apparently undisturbed geothermal areas are spatially distinct (e.g., Given 1980, Burns & Leathwick 1993), suggesting that plant composition and structure may reflect underlying environmental gradients.

3. Objectives

- Measure appropriate environmental variables and vegetation composition and structure over the full range of geothermally influenced sites.
- Determine which environmental variables are most strongly correlated with vegetation composition and structure.
- Use these variables to model likely changes in the composition and structure of geothermal vegetation with environmental variation.

4. Methods

Study area boundaries were chosen to include all geothermal vegetation, using enlargements of the most recent (1991) NZ Aerial Mapping colour aerial photos (scale = 1: 3300) (see Part I). Parallel E-W transects were systematically located over this study area every 200 m, and vegetation composition and structure were described on plots spaced at 100-m intervals along these transects, giving a total of 49 plots. At each plot, vegetative cover by tier was recorded for all vascular plants and bryophytes in quadrats varying between 9 m^2 (low vegetation) and 25 m^2 (tall vegetation) in area. Small samples of plants (particularly bryophytes) were sometimes taken to later verify identification.

At each plot, the following environmental and site data were collected: soil temperature at 0, 5, 10, and 15 cm depths, altitude, slope, canopy height, groundcover, and topographic position. Soil temperature was measured with a Digitron portable thermometer (model 3200KC) fitted with a 25 cm "bitumen" probe (model S016K). Groundcover was recorded as the percentage ground surface covered in five categories: bryophytes, vascular plants, rocks, bare soil, and litter. Topographic position was described using the nine-unit landsurface model of Dalrymple *et* al. (1968). In addition, at every second plot a soil sample was taken. Each sample consisted of at least 20 soil plugs to 10 cm depth extracted using a Hoffer tube and aggregated. Samples were analysed for pH (in H_20), conductivity, % soluble salts, $CaC1_2$-extractable Al, water-soluble S04, and DPTA-extractable Fe, Mn, Zn, and Cu (Blakemore *et* al. 1987, Hoyt & Nyborg

1972, Johnson & Nishita 1952, Lindsay & Norvell 1978). These soil variables and elements were chosen from the many possible tests available as those most likely to indicate restrictions on plant growth in geothermally altered soils, and as being feasible within the available budget (K. Giddens, pers. comm.).

The species and environmental data were analysed using detrended canonical correspondence analysis as implemented by the program CANOCO (ter Braak 1988). This provides a direct ordination diagram in which axes are a linear combination of the environmental variables supplied, and "optimally displays how community composition varies with the environment" (ter Braak 1988). Soil temperatures at 0, 5, 10, and 15 cm depth were highly intercorrelated, and since temperature at 15 cm provided the greatest range over which to separate species by their temperature response, only this variable was used in the analysis. Relationships between cover abundance of the major plant species and the dominant environmental variable were analysed using the non-parametric regression technique of Generalised Additive Models (Hastie & Tibshirani 1990, Yee & Mitchell 1991).

5. Results

5.1 SOIL CHARACTERISTICS

Soil characteristics of plots were grouped according to the vegetation types developed in Part I to examine variation across the geothermal area (Table 1). Temperature measurements taken at 15 cm depth indicate that these vegetation types fall broadly along a gradient of decreasing temperature. However, many other soil characteristics are similar throughout the different vegetation types, e.g., soils are uniformly extremely acidic, with very low conductivity and soluble salts (Table 1; Blakemore *et* al. 1987). Aluminium levels in almost all plots are extremely high - an order of magnitude greater than levels considered to be toxic for many crop plants (Singleton *et* al. 1987). Zinc and Cu levels are extremely low, Mn levels are moderate, and Fe levels are extremely high in relation to crop tolerance levels (Lindsay & Norvell 1978, Kabata-Pendias & Pendias 1984). Iron levels also increase as soil temperature declines. Water-soluble sulphate levels are also very high (when compared with the more aggressively extracted phosphate-soluble sulphate ratings given in Blakemore *et* al. 1987), and decrease with ground temperature.

5.2 ORDINATION

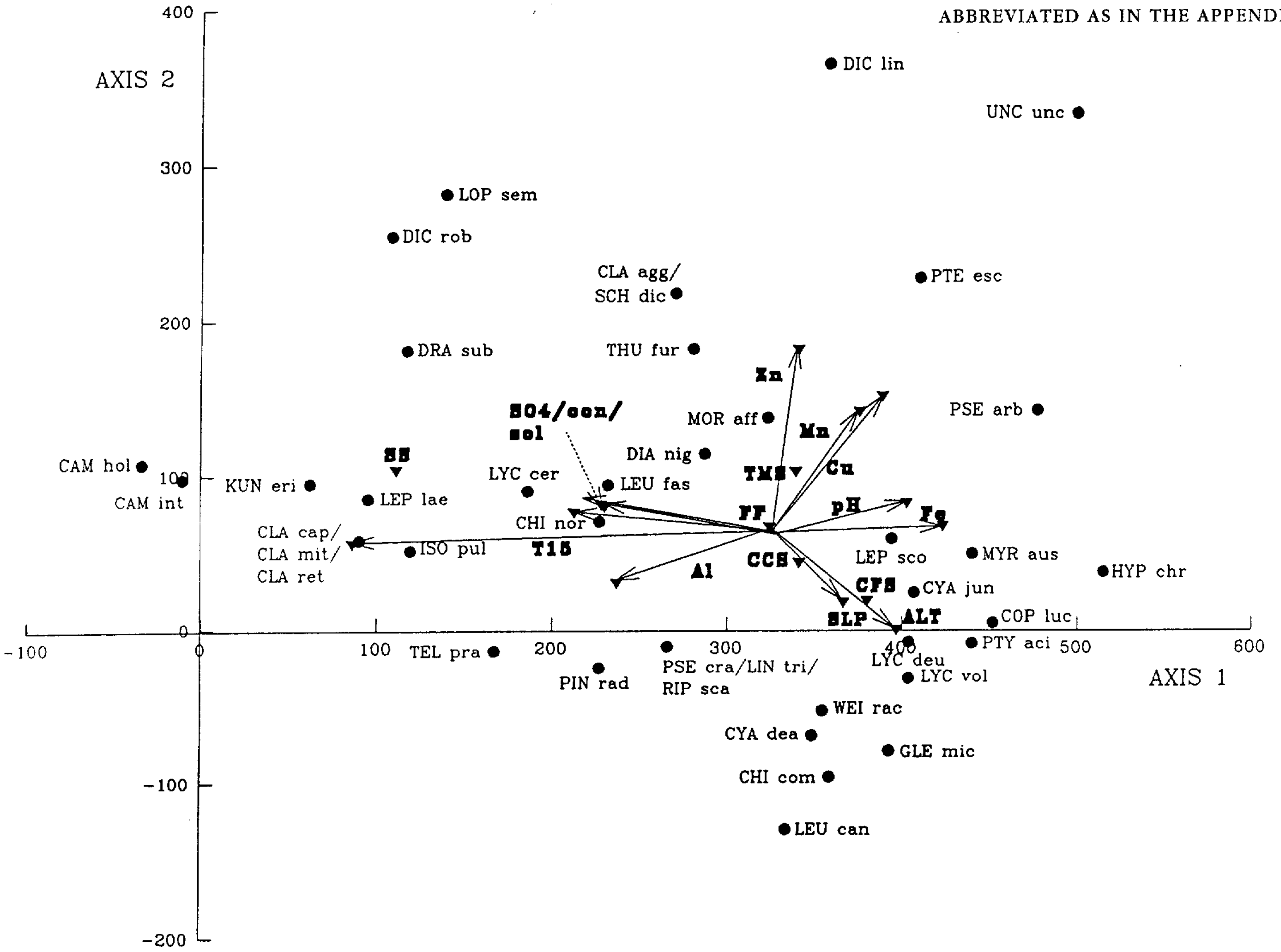
Two separate ordinations were carried out. The first used all plots for which only a limited number of site factors were consistently available. The second used the subset of plots for which soil sample results were available, and therefore used the full range of environmental variables measured. These two analyses provided strikingly similar results, and therefore only the latter is presented here.

TABLE 1 RESULTS OF SOIL ANALYSES GROUPED ACCORDING TO THE CLASSIFICATION OF PLOTS BY VEGETATION TYPES DERIVED IN PART I. MEANS ONLY ARE PRESENTED; MEANS WITH DIFFERENT SUPERSCRIPTS ARE SIGNIFICANTLY DIFFERENT AT THE 0.05 LEVEL USING TUKEY'S HSD TEST. VEGETATION TYPE NAMES FOLLOW THE CRITERIA OF ATKINSON (1985).

VEGETATION TYPE	n	T15	pH	Con.	Sol.	Al	SO_4	Fe	Mn	Zn	Cu
Prostrate kanuka / *Campylopus* spp. moss-shrubland	6	62.0^{a}	4.68^{a}	0.09^{a}	0.03^{a}	55.9^{a}	131.5^{a}	31.4^{a}	5.05^{a}	0.18^{a}	0.05^{a}
Prostrate kanuka - mingimingi shrubland	1	51.0	4.00	0.10	0.04	108.2	128.0	64.2	2.50	0.60	0.00
(Pine) / mingimingi - manuka scrub	2	21.5^{b}	3.70^{a}	0.13^{a}	0.05^{a}	112.7^{a}	59.0^{a}	108.9^{ab}	2.65^{a}	1.50^{a}	0.65^{b}
Manuka - kamahi / *Cyathodes juniperina* scrub	10	18.0^{b}	4.58^{a}	0.09^{a}	0.03^{a}	48.6^{a}	81.3^{a}	123.9^{b}	7.45^{a}	0.82^{a}	0.25^{ab}
Kamahi - fivefinger forest	3	16.0^{b}	4.60^{a}	0.06^{a}	0.02^{a}	48.2^{a}	47.3^{a}	152.9^{ab}	7.07^{a}	1.00^{a}	0.47^{ab}

T15 = soil temperature at 15 cm depth
Con. = soil conductivity (mmho/cm (K_{25}))
Sol. = soluble salts (%)
Al = $CaCl_2$-extractable Al (µg/g)
SO_4 = water soluble SO_4 (µg/g)
Fe = 0.005M DPTA-extractable Fe (µg/g)
Mn = 0.005M DPTA-extractable Mn (µg/g)
Zn = 0.005M DPTA-extractable Zn (µg/g)
Cu = 0.005M DPTA-extractable Cu (µg/g)

FIGURE 4 SPECIES SCORES FOR FIRST AND SECOND AXES OF A DCCA ORDINATION OF TE KOPIA GEOTHERMAL VEGETATION PLOTS. VECTORS INDICATE THE DIRECTION OF MAXIMUM CHANGE FOR A SITE VARIABLE AND THE STRENGTH OF THEIR CORRELATION WITH THE ORDINATION AXES. SPECIES NAMES AND VARIABLE NAMES ARE ABBREVIATED AS IN THE APPENDIX.



Results from the CANOCO analysis are shown in Fig. 4, with species positions on the axes (shown with symbols) indicating their broad relationships with environmental factors (shown by vectors indicating their direction and magnitude of correlation with the axes) (ter Braak 1988). The change in vegetation composition was most marked in relation to axis 1, as indicated by the relative strength of the eigenvalues of the first two axes (axis 1 = 0.62, axis 2 = 0.30). The first axis was highly and most strongly correlated (inversely) with soil temperature, and reflects the thermal influence on the rooting zone (Fig. 4). Species with low axis 1 scores are those of sites near geothermal features with high soil temperatures, such as *prostrate kanuka*, arching clubmoss, *Campylopus holomitrium* (moss), *Cladonia capitellata* (lichen) and *Cladonia mitis* (lichen) (Fig. 4). Soil conductivity, soluble salts, Al, and S04 all decreased along the first axis, with Fe and pH increasing.

The second axis was less strongly correlated with measured environmental variables. Levels of extractable Mn, Cu, and particularly Zn all increased along the second axis, while slope and altitude generally decreased. Plots that have high axis 2 scores are located on fallfaces (FF, Fig. 4) close to the active Paeroa Fault scarp, or on transportational midslopes (TMS, Fig. 4) at the base of this scarp. These plots have extremely shallow soils, and are probably frequently disturbed by mass movement or have been recently burnt. Vegetation on these plots is dominated by manuka and fivefinger at cool soil temperatures. Plots with high axis 2 scores but with intermediate soil temperatures are also co-dominated by monoao. Plots that have low axis 2 scores generally have low soil temperatures and occur on colluvial footslopes (CFS, Fig. 4) with deeper soils. Vegetation is generally taller, and is dominated by kamahi and other species of later successional forest, e.g., ponga, rimu. We therefore interpret this second axis as reflecting the effect of disturbance history and/or soil instability and depth on vegetation composition. The changes in trace element availability in these soils are consistent with this interpretation, as these elements would be more available in the recently weathered soils near the fault scarp (high axis 2 scores) but become less available in the deeper, older soils (low axis 2 scores) owing to leaching or to being bonded into clays or organic matter complexes.

5.3 REGRESSION ANALYSES

The direct ordinations indicate that the gradient in soil temperature at 15 cm depth (T_{15}), which is also correlated with a large number of soil parameters, has the greatest influence on vegetation composition and structure. Changes in cover abundance of the most common canopy, understorey, and bryophyte species along this gradient show how different species are differentially tolerant of the stresses imposed by increased soil temperature and associated geothermal effects (Fig. 5). This gradual compositional change also leads to significant overall structural changes in the vegetation along this gradient (Fig. 6).

Below T_{15} = 20°C, the vegetation is tall (c. 8-10 m high) and dominated by kamahi and fivefinger, with karamu a common component. Turutu, bracken, and snowberry are common in the understorey. Leaf litter is the principal

FIGURE 5 BEST FITTING REGRESSION CURVES FOR CHANGES IN COVER ABUNDANCE OF COMMON SPECIES ALONG A GEOTHERMAL GRADIENT IN GROUND TEMPERATURE AT 15 CM DEPTH: (A) CANOPY SPECIES; (B) VASCULAR UNDERSTORY SPECIES; (C) BRYOPHYTE SPECIES. SPECIES NAMES ARE ABBREVIATED AS IN THE APPENDIX, AND ARE FOLLOWED BY THE R^2 RESULT OF THE REGRESSION IN PARENTHESES.

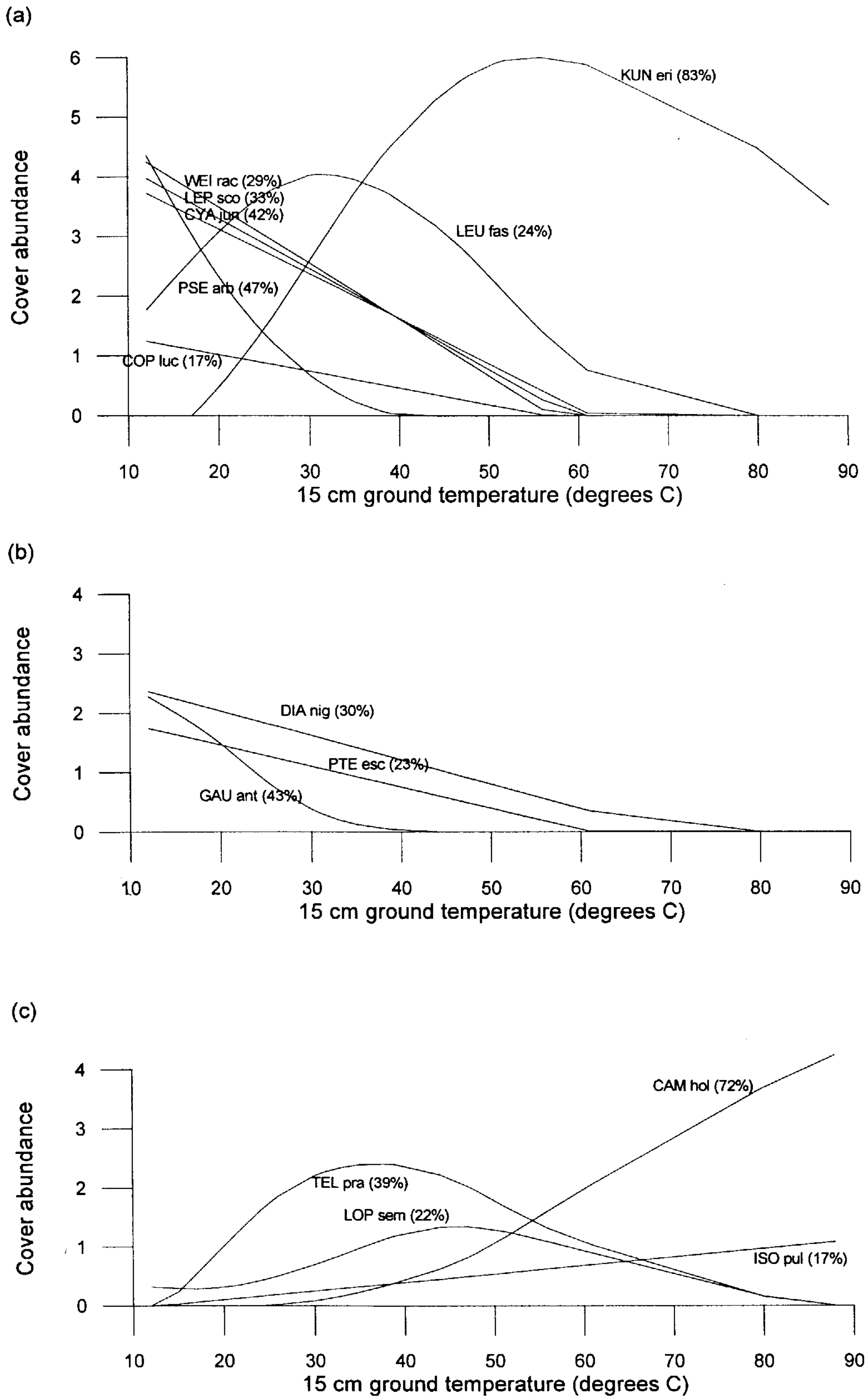
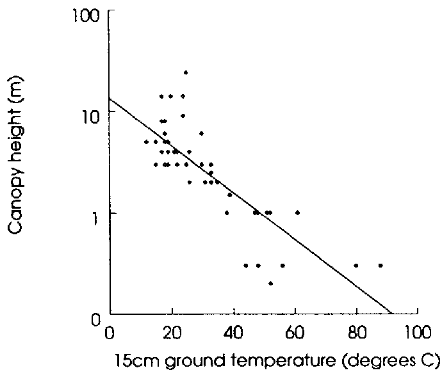
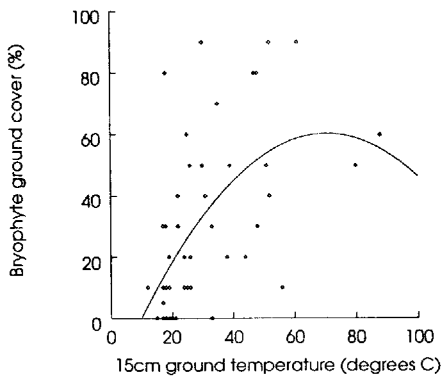


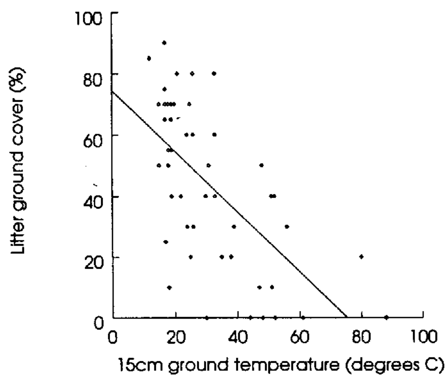
FIGURE 6 STRUCTURAL AND SPECIES RICHNESS CHANGES IN VEGETATION ALONG A GRADIENT IN GROUND TEMPERATURE AT 15 CM DEPTH (T_{15}).



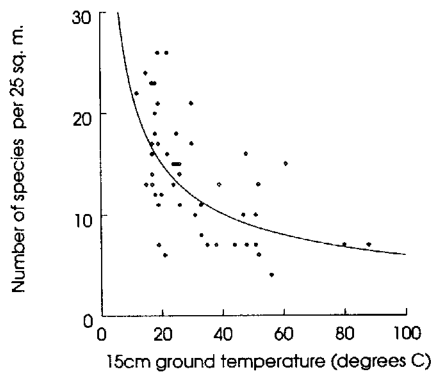
(a) Canopy height (HT) versus T_{15}: $LN(HT) = 7.206 - 0.053(T_{15})$. $R^2 = 0.658$, $p < 0.001$, $n = 49$.



(b) Bryophyte ground cover (B%) versus T_{15}: $B\% = -21.258 + 2.301T_{15} - 0.016\ (T_{15})^2$. $R^2 = 0.312$, $p < 0.001$, $n = 40$.



(c) Litter ground cover (L%) versus T_{15}: $L\% = 74.587 - 0.990T_{15}$, $R^2 = 0.387$, $p < 0.001$, $n = 49$.



(d) Species richness (SP) versus T_{15}: $SP = 87.549\ (T_{15})^{-0.568}$, $R^2 = 0.369$, $p < 0.001$, $n = 49$.

groundcover, and bryophyte biomass is generally insignificant. Species richness is relatively high (> 20 plant species/ 25 m^2).

As T_{15} increases from 20 to 30°C there is a dramatic shift in vegetation composition and structure. Canopies are shorter (2-4 m) and dominated by manuka, mingimingi, and prickly mingmingi, with kamahi, fivefinger, and karamu decreasing in abundance. Snowberry and bracken also decrease sharply in abundance over this range, although turutu increases. Large bryophyte mats, dominated at Te Kopia by the liverwort Telaranea praenitens, become common at these temperatures, and leaf litter is no longer the predominant groundcover. Species richness is on average between 10 and 20 plant species/25 m^2.

Sites with T_{15} values between 30 and 60°C are dominated by canopies of prostrate kanuka about 1 m tall, with less abundant mingimingi and monoao. Understories and groundcover comprise turutu and large mats of the bryophytes Telaranea praenitens, Lophocolea semiteres, and Lepidozia laevifolia. Species richness is generally < 10 species/ 25 m^2.

Above T_{15} = 60°C breaks in the short (< 1 m tall) canopy cover occur, and clumps of the moss Campylopus holomitrium and several lichen species are common. Another small moss, Isopterygiopsis pulchella, is found within these clumps. Where a vascular canopy does exist, it is almost entirely dominated by prostrate kanuka. Sites experiencing the hottest ground temperatures have as few as 4 (vascular and non-vascular) species.

7. Discussion

Soils throughout the geothermal area are poor for growth of most plants because of their low pH and unusual levels of trace elements. Although the pH levels of topsoils of the Waiotapu region surrounding Te Kopia are generally below average (Vucetich & Wells 1978), the soils of Te Kopia are even more acidic. However, the relatively uniform distribution of values across the area suggests that geothermally derived inputs to soil probably occur through dissolution of geothermal gases in rainfall, or condensation of steam emitted from fumaroles, affecting large areas more or less equally. If the populations of species present here are composed of stable genotypes specifically capable of growing on such poor soils, then these genotypes may be useful to rehabilitate other areas with soils of low pH or nutrient content, e.g., mine tailings.

Soil temperature, which is also correlated with a large number of soil parameters, apparently has the greatest influence on vegetation composition and structure. A generally predictable sequence of species occurs along this gradient, and provides an important and feasible basis on which to design a monitoring system as planned for objective 3. Species are differentially sensitive to temperature change, showing gradual increase or decrease in abundance with changing soil temperatures. Some show strong correlations of abundance with temperature, and changes in their distribution may be useful as indicators of change in the underlying geothermal conditions. Examples of temperature-sensitive species are *Pseudopanax arboreus*, *Kunzea ericoides*, *Gaultheria antipoda*, and *Campylopus holomitrium* (Fig.5).

The vegetation continuum (*sensu* Austin & Smith 1989) described at Karapiti by Given (1980) is similar to the hotter end of that described here. Given's coolest zones still had soil temperatures at 5 cm depth of 40-55 °C. The Te Kopia vegetation continuum is therefore a considerable extension of that previously published, particularly including the vegetation changes that occur over soil temperatures from 20-40 °C, and will be more applicable to vegetation in other geothermal areas.

Ongoing research should examine the variability of soil temperature at any point within a geothermal area, and by what process and over what time species adjust their distribution to a change in the temperature gradient. Also, how do stand processes change along the temperature gradient? For example, the replacement of a groundcover dominated by litter to one dominated by bryophyte mats as soil temperatures increase may suggest that litterfall decreases along this gradient, perhaps owing to a decrease in growth rate. Alternatively, this effect may result from an increase in available moisture for bryophyte growth from proximity to steam vents in hot areas. Objective 3 of this project may be able to examine some of these issues.

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8. References

Atkinson, IAE 1985 Derivation of vegetation mapping units for an ecological survey of Tongariro National Park, North Island, New Zealand. *New Zealand journal of botany* 23:361-378.

Austin, M.P., Smith, T.M. 1989. A new model for the continuum concept. *Vegetatio* 83: 35-47.

Blakemore, L.C., Searle, P.L., Daly, B.K. 1987. Methods for chemical analyses of soils. NZ Soil *Bureau scientific report 80.* DSIR, Lower Hutt.

Brownsey, P.J., Smith-Dodsworth, J.C. 1989. New Zealand ferns and fern allies. Auckland, Bateman.

Clarkson, B. 1984. Te Kopia Scenic Reserve - Thermal area vegetation. Botany Division, DSIR, unpublished report.

Dalrymple, J.B., Blong, R.J., Conacher, A.J. 1968. An hypothetical nine unit landsurface model. *Zeitschrift fur Geomorphologie N. F. 12, 1:* 60-76.

Dench, N.D. 1993. Geothermal Energy. Chapter 2 in Renewable Energy Opportunities for New Zealand. Eden Resources Ltd for Ministry of Commerce.

Given, D.R. 1980. Vegetation on heated soils at Karapiti, central North Island, New Zealand, and its relation to ground temperature. *New 2ealand journal of botany* 18: 1-13.

Hastie, T., Tibshirani, R.J. 1990. Generalised additive models. Chapman & Hall, London.

Hoyt, D.B., Nyborg, M. 1972. Use of dilute calcium chloride for the extraction of plant available aluminium and manganese from acid soil. *Canadian journal of soil science* 52: 163-167.

Humphries, E., Ecroyd, C. 1990. Te Kopia Scenic Reserve. *Rotorua Botanical Society newsletter* 20:26-27.

Johnson, C.M., Nishita, H. 1952. Microestimation of sulfur in plant materials, soils, and irrigation waters. *Analytical Chemistry* 24: 736-742.

Kabata-Pendias, A., Pendias, H. 1984. Trace elements in soils and plants. CRC Press, Boca Raton, Florida.

Lindsay, W.L., Norvell, W.A. 1978. Development of a DPTA soil test for zinc, iron, manganese and copper. Soil *Science Society of America* journal 44: 772-777.

Singleton, P.L., Edmeades, D.C., Smart, R.E., Wheeler, D.M. 1987. Soil acidity and aluminium and manganese toxicity in the Te Kauwhata area, North Island, New Zealand. *New Zealand journal of agricultural research* 30: 517-522.

ter Braak, CJF 1988 CANOCO - a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis (version 2.1). Technical Report LWA-88-02. Groep Landbouwwiskunde, Wageningen, The Netherlands.

Vucetich, C.G., Wells, N. 1978. Soils, agriculture and forestry of Waiotapu Region, Central North Island, New Zealand. *NZ Soil Bureau bulletin 31.* DSIR, Lower Hutt.

Wells, N., Whitton, J.S. 1966. The influence of hydrothermal activity on the element content of soils and plants. *New Zealand journal of science* 9: 982-991.

Wassilieff, M., Timmins, S. 1984. Register of protected natural areas in New Zealnd. Department of Lands and Survey, Wellington.

Yee, T.W., Mitchell, N.D., 1991. Generalised additive models in plant ecology. *Journal of vegetation science* 2: 587-602.

9. Appendix

Common names or descriptions of plants mentioned in Part I.

SCENTIFIC NAME	COMMON NAME OR DESCRIPTION
Aristotelia serrata	makomako
Baumea rubiginosa	baumea
B. tenax	baumea
B. teretifolia	baumea
Blechnum sp. I	kiokio
B. minus	swamp kiokio
Campylopus clavatus	moss
C. holomitrium	moss
C. introflexus	moss
Carex geminata	sedge
Chiloscyphus spp.	liverwort
Cladia leptoclada	lichen
Cladonia capitellata	lichen
Coprosma lucida	karamu
Cortaderia sp.	toetoe
Cyathodes juniperina	mingimingi
Dianella nigra	turutu
Dicksonia squarrosa	wheki
Dicranoloma sp.	moss
Dicranopteris linearis	
Dracophyllum subulatum	monoao
Gahnia setifolia	gahnia
Gaultheria antipoda	snowberry
Geniostoma rupestre	hangehange
Gleichenia microphylla	waewaekaka
G. dicarpa	tangle fern
Histiopteris incisa	water fern
Hypnum cupressiforme	moss
Hypolepis ambigua	
H. distans	
Knightia excelsa	rewarewa
Kunzea ericoides var. *microflora*	prostrate kanuka
Kurzia sp.	liverwort
Lepidozia glaucophylla	liverwort
Leptospermum scoparium	manuka
Leucobryum candidum	moss
Leucopogon fasciculatus	minimingi
Lycopodium cernuum	clubmoss
L. deuterodensum	clubmoss
L. volubile	clubmoss
Morelotia affinis	
Muehlenbeckia australis	pohuehue
Phormium tenax	harakeke
Phymatosorus diversifolius	kowaowao
Pinus radiata	radiata pine
Pseudopanax arboreus	fivefinger
Pteridium esculentum	bracken
Ptychomnion aciculare	moss
Pyrrosia eleagnifolia	leather-leaf fern
Scbizaea dichotoma	an fern
S. sp (cf. *flstulosa)*	comb fern
Schoenus tendo	sedge
Thuidium furfurosum	moss
Weinmannia racemosa	kamahi

Common names or descriptions of plants mentioned in Part 11.

SCIENTIFIC NAME	ABBREVIATION	COMMON NAME OR DESCRIPTION
Calochilus paludosus	CAL pal	orchid
C. robertsonii	CAI rob	orchid
Campylopus holomirrium	CAM hol	moss
C. introflexus	CAM int	moss
Chiloscyphus compactus	CHI com	liverwort
C. normalis	CHI nor	liverwort
Christella sp. (unnamed)	CHR sp.	fern
Cladia aggregata	CLA agg	lichen
Cladia retipora	CLA ret	lichen
Cladonia capitellata	CLA cap	lichen
Cladina mitis	CLA mit	lichen
Coprosma lucida	COP luc	karamu
Cyathea dealbata	CYA dea	ponga
Cyathodes juniperina	CYA jun	prickly mingimingi
Dacrydium cupressinum	DAC cup	rimu
Dianella nigra	DIA nig	turutu
Dicranoloma robustum	DIC rob	moss
Dicranopterls linearis	DIC lin	fern
Dracophyllum subulatum	DRA sub	monoao
Gaultheria antipoda	GAU ant	snowberry
Gleichenia microphylla	GLE mic	waewaekaka
Hypnum chrysogaster	HYP chr	moss
Isopterygiopsis pulchella	ISO pul	moss
Kunzea ericoides var. *microflora*	KUN eri	prostrate kanuka
Lepidozia laevifolia	LEP lae	liverwort
Leptospermum scoparium	LEP sco	manuka
Leucobryum candidum	LEU can	moss
Leucopogon fasciculatus	LEU fas	mingimingi
Lindsaea trichomanoides	LIN tri	fern
Lophocolea semiteres	LOP sem	liverwort
Lycopodium cernuum	LYC cer	arching clubmoss
L. deuterodensum	LYC den	clubmoss
L. volubile	LYC vol	clubmoss
Morelotia affinis	MOR aff	sedge
Myrsine australis	MYR aus	mapou fern
Nephrolepis sp. (unnamed)	NEP sp.	
Pinus radiata	PIN rad	radiata pine
Pseudopanax arboreus	PSE arb	fivefinger
P. crassifolius	PSE cra	lancewood
Pteridium esculentum	PTE esc	bracken
Ptychomnion aciculare	PTY aci	moss
Ripogonum scandens	RIP sca	supplejack
Schizaea dichotoma	SCH dic	fan fern
Telaranea praenitens	TEL pra	liverwort
Thuidium furfurosum	THU fur	moss
Uncinia uncinata	UNC unc	hooked sedge
Weinmannia racemosa	WEI rac	kamahi

Variables mentioned in Fig. 1.

Al = CaC12 - extractable Al (mg/g)
ALT = altitude above sea level
Con. = soil conductivity (mmho/cm (K25))
Cu = 0.005M DPTA-extractable Cu (mg/g)
Fe = 0.005M DPTA-extractable Fe (mg/g)
Mn = 0.005M DPTA-extractable Mn (mg/g)
SLP = slope (degrees)

Sol. = soluble salts (%)
T15 = soil temperature at 15 cm depth
Zn = 0.005M DPTA-extractable Zn (mg/g)

Topographic units mentioned in Fig. 1 (Dalrymple et al. 1968)

CCS = convex creep slope
CFS = concave footslope
FF = fallface
SS = seepage slope
TMS = transportational midslope