INDIGENOUS - INDUCED VEGETATION AND PINUS RADIATA ON VOLCANIC ASH SOILS

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INTRODUCTION

This paper presents the results of preliminary work on the vegetation of central North Island rhyolitic ash showers. It has three aims: first to record details of the fire induced seral vegetation of areas not yet subject to land development; second to compare such vegetation with the understorey vegetation of *Pinus radiata* plantations, and with the shrubland found in localised areas where *P. radiata* has failed to regenerate after clearfelling; third to examine, within each of the three types of vegetation, the variations in species composition with varying soils, with the ultimate end of evolving a site classification for forestry use, based on the understory and cutover vegetation.

The term "indigenous-induced" as used by Cockayne (1958) is appropriate to the three types of vegetation described in this paper. All three are induced by human activity and composed predominantly of indigenous plants.

1. The *Leptospermum scoparium — Pteridium esculentum — Dracophyllum subulatum — Poa caespitosa* fire-induced shrub and tussock land characteristic of these soils before intensive land use is started.
2. The understory of *Pinus radiata* plantations, 34 years old. Predominantly of tree ferns and macrophyllous mull-forming shrubs, this vegetation has developed after the natural opening of the canopy of these plantations.
3. Shrubland, dominated by the forest understory species and *Pteridium* found after clear felling, when the pine has failed to regenerate in localised areas.

The aim of this paper is to describe the variations of these three communities with soils of steeplands, hills and undulating plateaux.

Topography exerts a strong influence on the characters of soils developed from rhyolitic ash showers, especially in the distribution of the youngest member, the Taupo pumice. Previous work has expressed this influence of topography on soils and on the distribution of vegetation existing before intensive land use.

Between 1925 and 1932 a site classification was evolved for the area planted with *Pinus* spp. by the forerunners of N.Z. Forest Products Ltd. The late Owen Jones compiled the site classification shown in Figure 1.

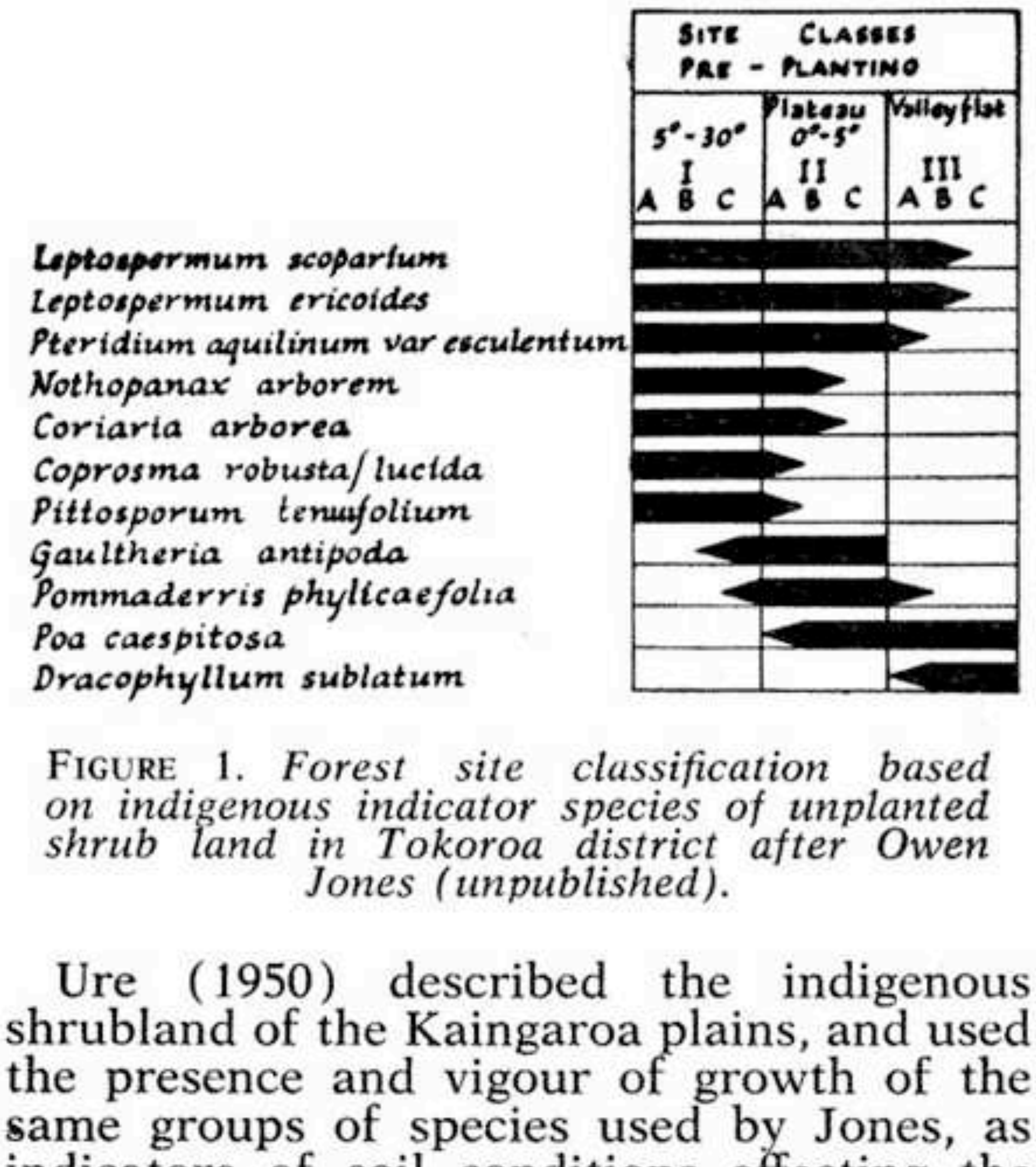

FIGURE 1. *Forest site classification based on indigenous indicator species of unplanted shrub land in Tokoroa district after Owen Jones (unpublished).*

Ure (1950) described the indigenous shrubland of the Kaingaroa plains, and used the presence and vigour of growth of the same groups of species used by Jones, as indicators of soil conditions affecting the growth of *Pinus* spp. in adjacent plantations. As conditions are more extreme at the higher altitude of Kaingaroa, and the pumice cover is generally coarser in texture, the presence of *Cladonia* spp., *Raoulia australis* and *Pimelea prostrata* were taken into acount by Ure as indicators. He also pointed out the significance of the depth of Taupo pumice as a function of distance from topsoil to the finer textured and more weathered older ash showers beneath. Where Taupo pumice was shallow, on slopes the shrub growth was more vigorous and richer in species. Van't Woudt (1956) also pointed out a similar relationship.

Baumgart (1952) and Druce (1952) dealing with the West Taupo area also described the pattern of scrubland vegetation in its relation to pumice cover; with *Pteridium, Coriaria arborea, Leptospermum scoparium, Nothopanax* and *Weinmannia racemosa* on slopes from which much Taupo pumice has been eroded exposing more weathered showers; and *Poa caespitosa — Dracophyllum subulatum* on valleys filled with deep pumice.

Henry (1954) first described the understorey of *Pinus radiata* plantations in the Tokoroa area, and contrasts the xerophytic shrubland before planting with the mesophytic nature of the shrubs invading these plantations after natural mortality has opened the pine canopy. Following clearfelling of a stand of *P. radiata* 23 years old planted on a *Poa caespitosa* covered flat on deep pumice he describes the invasion of the site by tall *Pteridium,* previously restricted to slopes with relatively shallow pumice cover.

With this foundation of work, described above, the present paper describes more fully the vegetation changes on three different soils from unplanted shrub and tussock land through pine forests to the shrubland of cutover areas; and is a preliminary stage in the building up of a new site classification based on the interaction between soil, vegetation and forest.

LOCATION, TOPOGRAPHY AND CLIMATE

The areas examined lie within or immediately adjacent to the boundaries of land owned by N.Z. Forest Products Ltd., on N.Z. M.S.1, sheets N84 and N85 at Lat. 38° S. (Fig. 2). The country lies between 500 ft. and 2000 ft. altitude and the topography is a combination of ignimbrite plateaux and remnants of these plateaux eroded to form broken hilly country. There are also extensive flat-bottomed pumice-filled valleys. The areas chosen for particular study are plateaux and hills lying between 1500 ft. and 2000 ft., receiving an annual rainfall probably greater than 65in. From Kinleith at 1200 ft. the following records from 1952 to 1957 give an idea of climatic conditions in the area.

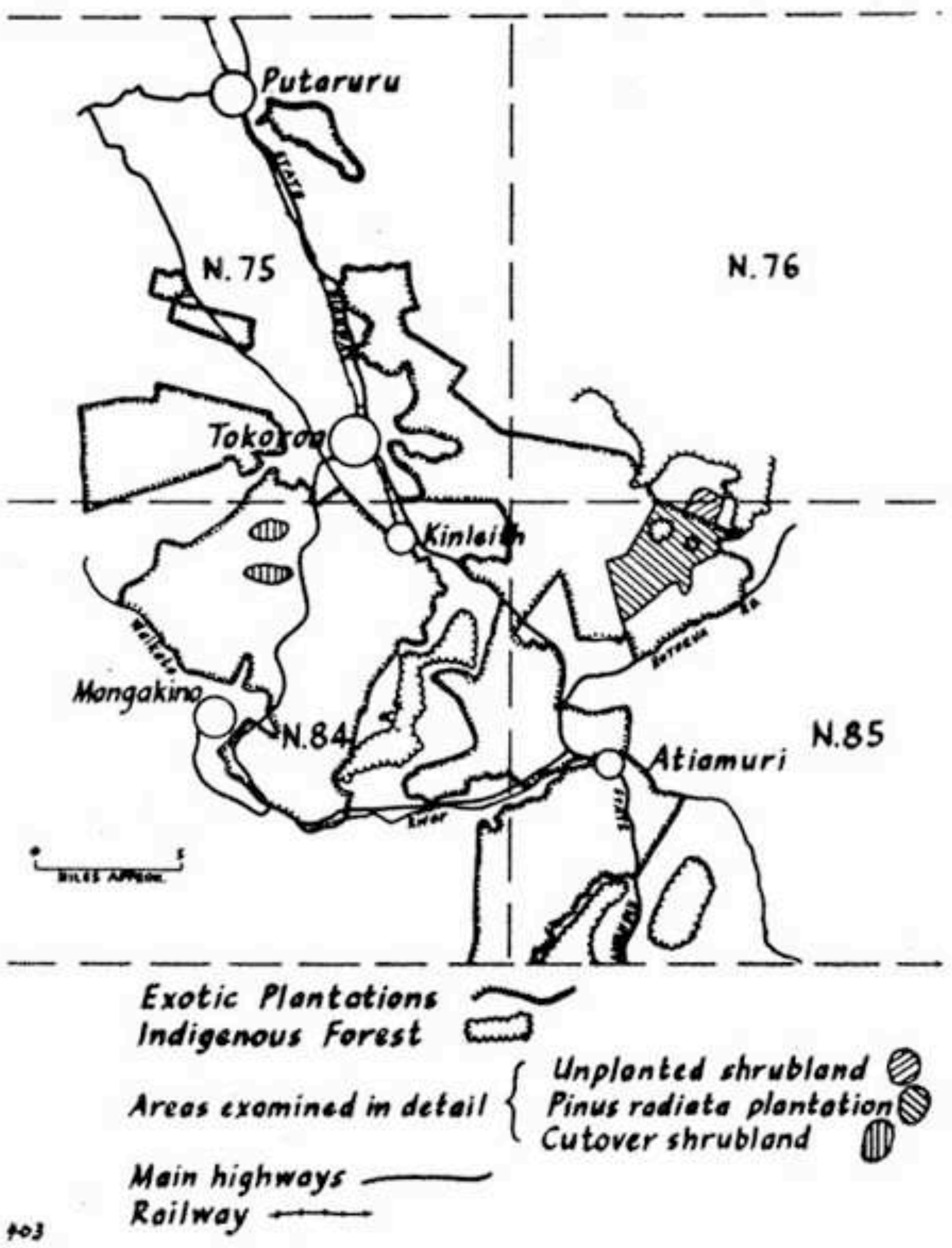

FIGURE 2. *Locality map.*

SOILS

Figure 3 is a generalised topographic profile, showing the relative positions and proportions of parent materials making up the three soil types in the area.

The parent materials are all acidic in petrologic nature, being derived from the Pleistocene to Recent rhyolitic cycle of volcanic activity in the central North Island. In stratigraphic order they are:

TAUPO PUMICE

An ash shower of paroxysmal origin dated at 130 A.D. by 14C methods (Fergusson and Rafter 1950).

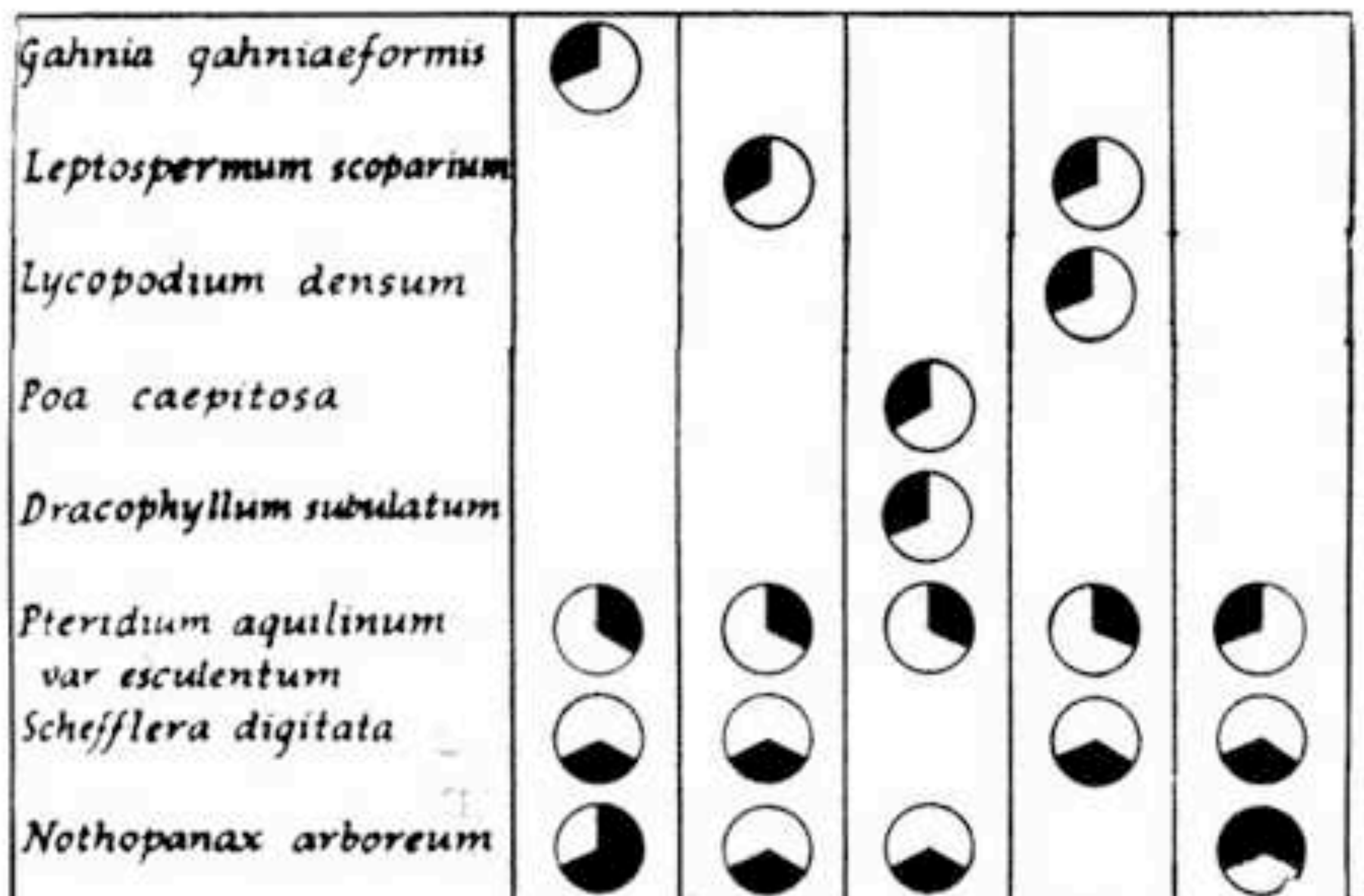

FIGURE 3. *Indicator species of unplanted shrub land forest understory and cutover shrub land for soil types and aspects (above) and a schematic representation of distribution of soil parent materials with topography (below).*

Below the upper shower of sandy silt texture there are lower showers of sand to coarse sand texture on undulating surfaces. Soils formed from Taupo pumice are well supplied with nutrients and have exceptional moisture retention capacity for their early stage of weathering (Packard 1957).

BROWN ASH

This term is suggested for general use by Vucetich (pers. comm.) to include the beds Mamaku 1 and Mamaku 2 of Grange (1937) and Tirau ash of Grange, Taylor and Rigg (1932). These ash showers were of intermittent origin and composed of fine sand and silt, weathered since their deposition about 17,000 years ago (J. Healy pers. comm.) to a silt loam or sand loam. Included is a small admixture of andesitic ash from the large central volcanoes, as shown by the higher amounts of Ca, Mg and P than are normal in purely rhyolitic showers (Grange *et al.* 1932). Brown ash has a higher clay content than Taupo pumice soils, and appears to have even greater moisture retention capacity than these soils.

IGNIMBRITE (with some rhyolite and pumice breccias)

Mapped by Grindley (1959) as Lower Pleistocene—Recent the ignimbrite sheets form the underlying rocks over most of the area. They are not hard, but massive and form flat to undulating plateaux. Where these plateaux have been eroded, their remnants form a characteristically broken, irregular landscape, with much of the drainage subterranean. The contribution of these rocks to soil profiles varies from the lithosols of bluffs, to gravel included in either ash

TABLE 1. *Meteorological data, Kinleith, Aug.* 1952–*Dec.* 1957

	J.	F.	M.	A.	M.	Ju.	Jy.	Au.	S.	O.	N.	D.
Mean Rainfall* (in.)	3.6	3.2	4.1	6.4	5.8	8.3	6.2	5.5	3.3	5.8	6.6	6.1
Mean Temperature (°F)	63	64	60	56	51	45	44	47	50	52	56	60
Mean Maximum Temp. (°F)	81	82	80	73	69	62	60	62	70	70	74	78
Mean Minimum Temp. (°F)	43	41	37	34	29	26	26	28	30	31	36	39
Mean Relative Humidity (%)	76	81	82	87	88	91	89	74	82	79	77	77

* Mean annual rainfall 64.85 in.

showers above or occasionally a coarsening of texture by complete breakdown to sand.

The three soil types examined are:

1. Oruanui sandy silt, undulating phase
2. Oruanui sandy silt, short hill slopes
3. Tauhara steepland.

These are all manuscript names from C. G. Vucetich (pers. comm.) for incorporation in the forthcoming bulletin on the soils of N.Z.M.S.1 N85. The following notes on each soil have also been supplied by him, together with additional field observations by the writer.

1. ORUANUI SANDY SILT, UNDULATING PHASE (slopes of 0° to 5°). This occupies rather exposed undulating plateau surfaces. The topsoils are shallow, ranging from 5 in. to 10 in., and are blacker (almost peaty) under shrubland compared with profiles on neighbouring rolling slopes (Oruanui sandy silts). The upper part of the profile is formed of compact sandy silt, of about 6 in. to 20 in. depth resting on about 12 in. to 18 in. loose coarse sand of pumice and dark rhyolite ash, both layers being from the Taupo pumice. Below this is the silt loam formed from brown ash. The depth of pumice from the soil surface to brown ash, (up to about 40 in.) together with the interposed loose coarse layer are characteristics of this soil. Two-tiered root systems are found in pines on these soils, with one tier in the sandy silt of Taupo pumice, and the other in the silt loam of brown ash. There are few roots in the coarse sand layer of Taupo pumice.

2. ORUANUI SANDY SILT, SHORT HILL SLOPES (slopes of 10°–30°). Taupo pumice on these soils ranges from 0 in. to 20 in. deep, with brown ash occasionally forming the topsoil. The pumice topsoil under shrubland is far looser in consistence, and with better developed crumb structure than in Oruanui sandy silt on deep sand. Pumice gravel is frequent in the lower parts of the horizons, and creep processes have frequently worked these particles into the upper horizons. Root penetration to brown ash has apparently been easy and tree root systems are spread through both Taupo pumice and brown ash. There appears to have been less change in topsoil consistence resulting from the growth of *Pinus radiata* forests than is the case with the Oruanui sandy silt on deep sand.

3. TAUHARA STEEPLAND (slopes over 30°). On slopes up to 35° Taupo pumice still contributes to these soils, generally in pockets up to 12 in. deep. On steeper slopes, (50% to 75% of the area of Tauhara soils mapped by Vucetich) brown ash forms the soil, and on very steep slopes fragments of soft glassy ignimbrite contribute to the profile. Pumice derived topsoils generally not more than 12 in. deep are silty sands with occasional pumice gravel, very friable with soft fine crumb and granular structure. From brown ash the topsoils are silty — sandy loams, friable, loose, with similar structures to pumice topsoil. A sandy texture is found in topsoils derived from fragments of ignimbrite, and gravels from this rock are present in the subsoils. Brown ash is easily accessible to roots in all three facies of this soil type, and all plants have roots distributed throughout the profile. The presence of boulders of ignimbrite on very steep slopes can limit this root distribution.

In addition to the topographic pattern expressed by the variation in parent material of these soils, the microclimate also varies.

Although the Oruanui sandy silt, undulating phase, is a soil of plateaux, there appears to be some cold air drainage on a small scale into depressions on plateaux. This effect is seen in the pattern of vegetation, where such small hollows are dominated by *Poa caespitosa* while elevated areas carry *Leptospermum scoparium, Dracophyllum subulatum* and *Poa caespitosa* in equal proportions.

The difference in aspect on hill and steepland soils has a considerable effect on vegetation in all three stages considered, both directly through the varying rates of evapotranspiration on warm and cold faces, and indirectly in the frequency of burning, in its effects on the soils. This is, as would be expected, most noticeable on the steepland soils where the warm faces under *Leptospermum* shrubland have truncated soils on bare areas between shrubs. Under equivalent aged *Pteridium* on a cold face the vegetative cover is complete and there is up to 12 in. of organically melanized topsoil.

METHODS

Frequency, in the sense of Braun-Blanquet (1932), percentage aerial cover along a line transect, and heights of plants or parts of them intersecting this transect were chosen as easily recorded variables for comparison. Frequency was recorded as the occurrence of any species either on the line transect or visible from it, and calculated as a percentage representing the number of plots carrying a particular species in a particular stratification. (See species list Table 4.)

In shrubland and tussock grassland areas, both on unplanted and cutover land the transect used was 50 ft. long sited across slope, and the cover in feet doubled to give a percentage. Transects were sited by aerial photograph and ground examination for relative homogeneity of communities. Transects were generally in groups, aimed at showing a graphic representation of visually recognisable communities. The limited areas of shrubland of uniform age on all soil types and aspects, both on unplanted land and cutover, further enforced this grouping.

In forest the sampling pattern was extensive, and was aimed at determining a pattern of vegetation. The vegetation survey was accomplished in conjunction with an assessment of timber volume with a sampling intensity of one plot to 40 acres. The sampling pattern used for this assessment is a square grid; originally laid out on contoured plane table maps, the plot centres were transferred visually to 20 chain aerial photographs. This resultant grid pattern, not always accurately orthogonal, was then transferred from the photographs to a 40 chain outline tracing by means of a Zeiss "Sketchmaster". The pattern of plots on this tracing was used as an overlay on the soil maps and together with a field check of soil at each plot, all plots were stratified for soil type and aspect. A 100 ft. line transect was used in the forest, sited across slope. As the volume assessment plot had to be slashed clear of vegetation for optical basal area measurement the transect was sited 100 ft. from the plot centre on a similar slope and aspect. As well as recording the vegetation cover and species seen from the transect the basal area was measured of trees whose canopies overtopped the transect.

Having established the frequency of occurrence of species by plots for each stratification the next step was to select species for study of cover and height. This was carried out as follows:

1. In unplanted shrubland there were a total of 24 transects in an area of about 100 acres. Only the species found on all transects of any one stratification of aspect and soil were selected for comparison of cover.

2. In forest there were 104 transects in an area of about 5,000 acres. In addition to species already selected for unplanted shrubland in (1) all these species above 60% frequency (class III on Table 4) were selected. Distribution maps were compiled and only those species with a reasonably uniform distribution were used for cover comparisons.

3. In cutover shrubland there were 34 transects in an area of about 100 acres. Any species over 60% frequency (class III on Table 4) not already selected in (1) and (2) were then chosen for comparison.

The mean cover, as plotted in Fig. 3, was calculated by summing the cover in feet for each species and expressing it as a percentage of the total length measured for each soil type and aspect stratification.

DISCUSSION OF RESULTS

Table 4 shows the distribution of the vascular flora in the three types of vegetation, and their respective soil types and aspects. The majority of this flora is indigenous, only *Erica lusitanica, Rubus fruticosus* and of course *Pinus radiata* being physiognomic. The latter species exerts a strong influence on the indigenous vegetation in the change from unplanted shrubland through plantation conditions to cutover shrubland.

Frequencies alone were not considered sufficiently indicative of the reactions of plants to their environments, and all further graphic interpretations are based on percentage cover and height. The frequencies generally follow the trends of cover, but there are certain anomalies which point to the need for further work, both in sampling methods and interpretation, particularly in the case of larger plants such as *Cyathea medullaris*.

Uniformity of age is desirable in attempting to compare the reactions of plants to soils and the micro-climatic effects of varying aspects. In the area of unplanted shrub-

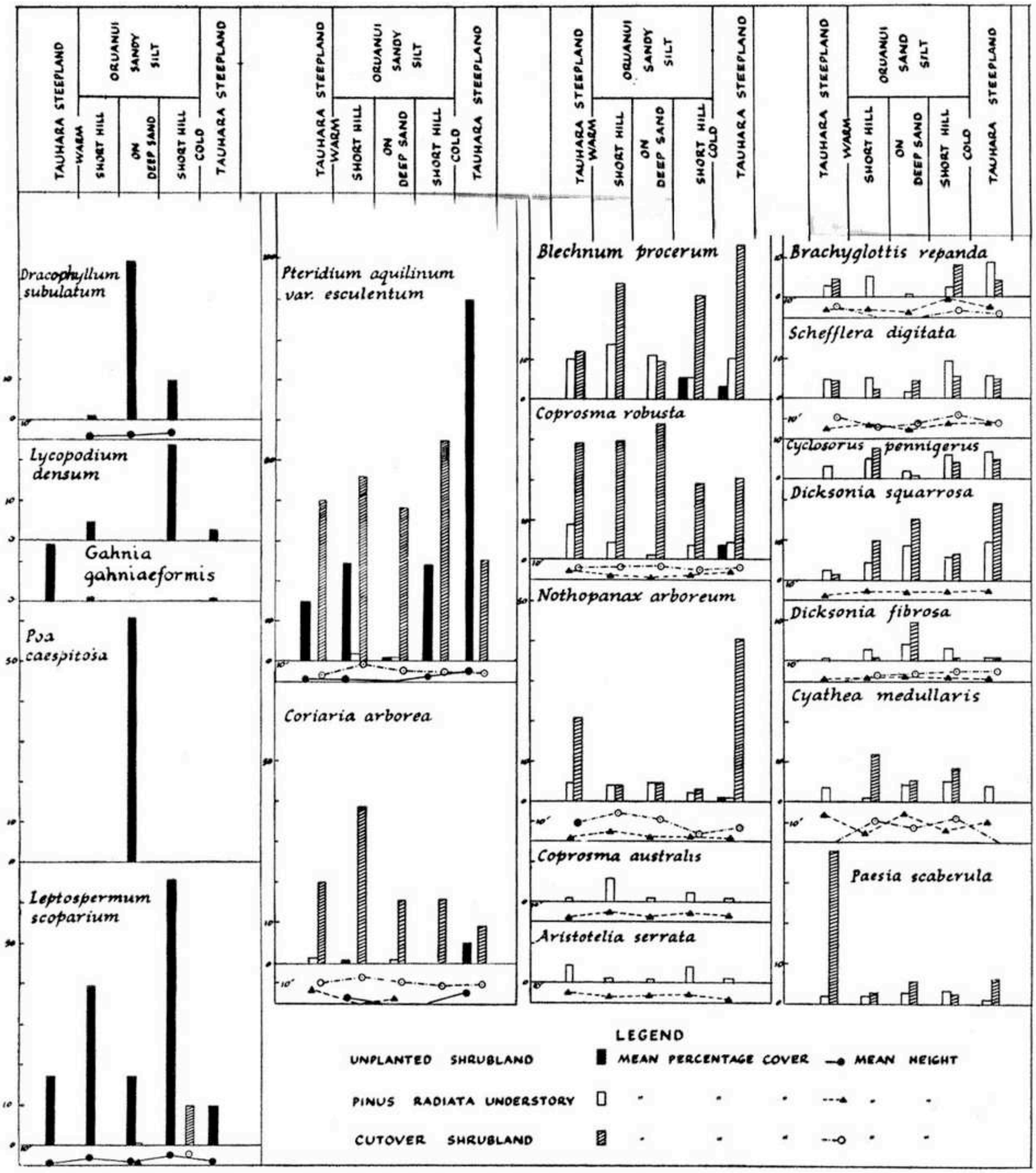

FIGURE 4. *Mean percentage cover of species in unplanted shrub land, forest understorey and cutover shrubland, plotted against soil types and aspects.*

land the communities examined appear to have originated following a fire about 12 to 14 years ago. An aerial photograph, taken in 1948 showed a distinct boundary of taller vegetation around the area. Ring counts of *Leptospermum scoparium*, *Dracophyllum subulatum* and coppice shoots of *Weinmannia racemosa* all showed age ranges up to 14 years. The forest understorey vegetation, according to Henry (1954) started to develop about 20 years after the pines were planted, the ferns generally being pioneers. The stands, examined in 1959, were planted in 1926 so that the vegetation could be 13 years or younger in age. Ring counts of woody species in this vegetation proved impracticable. The shrubland on cutover which did not regenerate can be accurately dated from the Company's logging records, and the areas examined were logged between 1951 and 1953. Their age at 1960 was then 7 to 9 years. They are younger than the other types of vegetation examined but generally show no sign of invasion by characteristic species of unplanted shrubland.

In the forest understorey the geographic distribution of species of high frequency was examined before selecting possible indicators. Table 2 shows the distribution or restriction of these species, together with their type of seed or spore. In no case was a restricted distribution related to soil types or areas of grouped similar soils. The most common pattern is that of a generally southeasterly pointing "lobe" coming from areas of indigenous forest to the north west.

Also in the forest understorey a test was made for relation between basal area of *P. radiata* trees whose canopies overtopped the transect, and total vegetation cover. Basal area was chosen as a simple expression of crown size following a suggestion by P. J. McKelvey (pers. comm.).

Only in cold aspects of the Tauhara steepland soils was there a statistically significant correlation (highly significant at a 5% confidence level, P. J. Dohrn (pers. comm.)). This result was not unexpected as it would be most likely that radiant energy could become a limiting factor for understorey under these conditions. Therefore, in the following interpretation of results it is felt unwise to draw any conclusions from variations in cover of individual species on cold aspects of Tauhara steepland soils until the cover of each species has been tested against the basal area.

The varying cover of species shown in Fig. 3 can be interpreted in two ways. The first set of variations show the changing specific composition, and variations in cover of individual species in the three biotically induced ecosystems of unplanted shrubland, understorey of pine plantations and cutover shrubland. The second set of variations may be seen in the reactions of species to the soils in which they grow in each ecosystem, and to the differing aspects of each soil.

CHANGES IN SPECIFIC COMPOSITION OR PROPORTIONS OF SPECIES WITH BIOTICALLY INITIATED CHANGES

The first group (I in Table 3) are those present only on unplanted shrubland. Physiognomic species of this group are *Draco-*

Table 2. *Distribution of species*

Uniformly distributed		Restricted	
DRY FRUIT OR SPORE	SUCCULENT FRUIT	DRY FRUIT OR SPORE	SUCCULENT FRUIT
Blechnum procerum	*Coprosma australis*	*Acaena sanguisorbae*	*Fuchsia excorticata*
Brachyglottis repanda	*C. robusta*	*Cyathea smithii*	*Melicytus ramiflorus*
Cyathea dealbata	*Nothopanax arboreum*	*Geniostoma ligustrifolium*	*Rubus fruticosus*
C. medullaris	*Schefflera digitata*	*Histiopteris incisa*	
Cyclosorus pennigerus		*Pteridium aquilinum* var. *esculentum*	
Dicksonia fibrosa		*Weinmannia racemosa*	
D. squarrosa			
Paesia scaberula			

phyllum subulatum, *Lycopodium densum* and *Gahnia gahniaeformis* (Fig. 4), in the deep sand soils. *Celmisia gracilenta* and *Leucopogon fraseri* are also present only in unplanted shrubland.

In other parts of New Zealand, apart from the locally endemic *Dracophyllum*, these species are found in vegetation receiving high light intensities and are often characteristic of leached soils (*Lycopodium densum*, *Lepidosperma australe*) or of soils exposed to conditions of high evaporation. (*Celmisia gracilenta*, *Leucopogon fraseri*.) Their absence from the cutover vegetation even in the early stages of succession following felling, and in the 7 to 9 year old stages considered here, suggests that considerable modification of soil conditions has taken place, both in nutrient and moisture conditions.

The second group of species (II in Table 3) are those physiognomic of unplanted shrubland, rare in forest and cutover shrubland. They are *Poa caespitosa* and *Leptospermum scoparium*. In the forest understorey they occur only on the Oruanui sandy silt, undulating phase, a soil which appears to have a lower available moisture supply than the other soils. *Leptospermum* also occurs in small quantities in cutover shrubland, on hill soils where both Taupo Pumice and most of the brown ash have been removed during logging operations and ignimbrite contributes to the profile. It will be seen (Fig. 4) that its height growth is greater on such sites than in unplanted shrubland. *Poa caespitosa* is frequently found on cutover land, especially on soils on deep pumice sand during the first three years following clearfelling, but is later rapidly overtopped by regrowth of mesophytic species from forest understorey vegetation, and was not encountered in older cutover shrubland.

The third group (III in Table 3) are also physiognomic plants of unplanted shrubland, but found only on the least frequently burnt soils with brown ash forming the soil on the cold faces of Tauhara steeplands. These soils appear to have the most favourable moisture regime. Species of this group are *Pteridium aquilinum* var. *esculentum* and *Coriaria arborea*.

Pteridium in forest is not a significant part of the understorey, but in cutover shrubland is often dominant. Particularly noticeable in the extension of its range, as a vigorous tall growing plant from the cold face Tauhara soils on to the Oruanui sandy silts of both hill and undulating phase. On the latter soils it remains dominant at 7 to 9 years but is generally being suppressed by shrubs on hill and steepland soils at the same age. Its height growth is greater on all soils after clearfelling than on the same soils before planting; height growth was used as a site quality indicator both by Ure (1950) at Kaingaroa, and locally by Owen Jones (unpublished).

Coriaria arborea also shows a similar pattern of response to changed conditions, being prominent in cutover shrubland on warm aspects of the steepland and hill soils, and on the soils of undulating country. It is absent or poorly represented on similar sites in unplanted shrubland.

The fourth group (IV in Table 3) are *Coprosma robusta*, *Blechnum procerum*, *Nothopanax arboreum*. All are present in unplanted shrubland at 12 to 14 years of age only on the cold aspects of steepland soils. They are however more widespread at later stages in the undisturbed succession at about 50 years of age on both aspects of hill soils, where *Nothopanax* is co-dominant with *Leptospermum* and *Coprosma robusta* and *Blechnum procerum* prominent in the sub-canopy.

They are amongst the most common species of the pine forest understorey at about 13 years of age. Their appearance on hill soils and soils of undulating country has been accelerated by the planting of *Pinus radiata*, which has acted as a "nurse" at a far earlier age than in the natural *Leptospermum* succession. The range of these species under forest, especially on the soils on deep sand, is modified once again in cutover shrubland. Apparently *Blechnum procerum* and *Nothopanax* are unable to thrive on these soils in the open, and their tenderness to frost, as observed in gardens as well as in the field, may contribute to their reduction in vigour.

The remaining two groups (V-VI in Table 3) of species are not found in unplanted shrubland at 12 to 14 years or even at about 50

TABLE 3. *Occurrence of species in the Tokoroa district on ash showers, compared with their occurrence, when found at Taita on soils derived from greywacke.*

		PRESENT WORK, TOKOROA ASH SHOWER SOILS			DRUCE 1957, TAITA GREYWACKE SOILS	
		UNPLANTED SHRUBLAND	UNDERSTOREY *P. Radiata*	CUTOVER SHRUBLAND	HARD BEECH SUBSERE	BROADLEAVED SUBSERE
I.	*Dracophyllum subulatum*	XX				
	Erica lusitanica	X			XX	
	Gahnia gahniaeformis	XX				
	Lepidosperma australe	XX			X	
II.	*Leptospermum scoparium*	XX			XX	
	Poa caespitosa	XX				
III.	*Pteridium aquilinum* var. *esculentum*	XX	X	XX	XX	XX
	Coriaria arborea	X	X	XX	X	X
IV.	*Blechnum procerum*	X	XX	XX	XX	XX
	Coprosma robusta	X	XX	XX	X	XX
	Nothopanax arboreum	X	XX	XX	XX	XX
	Coprosma australis		X		XX	XX
	Aristotelia serrata		X			X
V.	*Brachyglottis repanda*		XX	X	X	XX
	Cyclosorus pennigerus		XX	X		X
	Schefflera digitata		XX	XX		X
	Dicksonia fibrosa		XX	XX		X
	Dicksonia squarrosa		XX	XX		
	Cyathea medullaris		XX	XX		XX
	Paesia scaberula		XX	XX	X	X

XX — Physiognomic.
X — Less important.

years, although they are present at later stages in succession when a high forest structure is reached.

The fifth group (V in Table 3) consists of *Coprosma australis* and *Aristotelia serrata*. They are found only in the forest understorey and are absent from cutover shrubland. *Aristotelia* is a common member of vegetation on sites from which podocarp forest has been felled around the Tokoroa district, and its absence from *Pinus radiata* sites is a topic worth further study.

Species of the sixth group (VI in Table 3) form a considerable proportion of the forest understorey of *Pinus radiata* and all tolerate the conditions of cutover shrubland. They are *Brachyglotis repanda, Cyathea medullaris, Cyclosorus pennigerus, Dicksonia fibrosa, D. squarrosa, Schefflera digitata.* Of the species grouped above the majority are widespread in the North Island and their tolerances in soils derived from sedimentary rocks at Taita have been described by Druce (1957).

The vegetation at Taita, on well drained soils has been divided into two subseres. The hard beech subsere is characteristic of residual and moderately leached hill soils and the broadleaved subsere is found on more recent less leached colluvial-alluvial soils.

The vegetation of the hard beech subsere is characteristically xerophytic or sub-xerophytic, small leaved, with a small number of species of ferns, apart from filmy ferns, By contrast the vegetation of the broadleaved subsere except for some of the pioneer species, is mesophytic and large leaved. Ferns apart from filmy ferns are numerous in species.

These differences in morphology and life form are paralleled on the ash shower soils of the present study. The vegetation of unplanted shrubland, apart from that of cold steepland faces, is xerophytic, small leaved, and ferns are low in number, similar to that of the hard beech subsere. The vegetation of the forest understorey and of the cutover shrubland is mesophytic, large-leaved and ferns are numerous.

In a floristic comparison of species, the species of groups I and II (Table 3) *Lepidosperma australe, Leptospermum scoparium,* physiognomic of unplanted shrubland only are also physiognomic only of the beech subsere.

Species of groups III and IV found in unplanted shrubland, in forest and cutover shrubland on ash shower soils are also tolerant of both subseres at Taita. The majority of species of groups V and VI found only in understorey vegetation and cutover shrubland are physiognomic or present only in the broadleaved subsere at Taita. They are: *Aristotelia serrata, Cyclosorus pennigerus, Schefflera digitata, Dicksonia squarrosa, Cyathea medullaris.*

The indications of vegetation from these relationships are then that soil conditions of the hard beech subsere on greywacke soils have features in common with the conditions prevailing on ash shower soils, where vegetation has been frequently burnt.

A feature of the hill soils from greywacke, carrying the hard beech subsere, is their sedentary nature, with consequent opportunity for a long period of weathering to fine textures and leaching. The ash shower soils, far younger in origin, are coarser textured and far less weathered. They have an adequate supply of nutrients, and exceptional moisture storage capacity (Packard, 1957). The nutrients are apparently not fully available, and appear to be "locked up" in the almost peaty topsoils of unplanted shrubland (Grimmett, 1954).

The changes in physiognomic species on ash shower soils, associated with one rotation of *Pinus radiata* have been from species associated with soils of low nutrient status at Taita (the hard beech subsere) to those associated with soils of higher nutrient status (the broadleaved subsere).

The possible factors operative in this change are postulated and form a basis for further work.

1. Protection from burning, alone, allows the ingress of mesophytic species into unplanted shrubland. The time sequence of natural undisturbed succession has not yet been established locally but the appearance of *Coprosma robusta, Coriaria arborea, Nothopanax arboreum, Blechum procerum* at 12 to 14 years in the most favourable sites (cold steeplands) and their prominence in

other hill sites at about 50 years gives some idea of the time range involved. Protection from burning alone allows the more mesophytic and frost tender plants to establish under natural communities, but frequent burning keeps the vegetation at a xerophytic and frost tolerant level of life forms.

2. The presence of *Pinus radiata* as a fast growing shelter allows mesophytic species to enter all the soils and aspects considered about 20 years after establishment of the plantation, thus speeding up the natural succession. Among the understorey of pine forest is *Coprosma robusta* which is believed to fix atmospheric nitrogen (Stevenson 1959). The same author (1959) also produces evidence that *Pinus radiata* alone is capable of atmospheric nitrogen fixation. It seems likely that both canopy and understorey plants may play some part in revitalising a soil from which nutrients have been depleted or kept out of cycle by repeated burning.

3. In soils where sandy silt or sandy pumice forms part of the profile bleached patches are frequently found in organically rich horizons under *P. radiata*. This bleaching appears related to the activity of a fungus, which also causes particle aggregation. Will (pers. comm.) has shown that this fungus effectively removes most organic matter from mineral particles. The bleaching activity of this fungus is not static and such bleached areas are subsequently remelanised as the fungal colony moves into other areas where the original pre-forest organic matter has not been altered. A fungus similar in its aggregating capacity has been described by Thornton *et al.* (1956) from non-pumiceous sands under *Pinus radiata*. It is described as aggregating sand particles into larger aggregates, imparting a fluffy appearance to soil. This aggregation and fluffiness have been noted in the present study and it appears that soil structure is also improved under *Pinus radiata* on pumice soils.

VARIATIONS IN SPECIES COMPOSITION AND PROPORTION WITH SOIL AND ASPECT, WITHIN THE THREE ECOSYSTEMS

The previous section has dealt with the variation of species under the three biotically induced ecosystems of unplanted shrubland, pine forest understorey and cutover shrubland. Within each of these ecosystems the vegetation on the same three soil types has been examined and the variations in physiognomic species may be used as indicators of the soil types. These indications generally take the forms of variations in proportions of species rather than in absolute presences and absences. This interpretation is particularly used in forest understorey and cutover communities, it appears that in these communities the differences between soil types have become less pronounced during and following the growth of stands of *Pinus radiata*.

In the unplanted shrubland, 12 to 14 years of age the indicator species are clearly defined by presence or absence or by gross differences in cover (Figure 4).

The cold aspects of the Tauhara steepland soils are characterised by the dominance of *Pteridium* accompanied by the mesophytic shrubs *Coprosma robusta, Nothopanax arboreum*, and *Coriaria arborea*. This soil type on its cold aspects appears to have been the least burnt, and has a deep loose organic horizon.

In contrast the warm steepland faces have suffered from repeated fires and some truncation to unmelanised brown ash has occurred; the characteristic species *Gahnia gahniaeformis*.

The hill soil vegetation is dominated by *Leptospermum scoparium* and the cold aspects are characterised by *Lycopodium densum*.

The vegetation of warm aspects of hill soils is characterised only by the lower height of *Leptospermum*, and by a small quantity of *Dracophyllum subulatum*.

The Oruanui sandy silt, undulating phase, is the only soil on which *Poa caespitosa* was found together with a considerable cover of *Dracophyllum subulatum*.

In this sequence of indicator species there appears to be the expression of a soil moisture gradient from the soils with the most favourable moisture regime to those with the least favourable. The soil with the most favourable moisture regime is the Tauhara steepland of cold faces; with lowest evaporation, by virtue of aspect, and the nearness of brown ash with a higher clay content, this soil supports vegetation of the most mesophytic character, tall *Pteridium, Nothopanax, Coprosma robusta* and *Coriaria arborea.*

The warm aspect of the Tauhara steepland soils together with both aspects of the Oruanui hill soils may have approximately similar moisture regimes. Some differentiation may be possible however in subsidiary species and the presence of *Dracophyllum subulatum* on the warm aspect of the Oruanui hill soils may be a response to lower levels of available moisture.

The Oruanui sandy silt, undulating phase, with dominance of *Poa caespitosa* and *Dracophyllum subulatum* would appear to be the soil with least favourable moisture conditions.

Under *Pinus radiata* forest are several species which also occur in unplanted shrubland. Of these two are restricted to the Oruanui sandy silt, undulating phase, *Poa caespitosa* and *Leptospermum scoparium,* and their occurrence would suggest that the physical properties of the soil still have an influence under forest. This supposition is supported by the diminished cover on such soils under forest of another shrubland species, *Coprosma robusta.*

As there is a positive correlation between canopy basal area and vegetative cover on the cold aspects of Tauhara steepland soils no indicator conclusion can safely be drawn for these soils.

On the other soils the following species may be used as indicators:

Aristotelia serrata is characteristic of cold aspects of the Oruanui hill soils and warm aspects of steepland soils. *Schefflera digitata, Brachyglottis repanda, Coprosma robusta* and *Nothopanax arboreum* are physiognomic on all slope soils, and *Coprosma australis* on hill soils only.

Of the above species only *Nothopanax arboreum* and *Coprosma robusta* are found in any quantity on the Oruanui sandy silts, undulating phase, and the cover of *Coprosma robusta* is diminished compared with soils which have brown ash nearer the surface. The soils of the undulating phase have *Dicksonia squarrosa* and *D. fibrosa* in quantity.

Here again there appears the expression of a moisture gradient, from the soils with brown ash near the surface to those on deep sand, although the expression is not as clearly shown as in unplanted shrubland.

On cutover shrubland the pattern of forest survivors and colonisers of disturbed soil present a pattern from which it is difficult to establish indicators for soil types.

A clear cut grouping of mesophytic species is found on the cold aspects of steepland soils: *Dicksonia squarrosa, Paesia scaberula* are found in quantity only on these soils, together with *Nothopanax arboreum,* found also on warm aspects of steepland soils. *Coprosma robusta* and *Pteridium* are found on all soils, with less cover on cold steeplands. The only species showing a distinct preference for soils of the undulating phase is *Dicksonia fibrosa.* Characteristic of these soils is also the absence or low cover of *Nothopanax aroreum.*

It appears then that the changes resulting from planting and clearfelling of *Pinus radiata* have tended to diminish the differences in soils as shown by the reactions of plants to soil conditions, and that at 7 to 9 years age of regrowth of vegetation, the only clearly defined vegetation corresponding to a soil type is on the cold steepland soils.

GENERAL CONCLUSIONS

The use of plants as indicators of the soil types studied is most positive in unplanted shrubland, is still practicable in first rotation *Pinus radiata* stands, but is doubtful for differentiation of most soil types in cutover shrubland at 7 to 9 years of age.

The soil changes under *Pinus radiata* postulated above may reasonably be associated with the lack of differentiation of species on cutover shrubland. At the age studied it is likely that two effects from logging are still operative in the soil. The first of these is the "cultivation", particularly on gentler slopes resulting from the logging operations and includes the scraping of topsoil by moving logs and compaction by heavy

TABLE 4. Species list with frequency classes on three ecosystems and warm and cold aspects of three soil types. Figures represent percentage of transects on which species were recorded: I = 0–20; II = 20–40; III = 40–60; IV = 60–80; V = 80–100.

SOIL TYPES	UNPLANTED SHRUBLAND					PINUS RADIATA FOREST					CUTOVER SHRUBLAND				
Slope	> 30° Tauhara		5° — 30° Oruanui		0° — 5° Sandy Silt	> 30° Tauhara		5° — 30° Oruanui		0° — 5° Sandy Silt	> 30° Tauhara		5° — 30° Oruanui		0° — 5° Sandy Silt
Aspect: W = Warm (NE-N-W) C = Cold (E-S-SW)	steepland W	C	short hill W	C	Undulate phase	steepland W	C	short hill W	C	Undulate phase	steepland W	C	short hill W	C	Undulate phase
Acaena sanguisorbae						I	II	II		III					
Aristotelia serrata						III	III	V	V	III	II				
Arundo conspicua				II				I	I						
Asplenium bulbiferum						I				I					II
A. falcatum		II				II		I	I	III					
A. flaccidum						III	II	III	IV	IV					I
A. lucidum						I			I	I					I
Blechnum fluviatile						I		I		I		I			I
B. lanceolatum						I	I	I				I			I
B. procerum		III		III		IV	IV	V	V	V	V	V	V	IV	V
Brachyglottis repanda						III	IV	IV	III	III	II	I		III	
Carmichaelia flagelliformis		V													I
Carpodetus serratus							I	I	I						
Celmisia gracilenta	V		II	II	III										
Chiloglottis cornuta							I	III		III					
Cirsium vulgare*				II		I			I	I		I			
Clematis indivisa												II			I
Coprosma australis						I	II	II	II	II					
C. lucida	III	V	II			II	I	I	III	I					
C. parviflora									I	I					
C. propinqua	III	II	V	II											
C. robusta		V				IV	V	IV	V	III	V	V	V	V	V
C. robusta x C. propinqua															I
Cordyline australis		II						II							
C. banksii						I	I		I						
Coriaria arborea		III	II	II		I	I			I	IV	III	V	V	III
Crepis capillaris*								I	I						
Cyathea dealbata						III	III	III	II	III	II	I		I	II
C. medullaris						II	III	I	III	II			IV	II	III
C. smithii						I	I	I		II			I	I	II
Cyathodes acerosa	V	V	V	V	II		I	I		I		I			
Cyclosorus pennigerus						III	IV	III	II	II		II	III	III	III
Danthonia gracilis				IV		I	I	I	I	I					
Deyeuxia avenoides var. brachyantha				II		I	I		I	II		I			
Dicksonia fibrosa						II	II	III	IV	III		I	I	I	II
D. squarrosa						III	IV	IV	IV	V	III	V	IV	IV	IV
Dianella intermedia	II						I	I		I					
Dracophyllum subulatum			IV	V	V										
Eleocarpus dentatus						I									
Epilobium erectum						I		I		I					
Erica lusitanica*	V	III	V		IV									III	
Erigeron canadense*						I	I	I	I	I					II
Fuchsia excorticata						II	III	II	II	II		II	IV	IV	IV
Gahnia gahniaeformis	V	III	II												
Gaultheria antipoda	V	V	V	IV		I	III	I	II	I	II	II	I	I	I
G. oppositifolia	IV	V	II												
G. paniculata	IV	III	IV	V										I	
Geniostoma ligustrifolium		III				III	III	II	III	II			II	II	
Geranium microphyllum										I					
Gleichenia circinata				II											
Gnaphalium purpureum							II			I	II	I			
Hebe salicifolia		II		V	II			I					I	I	II
Histiopteris incisa								III	II	III					II
Holcus lanatus*								I	I	I		II		I	II
Hypochaeris radicata*				II	IV	I			I	I					
Hypolepis rugulosa						I	I	II		I					
Lagenophora pumila				III											
Lepidosperma australe			V	IV	V									I	
Leptospermum ericoides														I	
L. scoparium	V	V	V	V	V					I					
Leucopogon fasciculatus	III	V		III		I		I	I	I					
L. fraseri	II				III										
Lotus corniculatus*															II
Lycopodium densum		III	IV	V											
L. fastigiatum			II	IV											
L. volubile				II											
Melicytus lanceolatus						I		I							
M. ramiflorus						III	III	III	III	I			I		II
Microsorium diversifolium						I		I		I		I			II
Mycelis muralis*						IV	III	V	V	V	II				
Nertera depressa						I		I	I	II					I
N. dichondraefolia								I							
Nothopanax arboreum		IV		II		V	IV	V	III	IV	V	V	II	II	III
Olearia furfuracea	II	III				I									
Paesia scaberula						III	II	III	III	III	V	V	III	II	III
Pimelea prostrata	IV		II	II	IV										
Pinus radiata*						I		I	I		III	I	II		III
Pittosporum tenuifolium subsp.—tenuifolium						II	I	II	II	II	IV	V		I	II
Poa caespitosa					V					I					
Polystichum sylvaticum							I	I	I						
P. vestitum						I		II	II	III					I
Pommaderris phylicaefolia	V		V	II		I	II	II		I	III		I		
Pteridium aquilinum var. esculentum	V	V	V	V	II	III	III	III	I	II	V	V	V	V	V
Pteris macilenta						I									
Ranunculus hirtus		II				I		I	I			I	I		I
Rhipogonum scandens						I		I							
Rubus cissoides								I		I					
R. fruticosus								I	I	I			II	II	III
Schefflera digitata						III	III	IV	III	II	II	III	III	III	II
Senecio jacobea*						I	II	I	I	I					
S. kirkii							I			I					
Uncinia uncinata						I	I			I					
Weinmannia racemosa	III	V				II	II	I	I	I	II				
Number of transects	5	5	5	5	4	17	9	14	12	32	4	7	6	7	10

machinery. Compaction (Packard 1957) improves the moisture status of pumice soils.

The second factor is the sudden influx to the soil nutrient cycle of large quantities of needles, twigs and dead rootlets from felled trees. The surface influx of needles and twigs is likely not only to add to the soil nutrient cycling but also to "mulch" the soil and improve its moisture holding capacity.

Future work on the three types of vegetation described in this paper is likely to be on the following lines:—

1. The determination of the "natural" succession in undisturbed shrubland.

2. The detailed study of soils in the three ecosystems, aimed at the determination of nutrient and physical variations caused by biotically induced changes.

3. The relationship between vegetation and growth characters of *Pinus radiata* in first and second rotation sands.

ACKNOWLEDGEMENTS

The writer wishes to express his appreciation to the Managing Director N.Z. Forest Products Ltd., for permission to publish this paper. The following have contributed materially with assistance in their various fields—Messrs. A. P. Druce, Botany Division, D.S.I.R., C. G. Vucetich, Soil Bureau, D.S.I.R., J. E. Henry, B. Bay, J. W. Ansell of N.Z. Forest Products Ltd.

Assistance in field and office was also given by members of the forest mensuration field party of N.Z. Forest Products Ltd.

SUMMARY

Studies have been made of vegetation on soils formed from Taupo pumice (silty sand to sand), the older brown ash (silt loam or sand loam) and the ignimbrite beneath. The vegetation is all biotically induced and from 7 to 14 years old and consists of: (1) fire-induced seral shrubland. (2) Understorey of planted *Pinus radiata* forest. (3) The shrubland resulting from clearfelling, where *P. radiata* has locally failed to regenerate. Changes between these types of vegetation are from xerophytic, mor-forming plants of unplanted shrubland to the mesophytic, mull-formers of forest and cutover shrubland. Variations in species composition with soil types are clearly defined in unplanted shrubland, less so in forest and least in cutover shrubland, and appear related to the soil changes initiated by the planting of *P. radiata*.

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