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THE SPREAD OF HEATHER, *CALLUNA VULGARIS* (L.) HULL, INTO INDIGENOUS PLANT COMMUNITIES OF TONGARIRO NATIONAL PARK

Summary: The vegetation of 10 quadrats from each of 26 sites, in and around the Tongariro National Park, which contained the introduced dwarf shrub, *Calluna vulgaris* (L.) Hull, was analysed using Reciprocal Averaging and Indicator Species Analysis. Six major plant communities were recognised and related to previous mapping units: tussockland with shrubs and herbs (red tussock tussockland); heathland with tussock and *Dracophyllum subulatum* (monoao-red tussock tussock-shrubland); communities of herb field and scoria slopes ([mountain inaka] gravelfield); Calluna-dominated tussock or heathland (heather-red tussock tussock shrubland and heathland shrubland); *Gleichenia*/*Empodisma* bog (red tussock/wire rush-gleichenia rushland); and weed/scrub communities of disturbed ground (unmapped). An ordination of the sites showed that the major directions of variation in the vegetation were associated with altitude and soil moisture. *Calluna* had increased in extent since the area was mapped in 1960, and has been observed to have increased further since this survey was completed in 1984. *Calluna* has a potential to spread in all the recognised communities, although increases have been greatest in tussock grassland and on disturbed ground at lower altitudes and least in boggy areas. *Calluna* thus remains a threat to the natural vegetation of the Park, although some areas may be equally liable to succeed to taller vegetation. It is suggested that future research should be directed towards the effective control of heather within the Park.

Keywords: Heather; *Calluna vulgaris;* plant communities; invasion; Tongariro National Park; indigenous vegetation; introduced species; New Zealand.

Introduction

Tongariro National Park lies in the centre of the North Island of New Zealand and is dominated by three volcanoes, Mts Ruapehu (2797 m), Ngauruhoe (2291 m) and Tongariro (1968 m). The mountains form a barrier stretching from north-east to south-west which intercepts the westerly flow of air resulting in high rainfall (1800-3000 mm) in the north and west of the Park and lower rainfall (1100 mm) in the south and east (Atkinson, 1981). The land forms result mostly from volcanic activity and the studied area is largely confined to the lower slopes of the volcanoes which are gently sloping and consist of ash-covered lava-flows and mudflows. Soils are mostly formed from weathered volcanic ash and, at lower altitudes «1100 m), are dark sandy loams and loamy sands which often have impeded drainage. At higher altitudes (1100-1300 m) soils become increasingly patchy with erosion exposing old surfaces, while above 1300 m there is little soil formation and the substrate is dominated by gravel and stones (Atkinson, 1981).

Mean annual temperatures are around l0ºC at 650 m and 7.0°C at 1100 m, and this lapse rate suggests a mean annual temperature of about 4 °C at 1600 m. This temperature range encompasses the altitudinal range of this study and is similar to that found for European heathlands (Gimingham *et al.,* 1979). Heather, *Calluna vulgaris* (L.) Hull, (Ericaceae, sub family Ericoideae (Stevens, 1970)) is characteristic of European heathlands, where its ability to adapt to a wide range of environmental conditions is explained by both plastic (e.g. Grant and Hunter, 1966) and ecotypic (e.g. Bannister, 1978) responses to different environmental conditions.

Heather was first introduced to Tongariro National Park in 1912 with the idea of turning its extensive, rolling tussock grasslands into heather moorland suitable for grouse *(Lagopus lagopus scoticus)* to produce a North Island 'Sportsman's Paradise'. Details of its introduction are described by Bagnall (1982). Since its introduction to north-western sector of the Park, *Calluna* has spread to such an extent that it now ubiquitous within this sector (Fig. 1).

Although the potential for the spread of *Calluna* after fire had been recognised (Atkinson, 1975, 1976), it was not until 1980 that *Calluna* was widely accepted as being a threat to the existence of some of the indigenous plant communities

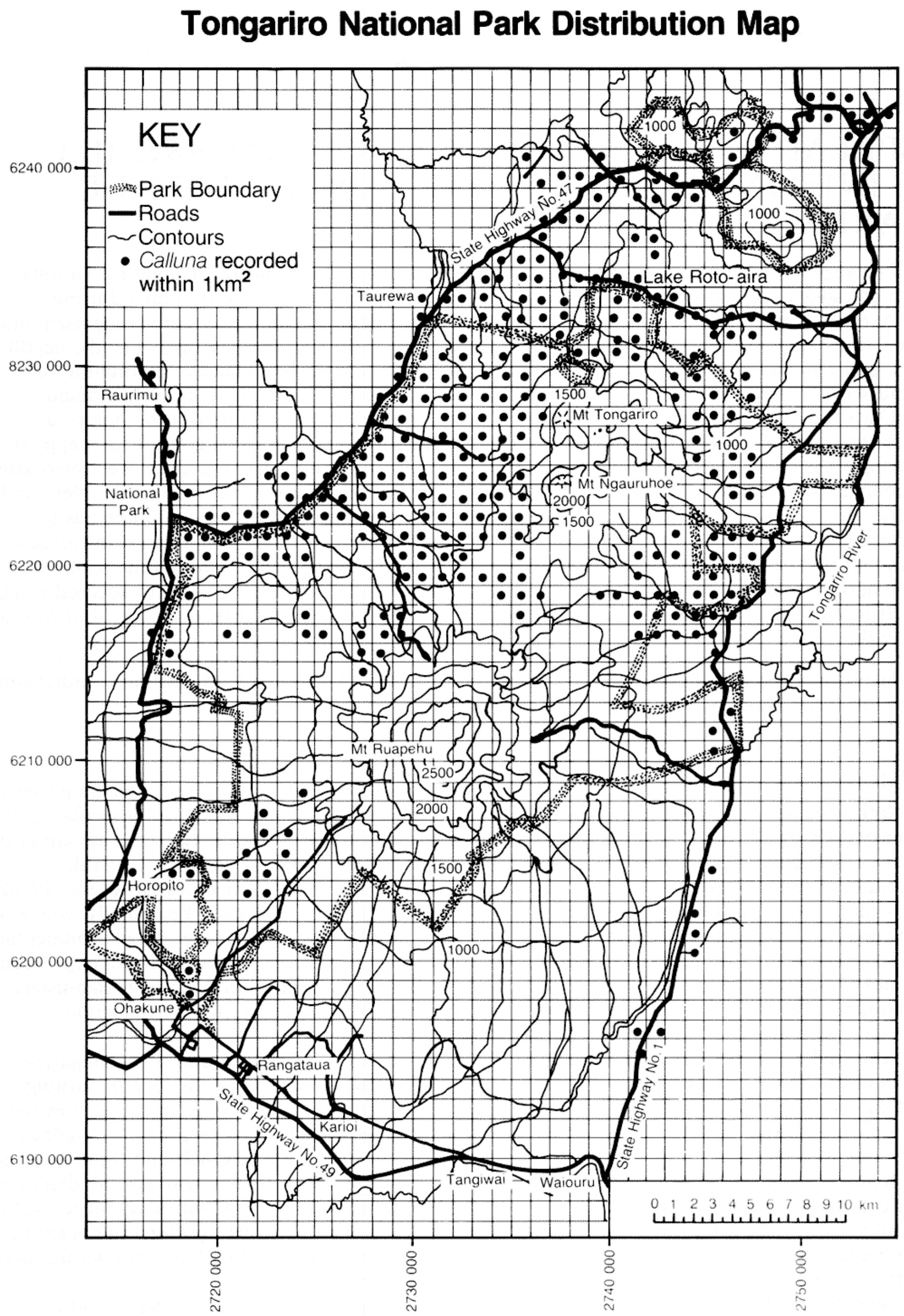

Figure 1: *The presence of Calluna vulgaris within 1 km² subdivisions of a map of the Tongariro National Park and environs. Data for* 1984.

within Tongariro National Park, particularly the red tussock *(Chionochloa rubra)* grasslands (Jefferies, 1988).

This paper addresses the consequences of the introduction of an exotic heathland shrub, *Calluna vulgaris* (L.) Hull, into the indigenous tussock grassland and heathland vegetation of Tongariro National Park. Its four main aims are to:

1. Classify the plant communities in which *Calluna* occurs.
2. Outline some of the environmental factors affecting the species composition of these communities.
3. Describe the species composition and physical environment of these communities.
4. Comment on the role of *Calluna* within, and its influence on, these communities.

Materials and methods

A series of 26 sites, containing *Calluna,* within Tongariro National Park and its environs were chosen to represent the range of environments and plant communities in which *Calluna* occurs. Site locations are indicated in Fig. 2.

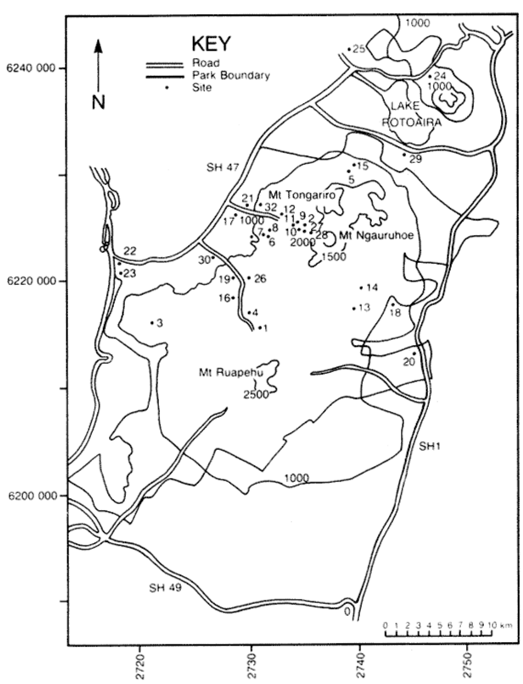

Figure 2: *Location of sites used in the study. Only sites 1-25 on this map (and site 31 - not shown) were used for vegetation analysis. Site 31 is off the map on State Highway 4 to the north of site 22.*

Site characteristics (Table 1)

The environmental variables considered in this paper include altitude (estimated from the 1:80,000 map of Tongariro National Park) and midsummer soil temperatures at 40 cm depth. An auger was used to bore two holes to a depth of 40 cm in each site; temperatures were measured with a soil thermometer in each hole. A soil pit was dug at each site to determine the soil depth and examine the soil profile.

Soil samples were collected over as short a period as possible on similar days so as to minimise the effects of season and day-to-day fluctuations in weather. Ten soil samples were collected from each site, they were taken from below the humus layer to a depth of 15 cm and stored in a deep-freeze until they were analysed. Soil organic matter, pH and soil moisture were determined as described by Allen *et al.* (1974). "Exchangeable" amounts of Ca, K, Na, Mg were extracted by neutral 1 M ammonium acetate and measured by atomic absorption flame photometry, whereas phosphorus was determined by the method of Olsen *et al.* (1954). The amounts of soil nutrients (Table 1) were determined as "MAF quick-test units" (Mountier *et al.,* 1966) and may be converted into _g/g dry soil by the following conversion factors: Ca, x125; K, x20; Mg,Na, x5; P, x1.1.

It should be noted that many of the environmental parameters in Table 1 are inter-correlated. In particular, altitude is inversely related to soil temperature, soil moisture is positively correlated with soil organic matter and soil depth and inversely related to pH, whereas the various soil cations (Ca, K, Mg, Na) are positively correlated with one another.

Floristic data

The presence of vascular plants, bryophytes and lichens was recorded within ten randomly-placed quadrats within each site. Quadrat size was determined by species-area curves and ranged from 1 m2 on species-poor sites to 4 m2 on species-rich sites. Species nomenclature follows Allan (1961) and Moore and Edgar (1970) for native vascular plants. Healy and Edgar (1980) and Webb *et al.* (1988) for introduced vascular plants and revised names follow Connor and Edgar (1987). The nomenclature of other species follows Allison and Child (1971, 1975) for mosses and liverworts and Galloway (1985) for lichens. Introduced species other than *Calluna vulgaris* are prefixed by an asterisk, e.g. **Hypochoeris radicata.*

Analysis of floristic data

Data were classified by Indicator Species Analysis (ISA; Hill *et al.,* 1975), and Reciprocal Averaging

Table 1: *Environmental variables measured in sites used for sampling vegetation in and around Tongariro National Park (sites arranged in altitudinal sequence).*

Site	Altitude (m)	40 cm Soil Temperature (°C)	Soil Moisture (% d.w.)	% Soil Organic Matter	Soil pH	Soil Ca (MAF quick test units - see text)	Soil K	Soil P	Soil Mg	Soil Na	Soil Depth (cm)
25	600	20	24.9	4.7	4.7	1	2	2	4	4	9
24	725	16	9.0	3.9	6.0	<1	2	2	4	4	13
22	800	16	43.3	9.7	4.8	<1	1	1	2	3	30
31	850	19	9.2	4.2	5.9	1	2	2	4	4	12
23	800	13	45.0	13.0	4.3	<1	2	1	3	2	50
21	950	12	43.3	27.2	4.3	<1	1	3	3	2	48
19	950	10.5	57.1	32.0	4.6	2	3	2	9	6	57
20	950	15	44.2	12.5	4.9	<1	2	3	3	3	80
18	1060	13	41.8	13.5	4.8	<1	2	3	3	2	55
17	1080	12	36.7	11.7	4.3	<1	2	3	4	3	120
15	1125	15	40.9	12.4	4.8	<1	1	2	2	3	60
13	1125	12.5	22.0	3.0	5.7	<1	<1	2	2	2	30
14	1125	13	28.0	6.9	4.8	<1	1	2	2	2	60
16	1125	11	38.0	12.2	5.5	<1	2	2	4	4	13
10	1150	14	21.4	4.6	4.6	<1	1	3	1	2	10
12	1150	12	31.5	7.5	4.7	<1	1	1	3	3	50
9	1160	14	19.4	3.0	5.1	<1	<1	2	2	3	30
11	1160	12	32.0	7.3	4.7	<1	1	3	3	3	50
8	1170	12.5	32.9	17.4	4.9	<1	2	3	3	2	48
7	1200	10	40.5	15.4	4.9	1	2	2	5	3	85
5	1210	14	38.8	11.8	4.8	<1	2	2	4	3	60
6	1210	13	8.8	28.9	4.7	<1	1	1	2	2	30
4	1250	12.5	29.3	9.1	4.9	<1	1	1	2	3	70
2	1350	12	18.5	2.8	5.5	<1	<1	2	2	3	28
3	1519	12	35.0	8.2	5.4	<1	1	3	3	3	52
1	1575	11	11.0	1.4	5.1	1	<1	2	2	2	40

(RA) (Hill, 1973) was chosen as a method of ordination because the two techniques are complementary.

Analysis of the relationship between environmental variables and floristic data

The influence of environmental factors on the floristic composition of sites was determined by a regression of the mean component scores for each site (from the RA ordination) against their appropriate variables. The site ordination score was used in preference to the quadrat ordination score because environmental variables were measured for each site, rather than for individual quadrats.

The principal investigations recorded here were completed in 1984; the sites were revisited by one of us (H.M.C.) in 1989, and observations on the spread of *Calluna* since 1984 are included in this paper.

Results and discussion

Classification of floristic data into quadrat groups

The classification of plant communities in which *Calluna* occurs was produced by setting the divisive level of the ISA so that the analysis terminated when eight final groups had been formed. On inspection of the groups it seems justifiable to amalgamate those groups which, from field experience, were ecologically very similar (Fig. 3). Groups 3 and 4 and Groups 7 and 8 were amalgamated, resulting in six interpreted quadrat groups (IQG's) (Horrill *et al.*, 1974). These were given the provisional names; 'tussock land with shrubs and herbs'; 'heathland with tussock and *Dracophyllum subulatum*'; 'herb field and scoria slopes'; '*Calluna* dominated tussock or heathland'; 'tussock and *Gleichenia* bog'; 'weed/scrub communities of disturbed ground'. All of these groups, except the last, can be correlated with the mapping units of Atkinson (1981). For ease of reference, Atkinson's names are given alongside the provisional names in the description of the IQG's. In the remainder of this paper the IQG's are called "plant communities", unless otherwise specified.

Some environmental factors affecting the species composition of the designated plant communities

The position of the sites in relation to the first two axes of the RA ordination is illustrated in Fig. 4 and that of the IQG's in Fig. 5.

Axis 1 of the ordination is associated with altitude ($r = -0.75$, $P<0.001$), soil temperature ($r = +0.52$, $P<0.01$) and available soil calcium ($r = +0.42$, $P<0.05$), sodium ($r = +0.48$, $P<0.05$) and potassium ($r = +0.50$, $P<0.01$). It describes a

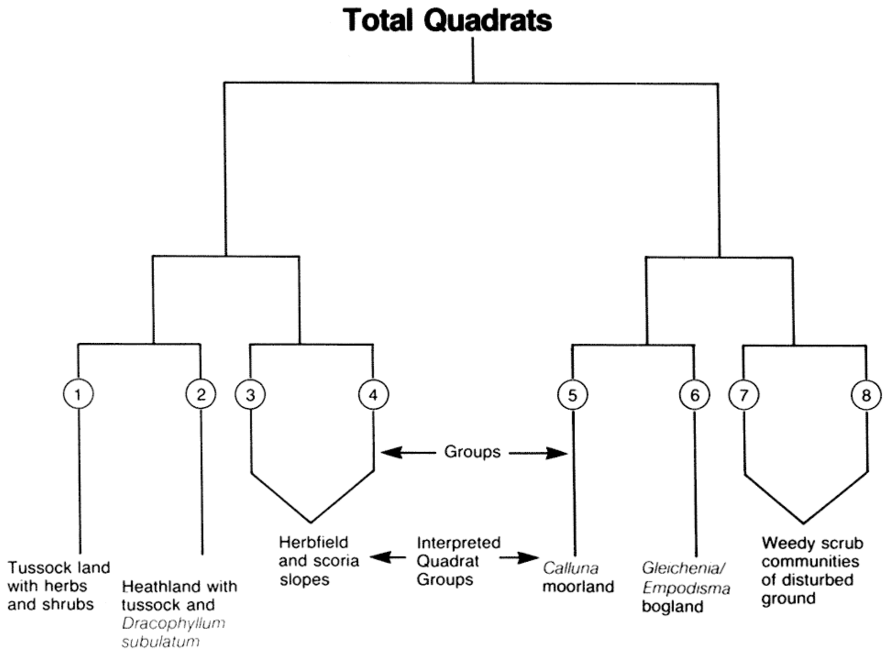

Figure 3: *The dendogram for the indicator species analysis showing the interpreted quadrat groups. Indicator species for each group are listed below.*

- *Tussockland with shrubs and herbs* (*35% of quadrats):* Anisotome aromatica, Calluna vulgaris, Poa colensoi, Rytidosperma setifolium.
- *Heathland with tussock and* Dracophyllum subulatum (*5% of quadrats):* Dracophyllum subulatum, Uncinia *sp.,* Brachythecium rutabulum, Oreobolus pectinatus, Gleichenia dicarpa, Empodisma minus.
- *Herbfield and scoria slopes* (*20% of quadrats):* Dracophyllum recurvum, Coprosma perpusilla, Celmisia gracilienta, Gaultheria colensoi, Rytidosperma setifolium, Andraea rupestris, Racomitrium lanuginosum.
- *Calluna moorland* (*10% of quadrats):* .Hieracium pilosella, Racomitrium lanuginosum.
- Gleichenia/Empodisma *bogland* (*5% of quadrats):* Gleichenia dicarpa, Dracophyllum filifolium, Empodisma minus, Griselinia littoralis, Astelia nervosa.
- W*eedy scrub communities of disturbed ground* (*20% of quadrats):* .Lotus pedunculatus, .Rumex acetosella, .Agrostis capillaris, .Hypochoeris radicata, .Cytisus scoparius, .Calluna vulgaris, Gonocarpus micranthus, Dicranoloma billiardieri, Brachythecium rutabulum, Hypnum cupressiforme.

vegetation gradient from low altitude roadside sites (e.g. 24 - Saddle Road and 25 - Te Whaiau Canal) through mid-altitude tussock grassland or moorland (e.g. 17 - Mangatepopo and 18 Ö Waihohonu) to high altitude scoria slopes (e.g. 13 - Rangipo Desert).

Axis 2 of the ordination is associated with soil moisture (r= -0.68, P<0.001), soil organic matter (r = - 0.52, P<0.01), soil depth (r = - 0.44, P<0.05), available magnesium (r = - 0.59, P<0.01) and potassium (r = - 0.43, P<0.05). Axis 2 describes a gradient from dry areas with shallow soils low in organic matter (e.g. 24 - Saddle Road and 10 - *Racomitrium* heathland) through tussock grassland or moorland (e.g. 17 - Mangetopopo and 18 - Waihohonu) to semi-waterlogged areas with deep organic soils (e.g. the *Gleichen;a - Empodisma* bog - site 19).

The increase in available soil nutrients at lower altitudes (Axis 1) may reflect the influence of fertilisers applied to adjacent agricultural and afforested areas, or the higher nutrient status of drier, less leached soils at lower altitudes. The increased potassium and magnesium in deeper, wetter, organic soils (Axis 2) is probably only a result of the low bulk density of organic soils - as the quick tests assume a uniform bulk density.

Species composition and environment of the plant communities

Tussock land with shrubs and herbs: (Red tussock tussockland or red-tussock land (Atkinson, 1981)).

About one-third of all quadrats, from a wide range of sites, are included in this IQG, most of which occur towards the centre of the RA ordination (e.g.

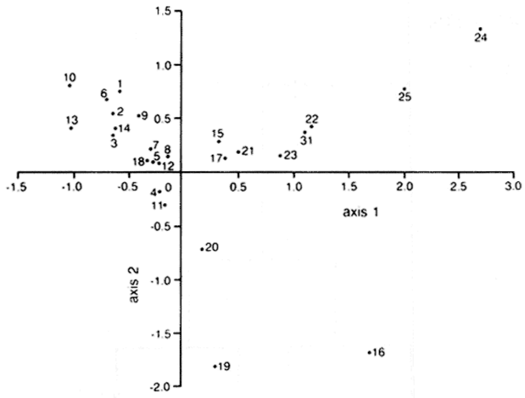

Figure 4: *Position of the sites on the normal reciprocal averaging ordination.*

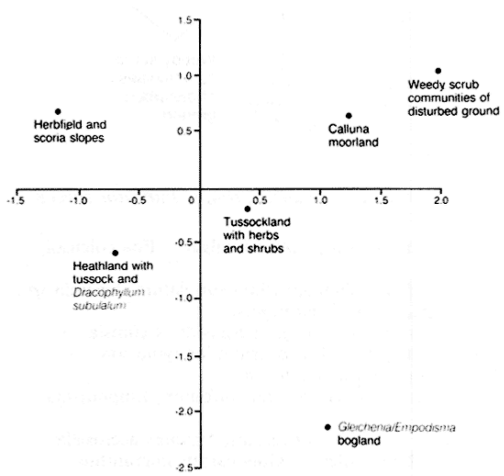

Figure 5: *Position of the interpreted quadrat groups on the normal reciprocal averaging ordination.*

8 - the north-eastern slopes of Pukeonake, 11 - tussock grassland near Mangetopopo Hut and 12 - tussock grassland and scrub near to the Mangatepopo Car Park). They are mid-altitude sites intermediate with respect to other sites in terms of soil depth, soil moisture and soil organic matter (Chapman, 1984). It is also the most diverse IQG in both sites and species composition, which partly explains its position towards the centre of the ordination diagram (Hill *et al.,* 1975). The plant community it describes is common in the northern and north-western sectors of Tongariro National Park but it also occurs in the north-eastern sector, where the presence of *Calluna* in the community is somewhat reduced. A mixture of red tussock (77.5% frequency) and *Calluna* (71 %) forms the dominant vegetation. There is an abundance of inter-tussock species such as the dwarf shrubs *Epacris alpina, Pentachondra pumila, Leucopogon fraser;* and *Pernettya macrostigma. Celmisia spectabilis* is the most abundant herb, while *Wah/enbergia pygmaea, Euphrasia cuneata* and *Anisotome aromatica* are common, as is the moss *Racomitrium lanuginosum.* The only exotic herb which occurs with a frequency as high as 50% is * *Hypochoeris radicata,* although **Lotus pedunculatus,* **Trifolium repens,* **Linum catharticum* and the grass **Holcus lanatus* are present.

The decline in red tussock between 1960 and 1984 is primarily due to an increase in *Calluna* (I.A.E. Atkinson, pers. comm.). The environmental factors associated with this community are ideal for *Calluna;* moist, infertile soils of low pH at altitudes of between 600-1200 m (Table 1; Chapman, 1984). *Calluna* increases in density at the expense of the tussock as the inter-tussock spaces provide an ideal site for the establishment of *Calluna* seedlings, which eventually shade out the tussock. Once established, *Calluna* spreads by both seed and vegetative regeneration. Inter-tussock species most threatened by *Calluna* are dwarf shrubs such as *Coprosma cheesemanii,* C. *perpusilla, Dracophyllum recurvum* and herbs such as *Celmisia spectabilis* and *Helichrysum bellidioides* (Chapman, 1984). However, the same species are vulnerable to competition from native shrubs such as *Leptospermum scoparium, Olearia nummulariifolia* or *Dracophyllum* spp., and there is evidence for the subsequent increase of these species within 'tussuck lands with herbs and shrubs' since 1984.

Such changes are not necessarily irrevocable; there is evidence for vegetation cycles between tussock grassland and scrub occurring on the Volcanic Plateau for thousands of years, initiated by volcanic eruptions, lightning and man-induced fires (Atkinson, 1976). Fires are essential for the maintenance of tussock grassland, without them there is a reversion to forest - either native forest with mountain toatoa and ultimately beech or colonisation by exotic trees such as lodgepole pine (Atkinson, 1981).

The Park Board prohibits fires and, as increasingly sophisticated fire-fighting techniques decrease the risk of fire, red tussock grassland would appear to be under threat of invasion by shrubs and trees even in the absence of *Calluna.*

If 'tussockland with shrubs and herbs' is to remain a feature of Tongariro National Park it will be necessary to manage an area of land for this purpose with a burning regime designed to allow for the maximum amount of both faunal and floral diversity. Any such management plan would be unavoidably complicated by the presence of C*alluna*. *Calluna* is able to re-establish after fires (Whittaker and Gimingham, 1962; Mohamed and Gimingham, 1970) more rapidly than C. *rubra,* which also responds to fife but has a slower growth rate than *Calluna* (Mark, 1969). *Calluna* is able to respond to fire by both germination of seed and by vegetative spread, while C. *rubra* shows an increased tiller growth and floral initiation.

There are no areas of red tussock grassland within the Park from which the absence of *Calluna* can be guaranteed; the scattered distribution of *Calluna* throughout extensive tracts of tussock grassland such as the eastern slopes of Mounts Tongariro and Ngauruhoe make a complete account of its distribution virtually impossible - as mature individuals may occur hundreds of metres apart they are easily missed. Once seed is shed, it can remain viable in the soil for at least eleven years (Gimingham, 1972) and seedlings have germinated from soils that had been under coniferous plantation for up to 45 years (Hill and Stevens, 1981). Seedlings are also difficult to locate as they often occur in sheltered situations such as tussock bases or small depressions.

Healthland with tussock and *Dracophyllum subulatum* (Monoao-red tussock tussock-shrubland (Atkinson, 1981))

This IQG represents about 50/0 of the quadrats and is found only in sites 18 - Waihohonu tussock grassland and 20 - Tussock grassland beside the Desert Road; each of which are in the eastern sector of Tongariro National Park. Their position on the RA ordination illustrates that this community occurs at mid altitude and on soils with a relatively high moisture and organic content (Fig. 4), (Chapman, 1984). The presence of red tussock and *Dracophyllum subulatum* with a high frequency of the shrubs *Olearia nummulariifolia* and *Coprosma cheesemanii* are unique to this IQG. The herb *Celmisia spectabilis* is very common, and other species indicative of damp areas, such as *Gleichenia dicarpa, Oreobolus pectinatus* and *Racomitrium lanuginosum* are well represented. The presence of exotic herbs is limited to **Hypochoeris radicata* and **Hieracium pilosella,* both of which occur at a low frequency.

Calluna shows a sparse, patchy distribution with a frequency of 12.5%; it is still a pioneer (Gimingham, 1972) in this community. Patches of *Calluna* of approximately 1.6 m in diameter typically include an established plant of between six to seventeen years old surrounded by small clumps of one to four year old seedlings. There has been active seedling regeneration from one such clump since 1984, where a permanent photographic site has shown *Calluna* to have spread over 20 m through *Gleichenia* and tussock.

Herbfield and Scoria slopes ((Mountain inaka) gravelfield (Atkinson, 1981))

About 20% of the quadrats belong to this IQG, and sites with a high percentage of quadrats in this IQG (e.g., 13 - Rangipo desert, 1 - Top of the Bruce Road) lie to the top left of the RA ordination (Fig. 4), where a combination of high altitude and infertile soils with a low moisture-holding capacity produce a harsh environment. This plant community occurs on the upper slopes of all three of the volcanoes, and on steep slopes, landslips and exposed ridges throughout Tongariro National Park. An unstable substrate, with much bare gravel and stonefield, is common to all the sites in this group, and the cycle of vegetation build-up and break-down has been described by Atkinson (1961, 1981).

Few species survive in this environment; *Dracophyllum recurvum, Gaultheria colensoi* and *Calluna* are the most common dwarf shrubs. *Anisotome aromatica* and *Celmisia spectabilis* are present, as is the grass *Rytidosperma clavatum* and the moss *Racomitrium lanuginosum*. The common occurrence of the moss *Andraea rupestris* (frequency 22%), is a major distinguishing factor of this IQG. *Andraea* is characteristic of higher altitude, rocky environments (Allison and Child, 1971). The presence of exotic herbs is restricted to **Lotus corniculatus* and .*Hieracium pilosella,* both of which occur at a very low frequency.

This community usually lies above 1060 m and *Calluna* shows little evidence of vegetative reproduction. As *Calluna* does not produce much seed above 1200 m (Chapman, 1984), it seems likely that *Calluna* has become established at these higher altitudes from viable seed brought from lower altitudes by wind, man or animals. The frequent build-up and break-down of vegetation patches (Atkinson, 1961) and other erosional forces (Atkinson, 1976) may prevent *Calluna* from becoming common in these habitats. However, it may stabilise the substrate to such an extent that it can increase in density, and *Calluna* has evidently increased on the upper slopes of all three volcanoes since 1984. Estimates of vegetative performance and biomass (Chapman, 1984) suggest that the vegetative growth of *Calluna* is unaffected by altitudes up to 1500 m.

Calluna-dominated tussock or heathland (Heather-red tussock tussock-shrubland or heathland shrubland (Atkinson, 1981))

This community is now an important component of the Tongariro National Park (present in about 10% of all sampled quadrats) and is increasing in area (I.A.E. Atkinson, pers. comm.). Sites comprising this IQG (e.g. 7 - the north west slope of Pukeonake, 17 - Mangetopopo moorland and 25 - Te Whaiau Canal) lie towards the centre of the RA ordination. The community is restricted to the original (1912-1918) *Calluna* plantings or else to roadside sites where the earlier vegetation has been either burnt or mechanically removed.

Calluna is the most common species in the IQG, while red tussock shows a sparse distribution. There are very few inter-tussock species, and most of those that do occur, such as *Celmisia spectabilis* and *Wahlenbergia pygmaea,* are present at low frequencies. Exceptions are the herbs *Aciphylla squarrosa, Nertera depressa, Hydorcotyle nova-zelandiae* var *montana, Gonocarpus micranthus, Microseris scapigera* and *Viola filicaulis,* all of which occur with their highest recorded frequencies in *Calluna*-dominated tussock grassland or heathland (Chapman, 1984).

The exotic component is relatively high; **Hypochoeris radicata, *Linum catharticum,* * *Dactylis glomeratus* and * *Holcus lanatus* are scattered throughout.

There is little evidence for continuing competition between *Calluna* and red tussock because most of the tussock has already been suppressed by *Calluna;* exceptions are semi-waterlogged hollows and stream banks.

Calluna spreads both by seed and from the burial and adventitious rooting of decumbent branches. The spread of ages of mature stems (12-20 years) and the paucity of degenerate *Calluna* bushes suggests a "steady state" where individual stems rather than complete bushes die and are replaced (cf. Forrest, 1971; Wallen 1980, 1981). Such a steady-state would account for the persistence of these stands since they were surveyed, as most the stems would now be 20-28 years old and mass degeneration would be expected. There is no evidence of this.

The highest biomass of *Calluna,* most of which is woody tissue, is found within this community (Chapman, 1984).

There is evidence for the invasion of this community by native shrubs such as *Leptospermum scoparium* and *Dracophyllum filifolium,* and in the absence of fire it would probably revert to native shrubland. Seedlings of *L. scoparium* become established under dense *Calluna* and eventually overtop it, while trees such as *Griselinia littoralis* or *Phyllocladus alpinus* become established in inter-bush gaps or on the edge of tracks. This is similar to the situation found in Europe where * *Betula pendula* and * *Pinus sylvestris* become established in a stand of heather if seed can germinate in a gap and grow quickly enough to overtop the *Calluna* (Gimingham, 1978).

Gleichenia-Empodisma bogs (Red tussock/wire rush-gieichenia rushland (Atkinson, 1981))

This community is represented by about 50/0 of the quadrats and is epitomized by site 19 *(Gleichenia-Empodisma* bog), low down on the Y axis of the RA ordination (Fig. 4). *Empodisma minus* and *Gleichenia dicarpa* dominate, and although *Calluna* is common, it provides far less cover than these wetland species.

Within *Gleichenia-Empodisma* bogs *Calluna* regenerates by adventitious rooting of semi-decumbent stems, and there is little evidence of seedling establishment. Performance, both in terms of annual diameter increment and *Calluna* biomass (Chapman, 1984) is low, and stems tend to have a high proportion of woody tissue. There is no evidence to suggest that *Calluna* might increase to such an extent that it alone would dry out a bog. However, once *L. scoparium* becomes established amongst *Gleichenia* or *Empodisma* and starts a drying out of the bog, then *Calluna* can increase. There is evidence for this in the boggy area along the Bruce Road, site 19.

Weed/scrub communities of disturbed ground (not described by Atkinson, 1981)

This IQG incorporates quadrats (about 20% of the total) from a limited number of sites lying towards the top right of the RA ordination (Fig. 4). These sites lie either outside the Park boundary or recently burnt land or near roadsides and tracks. *Calluna* is the most abundant species, while other exotics such as **Hypochoeris radicata, *Lotus pedunculatus* and **Agrostis capillaris* are also common.

Such areas usually lie at lower altitudes and on soils of higher pH which are associated with prolific flowering of *Calluna* (Chapman, 1984). *Calluna* from site 25 (beside Te Whaiau Canal) showed a higher proportion of flowers per stem than in any other sampled site. *Calluna* is able to become established before all native species and as fast as most exotics. There has been a huge increase in this community since 1984, especially alongside the Desert Road.

Conclusions

Calluna adopts a variety of different strategies within Tongariro National Park and its surrounds. It acts as:

(i) an aggressive species in tussock grassland where it is able to out-compete tussocks both by its ability to germinate in inter-tussock spaces and, later, by its strong vegetative growth and influence on its immediate environment;

(ii) a pioneeer species on disturbed ground and roadside verges;

(Hi) a weed of heathlands and herb fields at higher altitudes and on boggy, semi-waterlogged ground.

Calluna is increasing in both density and extent in tussock grassland, disturbed areas and at roadsides, and in communities at higher altitudes. All available evidence suggests that it will continue to do so, unless displaced by trees. or tall shrubs, such as *Leptospermum scoparium* and *Dracophyllum filifolium,* at lower elevations.

Calluna performs best between 600 m and 1060 m, on moist organic soils of low pH, or on roadsides where the less moist substrate has a higher pH (Table 1). However, it will survive at altitudes up to 1600 m and, because of seed transported by wind, animals or people, is likely to increase in abundance even at these altitudes.

Apart from its occurrence in various communities, the vegetative and reproductive performance of heather has also been studied within the Park (Chapman, 1984). Future work should perhaps be directed towards the control of *Calluna* (e.g. by heather beetle as suggested by Chapman (1984», and a study of the demography of *Calluna* in stands of different age and known history would form a valuable contribution towards this end.

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