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VEGETATIVE PRODUCTION AND PERFORMANCE OF *CALLUNA VULGARIS* IN NEW ZEALAND, WITH PARTICULAR REFERENCE TO TONGARIRO NATIONAL PARK

Summary: Aspects of the production and vegetative performance of *Calluna vulgaris* (heather) were examined in four areas of New Zealand between 1981 and 1983; Tongariro National Park in the North Island, together with Mount Cook National Park, the Wilderness Scientific Reserve, and Ben Callum peat bog in the South Island. The height and height/width quotient of *Calluna* bushes, the diameter increment of woody stems and the amount of flowers/stem all decreased with altitude. Other age-adjusted components of stem biomass were positively related to soil depth, soil moisture, soil organic content and soil pH. Biomass by direct harvest gave values between 300 g m⁻² and 2200 g m⁻² for plant communities with *Calluna*. These are similar values to recorded from British and European heaths, although the contribution of *Calluna* to the total biomass was often less in New Zealand. *Calluna* from New Zealand has a higher proportion of wood relative to total biomass than is normally found in Britain and Europe and this is probably related to the management of British and European heaths by burning. Multiple regressions indicated that increased woodiness is associated with lower altitudes and deeper, moister soils. Woodiness tended to decrease on more organic and more acidic soils, with a corresponding increase in the proportion of green shoots. Flowering declined with increased altitude, while the proportion of green shoots relative to total biomass increased. It is suggested that the upward extension of *Calluna* within Tongariro National Park is limited mainly by constraints on flowering and sexual reproduction.

Keywords: heather; *Calluna vulgaris*; performance; production; biomass; altitude; soil factors; Tongariro National Park; New Zealand.

Introduction

The role of heather (*Calluna vulgaris* (L.) Hull) as a highly valued and major floristic component of British and European heathlands has been well documented (Gimingham, 1972; Gimingham, Chapman and Webb, 1979; Miller, 1979). Much research has been directed towards the production and performance of *Calluna*, especially in relation to its management for herbivore production and, more recently, for the restoration of heather moorland (e.g., Willems, 1988; Gimingham, 1992). In New Zealand, however, *Calluna* is considered as an undesirable exotic weed which is capable of invading and radically altering native plant communities (Bagnall, 1982; Chapman, 1984; Chapman and Bannister, 1990). Consequently an understanding of its production and performance in New Zealand (e.g., Chapman and Bannister, 1995) will provide information useful to its management or eradication.

Earlier studies such as those of Watt and Jones (1948), Metcalfe (1950) and Nicholson and Robertson (1958), concentrated on subjective

estimates of performance with particular emphasis on the variation in height of *Calluna* with altitude. More recently, the variation in the annual diameter increment of stems has been used as a means of comparing relative performance (Grace and Woolhouse, 1970; Thorp, 1972; Wallén, 1980b). Considerable interest has also been shown in the measurement of biomass and net aerial production of *Calluna* which has been well documented by Chapman, Hibble and Rafarel (1975) and Chapman and Clarke (1980).

In this study, direct harvesting of quadrats, the variation of bush dimensions with altitude, and the annual diameter increment or biomass of individual stems, were used to estimate the vegetative performance of *Calluna* over a range of environmental conditions. Other aspects of performance, such as flowering and shoot extension, have been documented elsewhere (Chapman, 1984; Chapman and Bannister, 1995).

The four objectives underlying the investigations were (i) to examine the performance of *Calluna* within New Zealand; (ii) to compare biomass and production between a series of sites

within a particular area, Tongariro National Park; (iii) to relate any differences in performance and production between sites to environment, so as to deduce the optimal habitat for *Calluna* in Tongariro National Park; and (iv) to compare the estimates of performance and production with those from Britain and Europe.

Methods

Areas investigated

The principal area for this investigation was in and around Tongariro National Park, located in the centre of the North Island of New Zealand (39° 12'S, 175° 32'E). The Park is dominated by three volcanoes, Mt Ruapehu (2797 m), Mt Ngauruhoe (2291 m) and Mt Tongariro (1968 m). These form a barrier stretching from north-east to south-west which intercepts the westerly air flow, resulting in a higher rainfall (1800-3000 mm) in the north and west of the Park than in the south and east (1100 mm; Atkinson, 1981). The study area was located principally over the lower volcanic slopes, which were formed from gently sloping ash-covered lava-flows or mud-flows. Soils are derived mostly from weathered volcanic ash. Dark sandy loams and loamy sands, often with impeded drainage, are found at lower altitudes (1100 m). At higher altitudes (1100 - 1300 m) soils become increasingly patchy with erosion exposing old surfaces. Above 1300 m there is little soil formation and the substrate is dominated by gravel and stones (Atkinson, 1981). Recorded mean annual temperatures are around 10.0°C at 650 m, 7.0°C at 1100 m, and, by extrapolation from this lapse rate, about 4°C at 1600 m.

By 1980, *Calluna vulgaris* was widespread within the Park and occurred in a wide range of plant communities at altitudes between 600 and 1600 m. In order to investigate the status of *Calluna* within the Park, Chapman (1984) selected more than thirty sites for further study. These were chosen to reflect the range of altitude, topography and vegetation. Each site measured approximately 20 m x 20 m and was located in homogenous vegetation. Quadrats from these sites have been used to describe the plant communities containing *Calluna* (Chapman and Bannister, 1990) and in studies of phenology, flowering, and shoot extension (Chapman and Bannister, 1995). Twenty-five of the sites have been used to collect material for the various studies of production and performance described in this paper and are shown on Fig. 1. In order to allow ready comparison, site numbers used in Chapman (1984) and Chapman and Bannister (1990, 1995) have been retained. Fig.

1 differs slightly from previous maps (Chapman, 1984; Chapman and Bannister, 1990), as it corrects some site locations (notably sites 17, 19) within Tongariro National Park.

The areas in the South Island where *Calluna* occurs (Fig. 1) are much smaller than those in the North Island. Within the Mount Cook National Park (43° 44'S, 170° 06'E; 765 m a.s.l.), *Calluna* is scattered over a glacial moraine and probably dates from plantings made near the old Hermitage somewhere between 1884 and 1912 (Dennis and Potton, 1984). It does not appear to be spreading. This locality has a high annual rainfall (4100 mm) and a mean annual temperature of 8.4°C. Further south, the Wilderness Scientific Reserve (45° 32'S, 167° 51'E; 280 m a.s.l.) is an old fluvio-glacial terrace composed of greywacke quartz gravels with a grey sandy matrix which has some mafic mineral content. *Calluna* was planted sometime after the Second World War in an attempt to give the area a Scottish aspect. Seedlings have spread rapidly in recent years and *Calluna* is now competing with native vegetation. *Calluna* has been also become established in deep peat on two bogs beside Ben Callum Road (45° 55'S, 168° 29'E; 270 m a.s.l.) where it has been recorded for at least 80 years. The Wilderness and Ben Callum share a cool, wet, hill climate with annual precipitation of about 1100 mm and an annual mean temperature of 9.5°C.

Site characteristics

Measured environmental variables (Table 1) include altitude (estimated from maps), slope, aspect, and midsummer soil temperatures at 40 cm depth. A soil pit was dug at each site to determine the soil depth and examine the soil profile.

In Tongariro National Park, soil samples were taken from 22 of the 25 sites (excluding sites 27, 28, 30 for which only altitude was determined). Soil parameters measured in other areas are means for four sites at Ben Callum, three at the Wilderness and two at Mount Cook. Soil samples were collected over as short a period as possible, on days with similar weather, to minimize the effects of season and day-to-day fluctuations in weather. Ten soil samples were collected from each site, 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, and Mg were extracted by neutral 1 M ammonium acetate and measured by atomic absorption flame photometry. Phosphorus was determined by the method of Olsen *et al.* (1954). The amounts of soil

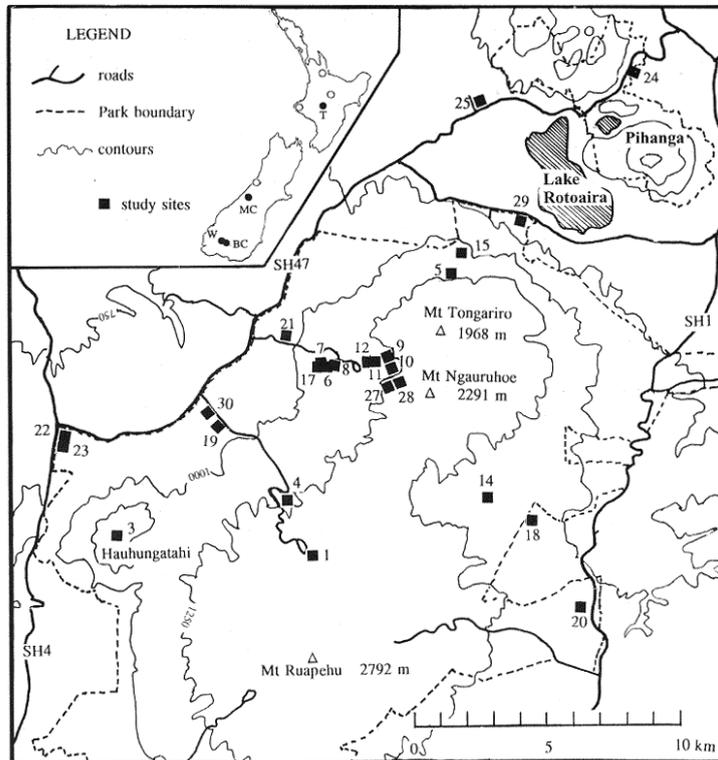


Figure 1: Location of sites at Tongariro National Park. The inset map shows the approximate location of Tongariro National Park (T) and areas investigated in the South Island (filled circles: MC = Mount Cook, BC = Ben Callum, W = Wilderness). Open circles indicate the approximate location of other areas where *Calluna* is found in New Zealand.

nutrients were determined as 'MAF quick-test units' (Mountier, Grigg and Oomen, 1966) and may be converted into $\mu\text{g g}^{-1}$ dry soil by the following conversion factors: Ca, x125; K, x20; Mg, Na, x5; P, x1.1.

Plant performance

Three aspects of *Calluna* performance were investigated: (i) the variation in height and width of *Calluna* bushes with altitude; (ii) the influence of environment on variation in stem diameter increment and stem biomass; and (iii) the influence of environment on above-ground biomass harvested from quadrats.

The logistics of access, collection, and transport meant that the same sites could not always be used for each of the three major investigations. However, in every case the number of samples was sufficient for robust statistical analysis of the data.

The height and width of thirty bushes, chosen at random within each of seventeen sites, were measured. The sites were chosen to represent as wide a variation in altitude as possible. Means of height, width and height/width quotient for each site were used to determine the effects of altitude on these variables.

Stem diameter increments (i.e., the annual increase in stem diameter) were obtained from regressions of basal diameter on stem age for each site. Twenty stems were collected from each of twenty sites at Tongariro National Park and from the Wilderness, Mount Cook National Park, and Ben Callum. Stems were selected to cover the range of diameters occurring at each site. Basal sections of each stem (where the stem emerged from the soil) were stained with phloroglucinol-HCl to highlight the annual rings, which were counted to give an estimate of stem age. The basal diameter of each aged stem was determined from the mean of three

Table 1: Environmental variables which had significant correlations with biomass and performance of *Calluna vulgaris* in sites from Tongariro National Park and in the South Island. Sites with no definable aspect are indicated by a hyphen (-); blank spaces in columns indicate that no measurements of the variable were made. "MAF quick-test units" may be converted into $\mu\text{g g}^{-1}$ dry soil by the following conversion factors: Ca, $\times 125$; K $\times 20$; Mg, Na $\times 5$; P $\times 1.1$.

Site	Environmental variables				Soil variables								
	Altitude	Aspect (m)	Slope (deg)	Depth (cm)	Temperature at 40 cm depth (°C)	Moisture (% dry weight)	Organic matter (% dry weight)	pH	Ca	K	P	Mg	Na
								(MAF quick-test units)					
1	1575	N	23	40	11	11.0	1.4	5.1	1	<1	2	2	2
3	1519	N	20	52	12	35.0	8.2	5.4	<1	<1	3	3	3
4	1250	E	22	70	12.5	29.3	9.1	4.9	<1	1	1	2	3
5	1210	N	18	60	14	38.8	11.8	4.8	<1	2	2	4	3
6	1210	-	0	30	13	8.8	28.9	4.7	<1	1	1	2	2
7	1200	NW	26	85	10	40.5	15.4	4.9	1	2	2	5	3
8	1170	NE	34	48	12.5	32.9	17.4	4.9	<1	2	3	3	2
9	1160	SW	26	30	14	19.4	3.0	5.1	<1	<1	2	2	3
10	1150	-	0	10	14	21.4	4.6	4.6	<1	1	3	1	2
11	1160	E	22	50	12	32.0	7.3	4.7	<1	1	3	3	3
12	1150	NW	2	50	12	31.5	7.5	4.7	<1	1	1	3	3
13	1125	-	2	30	12.5	22.0	3.0	5.7	<1	<1	2	2	2
14	1125	-	0	60	13	28.0	6.9	4.8	<1	1	2	2	2
15	1125	N	16	60	15	40.9	12.4	4.8	<1	1	2	2	3
17	1080	W	3	120	12	36.7	11.7	4.3	<1	2	3	4	3
18	1060	-	0	55	13	41.8	3.5	4.8	<1	2	3	3	2
19	950	-	2	57	10.5	57.1	32.0	4.6	2	3	2	9	6
20	950	-	0	80	15	44.2	12.5	4.9	<1	2	3	3	3
21	950	-	0	48	12	43.3	27.2	4.3	<1	1	3	3	2
22	800	-	0	30	16	43.3	9.7	4.8	<1	1	1	2	3
23	800	-	0	50	13	45.0	13.0	4.3	<1	2	1	3	2
24	725	-	2	13	16	9.0	3.9	6.0	<1	2	2	4	4
25	600	-	0	9	20	24.9	4.7	4.7	1	2	2	4	4
27	1550												
28	1450												
30	900												
Ben Callum	270	-	0	>100	10	86.5	92.3	5.0	3	3	7	17	
Wilderness	280	-	0	-30	13	29.9	7.5	5.7	2	2	4	6	
Mount Cook	765	-	0	-15	9.5	32.0	12.6	5.2	1	3	7	5	

different diameters, measured by vernier calipers to an accuracy of 0.1 mm. Multiple regression of stem diameter against age and various environmental variables was used to identify factors associated with changes in stem diameter.

A further series of twenty stems was collected from each of fourteen of the twenty-six sites within Tongariro National Park. The sites (see Table 2) covered the range of altitudes and vegetation types occupied by *Calluna*. Stems were aged as described above and then divided up into: (i) current year's green shoots; (ii) previous years' green shoots; (iii) woody stems; and (iv) flowers. This allowed comparison with British research (Mohamed and Gimingham, 1970; Miller, 1979) which had used a similar subdivision into components. The components were dried to constant weight at 105°C

(Chapman *et al.*, 1975). Analyses of covariance, using regressions of dry weight of each component against age for each site, were used to produce age-adjusted site means for each component.

Correlation and regression analyses were used to examine the relationship of these means to environmental factors.

Estimates of above-ground biomass were obtained by clearing three randomly placed 0.25 m² quadrats in each of ten sites from Tongariro National Park and one from Ben Callum. The vegetation was sorted into the following components: (i) *Calluna*; (ii) shrubs (other than *Calluna*); (iii) grasses; (iv) forbs; (v) mosses; (vi) lichens; (vii) wetland species (mostly *Empodisma minus* (Hook. f.) Johnson et Cutler and *Gleichenia dicarpa* R. Br.); and (viii) litter. *Calluna* plants

were separated into components as described previously, except for flowers, as the quadrats were harvested in autumn after most flowers had been shed. Components were oven-dried at 105°C and weighed to the nearest gram. The weights of the various components were analysed by a multivariate analysis of variance after logarithmic transformation.

Results

Size of *Calluna* bushes in relation to altitude

The average height, width, and height/width quotient of bushes decreased with increasing altitude (Fig. 2), indicating that bushes became smaller and more prostrate (i.e. less height per unit width) with increasing altitude. The decline in width with increasing altitude was significant only at $P < 0.1$, but the decline in height and height/width quotient were significant at $P < 0.05$.

Diameter increment and biomass of individual stems

Mean annual diameter increments (I, in mm) for each site (Table 2), including the South Island

Table 2: Estimates of vegetative performance of *Calluna vulgaris* derived from stems collected from various sites in Tongariro National Park (North Island) and from three locations in the South Island. Spaces in columns indicate that no measurements were made of that particular component.

Site	Diameter increment (mm yr ⁻¹)	Current year's green shoots	Weight of components (mg)			
			Older green shoots	Flowers	Wood	Total
Tongariro						
1	0.38	146	148	1	540	834
4	0.43	615	368	27	3010	4018
5	0.74	515	279	95	2874	3534
6	0.52					
7	0.53	784	701	83	4033	5096
8	0.49	304	126	31	4033	4494
9	0.41	308	233	19	1829	2389
10	0.92					
11	0.49	432	323	100	3080	3935
12	0.68	337	265	10	2033	2645
14	0.47	358	293	93	2022	2766
15	0.77	464	309	34	4306	5113
17	0.58	97	145	3	2278	2533
18	0.49	529	369	503	3366	4767
19	0.44					
20	1.06					
21	0.32					
22	0.61					
23	0.94	287	265	123	3521	4196
25	0.68	413	272	318	1611	2614
Ben Callum						
						0.52
Wilderness						
						0.99
Mt Cook						
						0.58

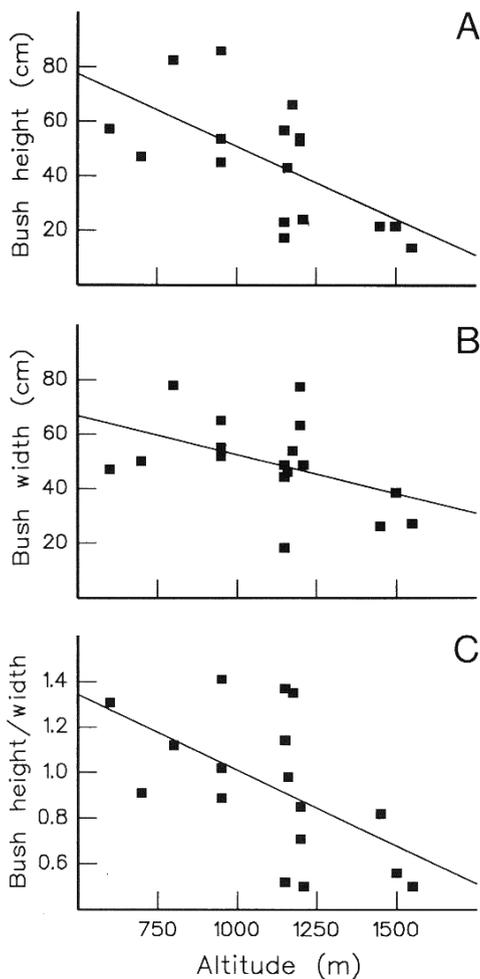


Figure 2: Variation in the (a) height, (b) width and (c) height/width quotient of *Calluna* bushes with respect to altitude, for 17 sites within Tongariro National Park. The sites are 3, 6, 7-10, 12, 14, 17, 20-25, 27, 28, 30 - see Fig 1 and Table 1.

Table 3: Significant correlations of environmental variables with components of the age-adjusted biomass of *Calluna* stems collected at Tongariro National Park (Table 2). Biomass of the components was expressed either as the natural logarithm of dry weight (ln wt) or as a percentage of total dry weight (% total). Correlation coefficients in italics are significant at $P < 0.1$, all others at $P < 0.05$; hyphens (-) indicate non-significant correlations ($P > 0.05$).

	Current year's green shoots (% total)	Older green shoots (% total)	Flowers (ln wt) (%total)		Wood (ln wt) (%total)		Total (ln wt)
altitude	-	-	-0.64	-0.61	-	-	-
soil depth	-0.51	-	-	-0.45	-	+0.61	-
soil temperature	-	-	-	+0.65	-	-	-
soil moisture	-0.63	-0.81	+0.52	-	+0.86	+0.59	+0.84
soil organic matter	-0.64	-0.87	-	-	+0.83	+0.69	+0.79
soil pH	+0.68	-	-	-	-	-	-
soil Ca	+0.59	-	-	-	-0.49	-0.59	-
soil K	-0.49	-	+0.54	-	+0.59	-	+0.61

Table 4: Biomass (above-ground standing crop, excluding litter) by direct harvest of quadrats from 10 sites from Tongariro National Park and in one site, Ben Callum, from the South Island.

Site	Age (years)		<i>Calluna</i> biomass (g m ⁻²)				Other plants' biomass (g m ⁻²)			Total biomass (g m ⁻²)
	mean	maximum	Total	Current shoots	Older shoots	Wood	Wetland plants	Shrubs, grasses, forbs	Mosses, lichens	
5	4.0	8	153	27	13	113	0	27	806	984
6	4.0	13	89	28	14	47	0	3	2129	2221
7	6.4	14	548	78	27	443	0	404	61	1013
8	5.3	15	210	22	7	181	0	461	29	700
10	4.9	9	73	21	1339	0	23	1313	1409	
12	5.9	15	581	69	43	469	0	74	14	669
15	4.6	9	434	48	39	347	0	198	22	654
17	7.0	19	849	47	41	761	0	25	510	1384
19	7.0	15	79	8	3	68	995	29	13	1116
21	6.5	19	142	29	22	91	0	7	149	298
Ben Callum	5.6	14	217	26	7	184	76	0	285	578

outliers, decreased with increased altitude (A) and soil organic matter (O) in a multiple regression accounting for 31% of the total variation ($P < 0.05$), viz.:

$$I = 1.100532 - 0.0004045A - 0.005438O$$

However, when separate multiple regression analyses of the diameter of every measured stem (i.e., 400 stems) against age and each environmental variable were used to account for the over-riding association with age, the partial regression coefficients for the following factors significantly ($P < 0.001$) increased the amount of variation accounted for by the regression. Stem diameters increased with increased soil pH, soil

moisture and soil organic content, and decreased with increased altitude, southerliness of aspect and depth of soil.

The logarithms of mean values of age-adjusted dry weights of various components of stems from Tongariro National Park were significantly correlated ($P < 0.05$) with a variety of environmental factors (Table 3). Logarithms of total stem dry weight and the dry weight of woody tissue were each positively correlated with soil moisture, soil organic matter and soil potassium. The logarithm of the dry weight of flowers showed a similar pattern, in that there were positive correlations with soil moisture ($P = 0.06$) and potassium ($P < 0.05$), but also a significant negative correlation with altitude ($P = 0.01$). In contrast, the dry weights of green

shoots were not significantly correlated with any of the measured environmental variables.

When wood, flowers, and green shoots are expressed as percentages of the total stem weight, some of the previous correlations remain, whilst others emerge. The relative proportion of wood remains positively correlated with soil moisture and soil organic matter, and the relative proportion of flowers decreases with altitude (Chapman and Bannister, 1995). However the relative proportion of wood is also positively correlated with soil depth and negatively correlated with soil calcium. In contrast, the relative proportion of both current year's and older green shoots is negatively correlated with soil moisture and organic matter whilst the relative proportion of current year's green shoots increases with soil pH and calcium.

It is possible to combine the data of Table 2 and Table 4, if wood (W) and green shoots (G) are expressed as a percentage of the biomass of *Calluna*. Selective multiple regressions indicate that the proportion of wood increases with soil depth (D) and soil moisture (M) but decreases with soil organic matter (O). For example, deep soils within the Tongariro National Park have low organic matter and a high content of volcanic sand or pumice. The regression (below) accounts for

57% of the variation in woodiness and is highly significant ($P < 0.001$).

$$\%W = 53.80 + 0.50M - 0.34O + 0.17D$$

In contrast, the proportion of green shoots is lower in soils of greater depth (D), higher pH and potassium content (K) but greater on soils at higher altitude (A) with a greater organic content (O). The following regression accounts for 64% of the variation in the proportion of green shoots and is highly significant ($P < 0.001$):

$$\%G = 130.09 + 0.03A + 0.53O - 18.08pH - 14.05D - 5.64K$$

Sites at Ben Callum differ from those at Tongariro in that the peat is deep and highly organic, with a high pH and cationic content (Table 1). Analysis of only the Tongariro sites (Fig. 3) indicates that the proportion of wood tends to increase on soils of greater depth (D) and higher pH but decreases at higher altitude (A), whereas the proportion of green shoots decreases in response to the same factors ($P < 0.001$ for both equations, which account for 62% and 63% of the variation in woodiness and proportion of green shoots respectively).

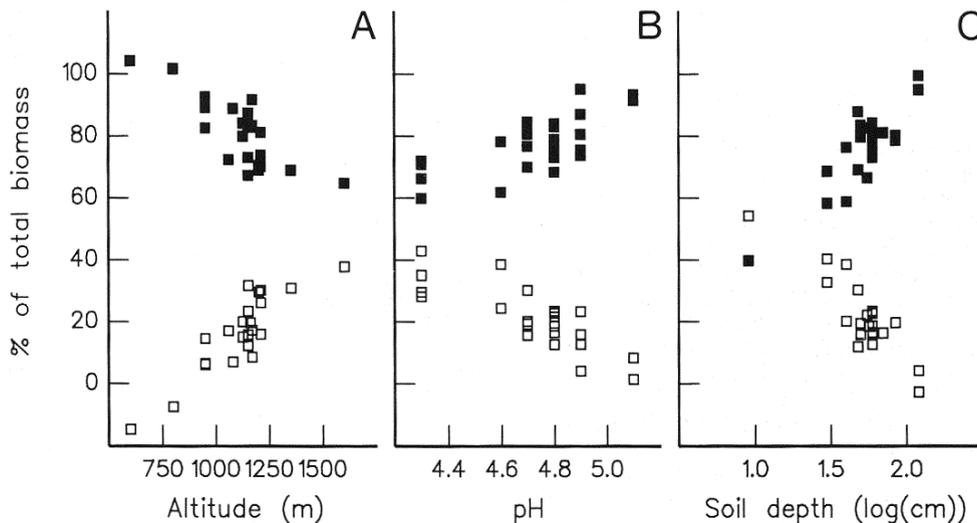


Figure 3: Trends in the proportions of *Calluna* wood (●) and green shoots (□) to altitude, pH and soil depth within Tongariro National Park. Data are derived from Tables 2 and 4 and adjusted values obtained from multiple regressions of the components on altitude, pH, and soil depth. As a result of the linear regression model used, some adjusted values may exceed 100% or be less than 0%. Graphs are: (a) with altitude at median pH (pH 4.8) and soil depth (60 cm); (b) with pH at median altitude (1150 m) and soil depth (60 cm); (c) with soil depth at median altitude (1150 m) and pH (pH 4.8).

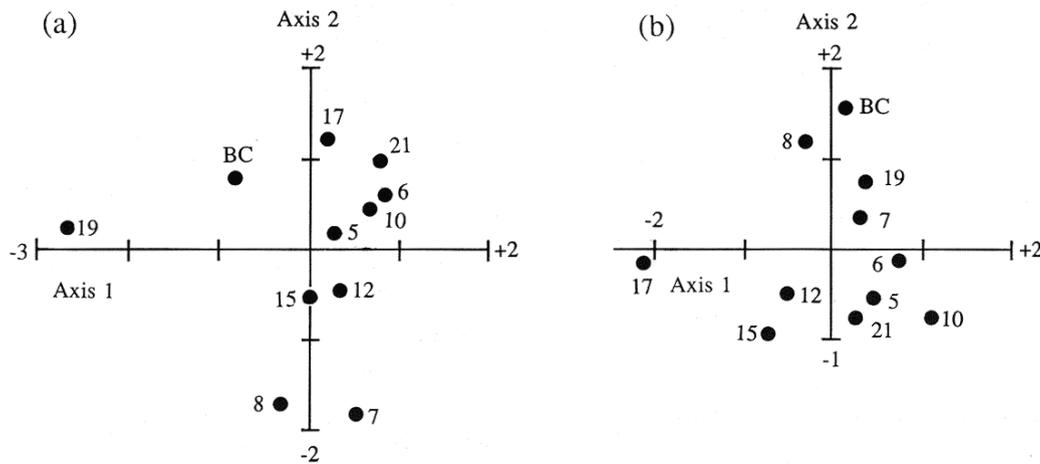


Figure 4: Relationship of sites used in estimates of biomass by direct harvest (Table 4) to the first two canonical axes derived from multivariate analyses of variance of (a) total vegetation biomass and (b) *Calluna* biomass.

$$\%W = -88.50 - 0.04A + 27.89pH + 21.00\ln(D)$$

$$\%G = 196.60 + 0.06A - 33.94pH - 19.75\ln(D)$$

Biomass

Results are presented in Table 4. Canonical discriminant analysis allowed the components of total biomass (by direct harvest) from the sites to be related to two canonical axes (Fig. 4a). The first (horizontal) axis is related to decreased wetness as it is negatively associated with the proportion of wetland species (mainly *Gleichenia dicarpa* and *Empodisma minus*). It is also negatively related to soil K, Mg and Na which are high in sites with high soil moisture and organic content (i.e., site 19 at Tongariro National Park and Ben Callum). The second (vertical) axis was related to decreased amounts of vascular plants (forbs, grasses and shrubs, other than *Calluna* and wetland species) and decreased slope (Table 5).

In a similar analysis that includes only the components of *Calluna* biomass (Fig. 4b), the first canonical axis is associated with decreased amounts of wood, decreased soil depth and increased pH. The second axis is associated with decreasing amounts of current year's and older green shoots, increased soil organic matter and associated cations (K, P, Mg, Na), and decreased soil temperatures (Table 5).

Table 5: Significant correlations ($P < 0.05$) of plant and environmental variables with the first and second axes of the canonical discriminant analyses of total vegetation biomass (Fig. 4a) and *Calluna* biomass (Fig. 4b).

	Total biomass axis 1	Total biomass axis 2	<i>Calluna</i> biomass axis 1	<i>Calluna</i> biomass axis 2
Wetland spp.	-0.89	-	-	-
Other vascular spp.	-	-0.96	-	-
<i>Calluna</i> wood	-	-	-0.70	-
Current green shoots	-	-	-	-0.93
Older green shoots	-	-	-	-0.93
Slope	-	-0.85	-	-
Soil depth	-	-	-0.64	-
Soil temperature	-	-	-	-0.64
Soil organic matter	-	-	-	+0.68
Soil pH	-	-	+0.60	-
Soil K	-0.71	-	-	+0.69
Soil P	-	-	-	+0.65
Soil Mg	-0.61	-	-	+0.64
Soil Na	-0.70	-	-	+0.64

Discussion

Variation in size of *Calluna* bushes with altitude

The significant decrease in both the mean height and the height/width quotient of *Calluna* bushes in relation to altitude within Tongariro National Park (Fig. 2) parallels British experience (e.g., Metcalfe,

1950; Gimingham, 1960). Height/width quotients of *Calluna* bushes have been shown to decrease in relation to increased exposure (Nicholson and Robertson, 1958), and the quotients found in the Tongariro National Park are similar to those recorded by Grant and Hunter (1962) for sites at high and low altitudes in Scotland. In Britain, there appears to be a genetic component to the growth form of *Calluna* bushes (Grant and Hunter, 1962; Bannister, 1978), but no experiments have been carried out to determine whether the variation in growth form of *Calluna* in the Tongariro National Park is merely a plastic response or has some genetic basis.

Diameter increment and biomass of individual stems

The diameter increments for stems of *Calluna* collected from New Zealand varied from 0.32 to 1.06 mm yr⁻¹ (Table 2) and are very similar to the range of 0.22 to 0.94 mm yr⁻¹ recorded by Thorp (1972) for heathlands in S.W. Scotland. In contrast, much lower increments were recorded (0.06 - 0.12 mm yr⁻¹) for *Calluna* from blanket bog at Moor House in Northern England (Grace and Woolhouse, 1970). The finding that mean diameter increments tended to decrease with increased altitude and with increased organic matter is in accord with Thorp (1972).

In contrast, when sites from Tongariro National Park are considered in isolation, both the diameter and biomass of individual stems increased with increased soil moisture and organic content (Tables 2, 3). This may be explained by the exclusion of the highly organic peat from Ben Callum (Table 1), and the observation that the drier and less organic soils within Tongariro National Park are associated with exposed scoria at higher altitudes where production would be expected to be limited by both drought and low temperatures. This is borne out by the significant negative correlations of altitude with organic matter and water content ($r = -0.49$, $P < 0.05$, and $r = -0.56$, $P < 0.01$) respectively) for the sites from which diameter increments were obtained. Annual shoot increments show a similar relationship with altitude (Chapman and Bannister, 1995). The factors which influence *Calluna* performance also influence the floristic composition of communities in which *Calluna* occurs within Tongariro National Park (Chapman and Bannister, 1990). Ordination showed that the primary separation of communities is with respect to altitude (and the associated decrease in soil temperatures), and secondarily to soil moisture, soil organic matter and soil depth.

In the current study, vegetative performance of *Calluna* was not correlated with altitude, although the relative proportion of green shoots increased with altitude, and flowering decreased with altitude. However, Chapman and Bannister (1995) found that, within Tongariro National Park, shoot annual increments tended to increase with altitude, whereas flower abundance and maturity decreased. Hence the vegetative growth of plants of *Calluna* which become established at higher altitudes is at least as good as that of plants from lower altitudes, even though their flowering is reduced. Estimates of *Calluna* production by direct harvest show similar relationships to environmental factors to those provided by analyses of single shoots. Woodiness tends to increase in deeper soils, organic soils, and more acidic soils, whereas higher green shoot production is associated with warmer, shallower, less organic and less acid soils (Tables 4, 5).

These apparently simple relationships are complicated by the correlation of environmental variables. Overall, soil moisture and organic content are positively correlated with each other and negatively correlated with altitude, whereas at Tongariro altitude is positively correlated with pH and uncorrelated with organic content. The inclusion of data from Ben Callum determines the negative correlation of soil organic matter with altitude, and the high pH (which probably results from the application of inorganic fertilizers to the surrounding farmland at Ben Callum) negates the positive correlation of pH with altitude that exists at Tongariro. Multiple regression accounts for these intercorrelations and indicates that on deep, moist, soils at lower altitudes (which are typically organic and with a low pH) decreases in organic matter and increases in pH are associated with increased woodiness. In contrast, on shallow, drier soils at higher altitudes (which typically have lower organic contents and higher pH) increases in organic matter and decreases in pH are associated with higher production of green shoots. These associations of altitude, soil organic matter and pH help explain the apparently contradictory responses to pH and organic matter obtained by simple correlations (Tables 2, 5) and by multiple regression (Fig. 3).

Biomass and productivity of *Calluna* in New Zealand and Europe

The climate of New Zealand sites is similar to those experienced by heaths and moors in Britain and Scandinavia (Table 6). Despite the lower latitude of the New Zealand sites, the mean annual temperatures are very similar (Table 6) due to the high altitude of the Tongariro sites and the

Table 6: Comparisons of the environment, above-ground biomass, and production of stands containing mature *Calluna vulgaris* in New Zealand and Europe (based on Gimingham *et al.*, 1979 with additional information from Barclay-Estrup, 1980; Chapman *et al.*, 1975; Forrest, 1971; Miller, 1979; Tyler *et al.*, 1973; Wallén, 1980a,b). Missing values are indicated by hyphens (-). The proportional contribution of *Calluna* to the total biomass is given by the quotient *Calluna/All*, and total above-ground annual production and the annual production of green shoots are also expressed relative to *Calluna* biomass (*Total/biomass*, *Shoots/biomass*, respectively).

	Environment					Above-ground biomass			Above-ground annual production (<i>Calluna</i> only)		
	Latitude (°)	Altitude (m)	Annual mean temp (°C)	Annual rainfall (mm)	Growing season (days)	All species (g m ⁻²)	<i>Calluna</i> only (g m ⁻²)	<i>Calluna/All</i> (%)	Total (g m ⁻² yr ⁻¹)	Total/biomass (%)	Shoots/biomass (%)
New Zealand											
Tongariro	39°S	1120	7.1	2750	150	1068	317	30	38	-	15
Ben Callum	46°S	270	9.1	1130	-	578	218	38	27	-	12
Scotland											
Elsick Heath	57°N	110	-	760	150	2305	1924	83	369	19	-
Kerloch Moor	57°N	150	7.0	960	184	-	2000	-	270	-	4
England											
Moor House	55°N	550	5.1	1180	184	1510	740	49	168	23	18
Dorset Heaths	51°N	60	10.7	800	250	2200	1800	82	300	17	14
Sweden											
Skanör Heath	55°N	10	7.6	625	184	920	741	80	232	31	20
Sandhammaren	55°N	50	-	-	-	851	760	90	-	-	-

Antarctic influence in the South Island. Rainfall is generally similar, except at Tongariro where it is much higher than any of the European sites. It is, however, difficult to compare the biomass or annual production of *Calluna* in New Zealand (Table 4) with that in Britain and Europe. *Calluna* was often at low density as a component of relatively unproductive vegetation in most of the New Zealand sites examined, in contrast to the dense monocultures of *Calluna* that exist in many British and European heaths or moorlands. The total vegetation biomass for the New Zealand sites varied between 300 g m⁻² and 2250 g m⁻² (Table 4); this is similar to Dorset Heaths which vary from about 300 g m⁻² in the post-burn phase to 2500 g m⁻² in old degenerate sites (Chapman *et al.*, 1975; Gimingham, Chapman and Webb, 1979). However, the biomass of *Calluna* in the New Zealand sites varied from about 75 - 850 g m⁻² which overlaps at the higher end with some of the less productive European sites listed in Table 6 such as Moor House (Forrest, 1971), Skanör Heath (Tyler *et al.*, 1973) and Sandhammaren (Wallén, 1980b) which show a range between 700 - 900 g m⁻². The values for *Calluna* biomass presented in this paper are, however, likely to be underestimates of potential *Calluna* biomass in Tongariro National Park. This is because they were derived from only

three small, 0.25 m², quadrats which were randomly placed in sites in which *Calluna* was assumed to be at an early stage of ingress. This attempt to include sites representative of all stages of heather invasion resulted in the selection of many sites in which the low density of heather increased the probability of random quadrats sampling areas with little or no *Calluna*. Many of these sites have shown little increase in heather cover in ten years since they were first sampled (G. Rogers, *pers. comm.*). Samples deliberately taken from dense stands of heather within Tongariro National Park, some ten years later than those reported in this paper, show a range of *Calluna* biomass from 1700-4600 g m⁻² (*pers. comm.* G. Rogers, G. L. Rapson, V. Keesing), although resampling at Ben Callum in 1992 gave a very similar value (244 g m⁻²) to that recorded by Chapman (1984).

A comparison of productivity is possible if the estimated annual production of green shoots is expressed as a percentage of the biomass of *Calluna*, as this eliminates differences due to the cover of *Calluna* and allows data from stem samples to be included with those from direct harvest of quadrats. The New Zealand sites show relative productivities ranging from 32% in the building phase (e.g., Site 6, Table 4) to 6% in a more degenerate phase (e.g., Site 17, Table 4),

whereas annual production of green shoots in British sites may be as high as 83% of biomass (two years after burning) and fall to about 7% in stands not burnt for 40 years (Miller, 1979). The mean value for production of green shoots of *Calluna* in the cleared plots at Tongariro National Park is 15% of biomass and 13% when the values for the other New Zealand localities are included in an overall mean (Table 6). These values are similar to 14% for mature sites in Scotland (Miller, 1979) and Dorset (Chapman *et al.*, 1975), although mature sites at Moor House (Forrest, 1971) with 18%, Elsick Heath (Barclay-Estrup, 1970) with 19% (including flowers) and Skanör Heath (Tyler *et al.*, 1973) with 20% (excluding flowers), all show higher values.

The studies of Chapman (1984) which are reported in this paper, suggested that *Calluna* in New Zealand was less productive than *Calluna* in many European heaths or moors. Both the proportion of current green shoots in relation to total stem biomass (see above) and the annual shoot increment (Chapman and Bannister, 1995) were low in comparison with Europe. However recent measures suggest that, in dense stands within Tongariro National Park, *Calluna* biomass is greater than either that estimated by Chapman (1984) or described from Europe. One reason for this apparent anomaly may be the high proportion of wood in the New Zealand samples (53-90% in sites with shoots of a maximum age of 9 - 19 years, whereas Miller (1979) records an increase from 10-70% wood in an ungrazed Scottish site over 40 years. New Zealand sites are usually neither burnt nor grazed, so that the high biomass may result from increased woodiness in aged plants, as stands at Tongariro and Ben Callum could be as much as 80 years old. Increased woodiness also implies a smaller investment in green shoots and thus a smaller potential for dry matter production from photosynthesis. The high rainfall at Tongariro may also depress production, as Miller (1979) has shown that the production of green shoots in different years is inversely related to annual rainfall. Furthermore, most British sites are systematically burnt in order to maximize the production of green shoots by *Calluna*, and the high productivity of pioneer stages is at least partly due to rapid regeneration supported by ample reserves contained in stem bases and enhanced by the minerals released from the plant ash. Systematic burning also reduces the proportion of wood in the standing crop of heather. *Calluna* in New Zealand is rarely burnt and its pioneer stages are dominated by colonising seedlings rather than regeneration from surviving stem-bases.

The annual production of green shoots is an underestimate of total aerial production as it may exclude flowers, and does not take the diameter increment of the main stem into account (which would be important in more woody stems). Averages from individual stems in this study indicate that flowers may account for up to 10% of stem biomass (Table 2; cf. Miller (1979) who gives means of 2-10% depending on age since burning) and suggest that the annual increment in wood could be of the same order as the shoot increment. Estimates of annual production of wood from British sites are only 1% of biomass in Dorset (Chapman *et al.*, 1975) and 5% at Moor House (Forrest, 1971), but about 9% in Sweden (Tyler *et al.*, 1973). Consequently, estimates of annual production for *Calluna* in New Zealand might show a greater similarity to those in Britain and Europe when the sparser cover of *Calluna* and its increased woodiness are taken into account.

Calluna at Moor House (Forrest, 1971) and Sandhammeren (Wallén, 1980b) has been claimed to be in a "steady state" with decumbent stems which continuously replace their oldest portions of the stem by the adventitious rooting of the younger growth in the peaty or sandy substrate. *Calluna* in Tongariro National Park and at Ben Callum behaves similarly, and the rooting of procumbent stems under a superficial layer of organic matter is more common than the degeneration of whole bushes. Furthermore, the oldest stems from the sites at Tongariro range from 8 - 19 years old with little evidence of degeneration (Table 4) even though some sites might have supported *Calluna* for the eighty years since its introduction - thus supporting the idea of a "steady-state". Colonisation of gaps by decumbent branches is now considered more common than previously thought (Gimingham, 1988; Scandrett and Gimingham, 1989a). Furthermore, modelling of *Calluna* population dynamics suggests that this mode of growth leads to a "steady state" which is characterised by a relatively constant distribution of stem ages within the community, and which results in relatively constant biomass and productivity in successive years (Scandrett and Gimingham, 1989b). This concept of a steady state is at variance with the suggestion that the large biomasses recorded recently at Tongariro National Park are a result of increased woodiness in older stems, and more work needs to be carried out on the demography of heather stems to resolve this issue.

In conclusion, studies of stem diameters and diameter increments (Table 2) suggest that the vegetative performance of *Calluna* in New Zealand is likely to be best on warm, shallow, mildly acid

mineral soils with adequate organic and moisture content (Tables 3, 5), but is limited by low temperature as diameters decrease with both increased altitude and poleward aspect. At Tongariro National Park, however, the frequent occurrence of porous mineral substrata with little moisture content at higher altitudes results in an association of higher vegetative production with moister soils, although deeper, wetter soils are associated with increased woodiness and a decreased proportion of green shoots. The annual production of green shoots by *Calluna* (as a percentage of biomass) increases with altitude in Tongariro National Park (Fig. 3), whereas stem biomass is unaffected (Tables 2, 3). This suggests that constraints on vegetative production are unlikely to limit the upward extension of *Calluna vulgaris* in the National Park. Indeed, *Calluna* has increased in abundance at higher altitudes in the Park since the completion of this study in 1984 (Chapman and Bannister, 1990), and we consider that its further spread is more likely to be limited by the restriction of flowering at higher altitudes (Table 4) than by reduced vegetative performance.

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