Control, Demography, and Post-control Response of Heather in the Central North Island

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1. Introduction

In the last 70 years, heather (*Calluna vulgaris*) has invaded and transformed most of the red tussock grassland of northern Tongariro National Park, and it now threatens Moawhango Ecological Region. The Department of Conservation is developing a policy and preparing a management strategy for the control of heather in Tongariro National Park, including the use of the defoliating beetle *Lochmaea*. A project is being undertaken in 1992-1995 by Landcare Research New Zealand Ltd, Native Plants and Animals Division, Rotorua, to study the community dynamics of heather, the effectiveness of conventional control techniques, and the wider community effects of a planned biological control agent as important inputs to the development of management policy.

Objectives

- To test the effectiveness of selective herbicides on heather stands of different ages and cover.
- To predict the initial and medium-term response of heather, tussock grasses, and shrubs to the control of heather.
- To determine whether and at what rate heather inhibits or allows successional development to native shrubland and forest.
- To comment on the potential for managing the community, including oversowing and revegetation, to control (or halt) the spread of heather into priority natural areas and remove it from high-value areas in which it has just arrived.

3. Methods

3.1 HERBICIDE TRIALS

Herbicide trials for heather control are being conducted with the co-operation and financial support of the Manawatu-Wanganui Regional Council and Dow-Elanco Ltd on Army land adjacent to State Highway 1 just north of Waiouru. Most herbicides are Dow-Elanco products and selective for woody species and not grasses or forbs. The broad-spectrum chemicals Escort and Roundup, manufactured by Monsanto, are included and were applied by hand-held techniques. A secondary objective of the trials is to assess the survival of native tussocks and herbs and the non-target damage to woody natives. Three techniques for applying chemicals are being trialed: helicopter, gun and hose,

and mist-blower. The different techniques will be appropriate for different sized stands of heather, ranging in size from extensive areas to isolated outlier nuclei. Sizes of trial plots are: aerial, 1 ha; brushgun, 5×10 m; and mistblower, 5×5 m. The plots are monitored for a minimum of 12 months after chemical application. One hundred frequency counts centred on a heather plant in each plot record the presence of dead, resprouted, and recently germinated heather, and the presence of dead or living native species. Resprouted heather includes both partly defoliated or debilitated plants and plants apparently dead that had basally resprouted. The trial is not assessing the seasonal effectiveness of herbicides.

The most encouraging chemicals from the first trial are to be reapplied in 1993 to assess their effectiveness on surviving heather and on newly germinated seedlings. Further, a previous herbicide trial conducted by Ivan Watkins-Dow in July 1982 near the end of Mangatepopo Road was revisited and observational impressions noted. Design details of this experiment can be obtained from the author of this report.

3.2 SOIL AND LITTER SEED BANKS

The composition of soil and litter seed banks is being assessed in germination trials of samples of litter and the top 5 cm of soil from 21 sites spanning a range of altitude and stand ages of heather. The samples have been incubated under greenhouse conditions for 18 months. Seedlings are removed at 3 month intervals and the soil is stirred. The experiment will give preliminary indications of the composition of the seed bank, the viability of heather seed in the soil, and the potential germination response of seeds after the biological control of heather.

3.3 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

Simulation of an outbreak of the heather beetle (Lochmaea) involves harvesting heather from 42 plots by completely removing the entire standing crop of heather or, alternatively, removing green shoots only. Heather is completely harvested by clipping stems at ground level, and green shoots are removed by clipping stems just below green foliage. The waste is removed from the site. Of the two harvesting techniques, clipping green shoots probably offers the best simulation of a population irruption of the heather beetle. The ideal simulation would be harvesting leaf tissue only and allowing decomposition of the foliage on site, but we consider clipping a good approximation within the resource limitations of the experiment. The simulated collapse of heather may induce both vegetative resprout and new germination of heather, and growth release and accelerated germination of natives. The resprout, germination, and release responses will be measured using frequency and size-class analyses in April 1993 and April 1995. Plot placement covers the key environmental gradients and differences in the demographic age, stature, and cover of heather. The biomass and demographic structure of heather are also sampled at each site.

3.4 SUCCESSIONAL ROLE OF HEATHER

The successional role of heather in open vegetation and the spread of native shrubs and trees through heather shrubland is being assessed from 50 plots on the ringplain between the Whakapapiti Stream and the Wanganui River. The cover of heather and the rates of spread of native shrubs through heather are compared with the rates of spread of native shrubs and trees through tussock grasslands in adjacent landscapes without heather. Point height intercept sampling measures species canopy cover and height, and the size and age classes of all woody plants in a range of communities spanning altitudinal, climatic, and age gradients of heather. The role of heather in non-forest ecosystems will be assessed by observation only.

3.5 SOIL CHEMISTRY

We are conducting a preliminary investigation into the capacity of heather to modify soil morphology and chemistry from that evident under red tussock and manuka and inaka. Soil pH, carbon and nitrogen content, and carbon-nitrogen ratios are measured at 12 sites within each community.

4. Results

4.1 HERBICIDE TRIALS

The herbicide trials were conducted in pioneer and building-phase stands of heather with a mean crown cover of 72% and mean crown height of 0.3 m. The proportion of plants in different growth phases in a representative sample was 55% pioneer, 30% building, 15% mature, and none in the degenerate phase.

Helicopter

There was a wide variation in herbicide effectiveness, and no one herbicide killed a high proportion of heather plants in the first application (Table 1). Hi Ester 2,4-D + Boost and Tordon 50-D were the most promising, killing 45% and 72% of heather plants respectively. Tordon 50-D + Boost also provided encouraging results. On the other hand, Grazon, both individually and in combination with Hi Ester 2,4-D, and Tordon Brushkiller were ineffective. The surfactant 'Boost', surprisingly, retarded the effectiveness of two chemicals, Tordon 50-D and Tordon Brushkiller. Most chemicals were more effective on mature and senescent plants with collapsed, decumbent form and low foliar biomass, whereas multi-branched, erect, juvenile plants with high foliar biomass showed superior resistence. There was little variation in the frequency of newly germinated heather, with a mean frequency of 44% of new seedlings throughout. None of the herbicides killed native forbs and grasses, but a proportion of prostrate and erect native shrubs succumbed (Table 2). Monoao,

the dominant native shrub invading western Waiouru tussock grasslands, is particularly susceptible to the herbicides.

Brushgun

Hi Ester 2,4-D without Boost produced an encouraging result, killing 88 % of plants. Tordon Brushkiller provided an improved result, when compared to the helicopter trial. However, in contrast to the helicopter trial, Tordon 50-D was only moderately successful at the highest concentration. Grazon again provided the worst performance of all chemicals. The two Monsanto herbicides, Escort and Roundup, mostly killed less than 50% of plants. Overall, the addition of Boost marginally improved chemical effectiveness. Although the non-target death of natives was not quantitatively assessed, Roundup appeared to kill some grasses and herbs, but Escort did not.

Mistblower

Overall, the mistblower provided the best results for the three applications. Tordon Brushkiller without Boost killed almost 90% of plants, as did Roundup with Boost. Only Escort performed poorly. Grazon, after performing poorly in the helicopter and brushgun trials, killed up to 79% of plants. The mistblower trials also had the lowest frequency of newly germinated seedlings.

TABLE 1: PERCENTAGE FREQUENCY OF RESPROUTED, DEAD, AND NEWLY GERMINATED PLANTS OF HEATHER IN HERBICIDE TRIALS AT WAIOURU. PEARSON PRODUCT-MOMENT IS A MEASURE OF THE CORRELATION BETWEEN THE FREQUENCY OF DEAD HEATHER PLANTS AND THE FREQUENCY OF NEWLY GERMINATED SEEDLINGS.

(A) AERIAL APPLICATION

CHEMICAL	FORMULATION NAME	APPLICATION RATE	TRIAL DATE	RESPROUT (%)	DEAD (%)	SEEDLINGS (%)
Triclopyr	Grazon	6.0 kg a.i.ha ⁻¹	12/90	96	4	43
Triclopyr+ Picloram	Tordon Brushkiller	3.0+1.0 kg a.i.ha ⁻¹	12/90	88	12	50
2,4-D + Triclopyr	Hi Ester 2,4-D + Grazon	11.0+2.0 kg a.i.ha ⁻¹	12/90	92	8	56
2,4-D + surfactant	Hi Ester 2,4-D + Boost	11.0 kg a.i.ha ⁻¹ and 1.5 lha ⁻¹	3/92	55	45	42
2,4-D + Picloran	Tordon 50-D	4.0+1.0 kg a.i.ha ⁻¹	3/92	28	72	57
2,4-D + Picloran + surfactant	Tordon 50-D+ Boost	4.0+1.0 kg a.i.ha ⁻¹ and 1.5 lha ⁻¹	3/92	57	43	37
Triclopyr+ Picloram	Tordon Brushkiller	3.0+1.0 kg a.i.ha ⁻¹	3/92	76	24	39
Triclopyr + Picloram+ surfactant	Tordon Brushkiller + Boost	3.0+1.0 kg a.i.ha ⁻¹ and 1.5 lha ⁻¹	3/92	86	14	37
Triclopyr + surfactant	Grazon + Boost	6.0 kg a.i.ha ⁻¹ and 1.5 lha ⁻¹	3/92	86	14	37
Mean				73.78	26.22	44.22
Standard deviation				22.53	22.53	8.11
Pearson Product-moment						0.223

(B) BRUSHGUN APPLICATION (TOTAL MIX 5000 lha⁻¹)

CHEMICAL	FORMULATION NAME	APPLICATION RATE	TRIAL DATE	RESPROUT (%)	DEAD (%)	SEEDLINGS (%)
Тгісlоруг	Grazon	180 g a.i. 100 l ⁻¹	12/91	84	16	24
Triclopyr + surfactant	Grazon + Boost	180 g a.i. 100 l ⁻¹	12/91	76	24	32
2,4-D + Picloram	Tordon 50-D	60.0+15.0 g a.i.100 l ⁻¹	12/91	81	19	66
2,4-D + Picloram + surfactant	Tordon 50-D +Boost	60.0+15.0 g a.i.100 l ⁻¹	12/91	81	19	56
2,4-D + Picloram	Tordon 50-D	120.0+30.0 g a.i.100 l ⁻¹	12/91	75	25	28
2,4-D + Picloram + surfactant	Tordon 50-D +Boost	120.0+30.0 g a.i.100 l ⁻¹	12/91	50	50	34
Triclopyr + Picloram	Tordon Brushkiller	90.0+30.0 g a.i.100 l ⁻¹	12/91	60	40	76
Triclopyr+ Picloram + surfactant	Tordon Brushkiller + Boost	90.0+30.0 g a.i.100 l ⁻¹	12/91	42	58	60
2,4-D	Hi Ester 2,4-D	216.0 g a.i.100 l ⁻¹	12/91	12	88	33
2,4-D + surfactant	Hi Ester 2,4-D + Boost	216.0 g a.i.100 l ⁻¹	12/91	41	59	49
Glyphosate	Roundup	360.0 g a.i.100 l ⁻¹	12/91	61	39	85
Glyphosate + surfactant	Roundup + Boost	360.0 g a.i.100 l ⁻¹	12/91	44	56	94
Metsulfuron	Escort	5.4g a.i.100 1 ⁻¹	12/91	80	20	60
Metsulfuron + surfactant	Escort + Boost	5.4g a.i.100 l ⁻¹	12/91	61	39	13
Mean				60.57	39.43	50.71
Standard deviation				20.91	20.91	24.37
Pearson Product-moment						0.072

(C) MISTBLOWER (NON-ULA) APPLICATION

CHEMICAL	FORMULATION NAME	APPLICATION RATE	TRIAL DATE	RESPROUT (%)	DEAD (%)	SEEDLINGS (%)
2,4-D + surfactant	Hi Ester 2,4-D + Boost	270.0+15.0 g a.i.10 1 ⁻¹	1/92	45	55	15
Triclopyr	Grazon	105 g a.i.10 l ⁻¹	1/92	21	79	21
Triclopyr + surfactant	Grazon +Boost	105+15.0 g a.i.10 1 ⁻¹	1/92	60	40	39
Triclopyr + Picloram	Tordon Brushkiller	52.5 g a.i.10 1 ⁻¹	1/92	11	89	57
Triclopyr + Picloram + surfactant	Tordon Brushkiller +Boost	52.5+17.5 g a.i.10 l ⁻¹	1/92	33	67	54
Glyphosate	Roundup	63.0 g a.i.10 l ⁻¹	1/92	30	70	24
Glyphosate + surfactant	Roundup + Boost	63.0+15.0 g a.i.10 l ⁻¹	1/92	8	92	15
Metsulfuron	Escort	7.5g a.i.10 l ⁻¹	1/92	86	14	44
Metsulfuron + surfactant	Escort + Boost	7.5+15.0 g a.i.10 1 ⁻¹	1/92	84	16	32
Mean				42.00	58.00	33.44
Standard deviation				29.19	29.19	15.99
Pearson Product-moment						-0.143

TABLE 2. PERCENTAGE SURVIVAL OF IMPORTANT NON-TARGET PLANT SPECIES IN AERIAL HERBICIDE TRIALS FOR HEATHER AT WAIOURU. MEAN FREQUENCY IS THE AVERAGE OCCURRENCE OF SPECIES IN ALL NINE TRIALS.

Moss	alive	29.4	15.1	100	100	100	100	100	100	100	100	100
Native grasses	alive	7.6	3.3	100	100	100	100	100	100	100	100	100
Lycopodium fastigiatum	alive/dead	6.8/1.0	4.4/0	100/0	89/11	89/11	100/0	90/10	100/0	100/0	100/0	100/0
Cassinia vauvill- iersii	alive/dead	6.2/1.0	3.4/0	91/9	75/25	75/25	100/0	100/0	88/20	80/20	86/14	92/8
Celmista gracilenta	alive	5.1	2.3	100	100	100	100	100	100	100	83	100
Penta- chondra pumilia	alive/dead	5.3/3.9	5.1/2.0	40/60	65/35	35/65	79/11	0/100	33/67	50/50	43/57	50/50
Coprosma cheese- manti	alive/dead	10.3/4.4	6.7/1/5	73/27	71/29	54/46	82/18	58/42	20/80	0/100	38/62	95/5
Monoao	alive/dead	2.8/4.3	1.5/2.2	0/100	57/0	33/67	36/64	0/100	25/75	0/100	0/100	0/100
Adventive grasses	alive	58.2	7.6	100	100	100	100	100	100	100	100	100
Hieracium pilosella	alive	14.0	15.0	100	100	100	100	100	100	100	100	100
Silver tussock	alive	27.4	9.8	100	100	100	100	100	100	100	100	100
Hard tussock	alive	9.4	3.9	100	100	100	100	100	100	100	100	100
Red tussock	alive	48.2	7.3	100	100	100	100	100	100	100	100	100
Species		mean frequency	standard deviation	Grazon	Tordon Brushkiller	Hi Ester 2,4-D + Grazon	Hi Ester 2,4-D + Boost	Tordon 50-D	Tordon 50-D +Boost	Tordon Brushkiller	Tordon Brushkiller +Boost	Grazon +Boost

General comments

Means and standard deviations (Table 1) indicate increased herbicide effectiveness from the helicopter to the brushgun to the mistblower, especially for Hi Ester 2,4-D, Tordon Brushkiller, and Grazon. The surfactant Boost mostly performed poorly with herbicides from Dow-Elanco. An exception was Tordon 50-D with Boost which doubled in effectiveness at high concentrations in the brushgun trial. Boost did, however, improve the performance of the Monsanto herbicides Escort and Roundup. But, overall, Escort performed poorly in both the brushgun and mistblower trials.

There were no significant correlations between the frequency of recently germinated seedlings and the frequency of dead heather plants (Pearson Product-moment correlations). In other words, the amount of defoliation and increased light conditions on the ground did not seem to influence the frequency of emergence of new seedlings.

A herbicide trial conducted by Ivan Watkins-Dow in July 1982 near the end of Mangatepopo Road produced poor results for heather control. All 15 plots contained dense heather shrubland, dominated by plants that predate in age the original treatment in July 1982. This apparent high survivability confirms the original impression of the herbicide company that the trial was conducted at an inappropriate time of year compromising the chemical effectiveness (B. Harris, Dow-Elanco, pers. comm. 1993).

4.2 HEATHER BIOMASS AND REPRODUCTIVE STRATEGY

Biomass varies in terms of stand structure; high levels (approaching 6 kg m⁻²) are recorded in old stands at low altitude, and low values characterise pioneer-building phase stands at high altitudes (Table 3). The figures for heather are in addition to the biomass of native plants, which contribute between 5 and 75% of the total biomass depending on the successional stage of the vegetation. Damp hollows at low altitudes have higher biomass than crests and sideslopes, but frosty hollows at high altitudes have lower biomass than crests and sideslopes.

TABLE 3: MEAN AERIAL BIOMASS (g m^{-2}) OF HEATHER FROM SITES IN TONGARIRO NATIONAL PARK. FIGURES ARE EXCLUSIVE OF NATIVE VEGETATION.

LOCATION	BRUCE ROAD		MANGATEI	TARANAKI FALLS	RANGIPO		
Altitude (m)	930	910	980	1080	1170	1300	860
Growth form	degenerate	mature	mature	mature	building mature	pioneer building	building mature
Mean cover (%)	42.0	72.3	48.7	75.3	36.0	18.0	60.5
Crest	2529	3255	2677	5793	3469	768	828
Side slope	2799	3231	2298	4636	3730	232	1663
Hollow	3190	3988	3535	1830	2963		

Heather seedlings are rare in undisturbed stands, especially those with mature and degenerate growth forms (Table 4). Regeneration appears to be mostly by basal resprout from the root crown and not by seed germination or layering from decumbent stems. Layering only appears important in acidic peat bogs where heather is a minor component of vegetation dominated by four-square sedge, tangle fern, and jointed rush. In undisturbed older stands on well-drained substrates the limited recruitment by seed germination occurred more on frosty hollows with low biomass than on crests and side slopes with high biomass and decumbent growth forms. Abundant seedlings in pioneer and building-phase stands result from heather exploiting high light conditions within the open community.

4.3 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

The removal of all aerial tissue of heather resulted in both new seedlings and basal resprout at all sites irrespective of the original stand structure of heather (Table 4). The greatest number of seedlings occurred in mature stands on the lower Mangatepopo Road and in building-phase stands in the Rangipo. Predictably, the clearance of heather stimulated seedlings in excess of those noted from undisturbed stands.

The removal of green shoots by clipping resulted in more basal resprout than new germination (Table 4). Pioneer and building-phase stands at high altitude and in the Rangipo did not differ strongly in their disturbance response to that of mature-degenerate stands, despite distinct differences in ground light conditions between the two.

Overall, there were no consistent differences in the frequency of seedlings and resprout between complete harvesting and clipping. Furthermore, there were no new seedlings of native shrubs in any plots for the 18 month monitoring

period, although catsear, adventive grasses, ferns, and *Hieracium* were common in the cleared plots, but not in the clipped plots.

TABLE 4: MEAN FREQUENCY OF NEW SEEDLINGS AND ROOT-CROWN RESPROUT OF HEATHER IN 1 ${\rm m}^{-2}$ Plots 18 months after complete Harvesting of Heather and Removal of Green shoots only in Tongariro National Park.

LOCATION	BRUCE ROAD		MANGATER	TARANAKI FALLS	RANGIPO		
Altitude (m)	930	910	980	1080	1170	1300	860
Growth form	degenerate	mature	mature	mature	building mature	pioneer building	building mature
Mean cover (%)	42.0	72.3	48.7	75.3	36.0	18.0	60.5
Existing seedlings	0	0	3.5	5.5	2.5	13	15.5
Seedlings in cleared plots	11	90.5	5	6.5	7	6	42
Resprout in cleared plots	3.5	16.5	2	11	14.5	8	6.5
Seedlings clipped plots	2.5	14.5	9	1	1.5	5	8.5
Resprout in clipped plots	17	10.5	17	6	5.5	8.5	42

4.4 SEED BANKS

The amount of germinable seed of both natives and heather in litter and soil varied widely in terms of altitude, successional age of the vegetation, and the amount of heather in the vegetation (Table 5). Heather dominates most of the samples, although ferns and herbs are important. The quantity of germinable heather seed from pioneer and building-phase stands at high altitude and in the Rangipo was substantially less than that under mature and degenerate stands on the lower Bruce and Mangatepopo Roads. The germinable seed of native shrubs is concentrated at intermediate altitudes.

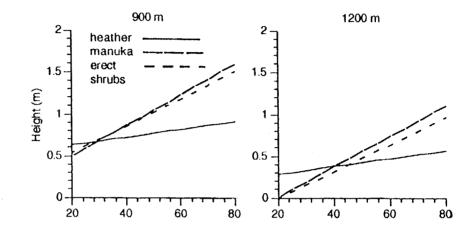
There is consistently more heather seed in the soil than in litter, probably because the fine seed is captured by the soil after filtering down through the litter. Heather seed was still germinating abundantly after 18 months, suggesting a minimum viability period of at least 2 years.

FIGURE 1. THE EFFECT OF TOPOGRAPHY, ALTITUDE, AND TIME SINCE THE LAST BURN, IN LOGISTIC REGRESSION MODELS, ON THE HEIGHT OF THE IMPORTANT SHRUBS IN NORTHERN TONGARIRO NATIONAL PARK.

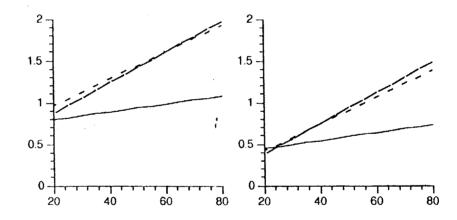
The graphs show changes in the estimated probability of species.

"Erect shrubs" includes: manuka and inaka

CRESTS



SIDESLOPES



HOLLOWS

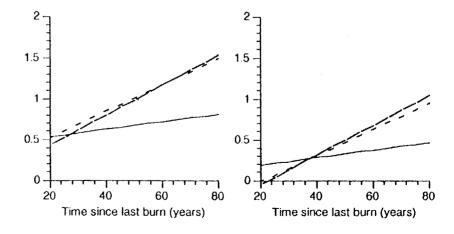


FIGURE 2. THE EFFECT OF TOPOGRAPHY, ALTITUDE, AND TIME SINCE THE LAST BURN, IN LOGISTIC REGRESSION MODELS, ON THE COVER OF THE IMPORTANT SHRUBS IN NORTHERN TONGARIRO NATIONAL PARK.

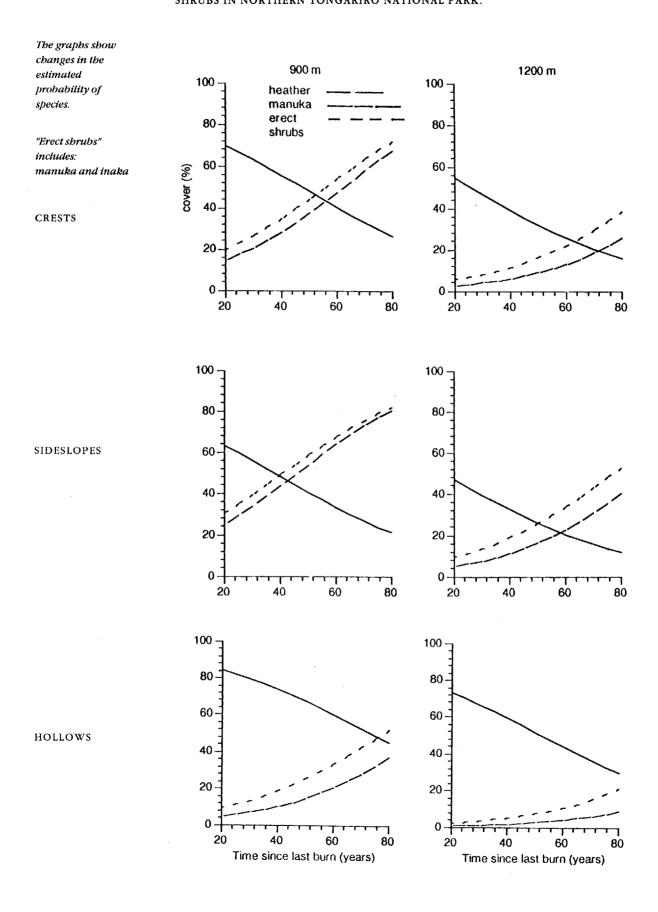
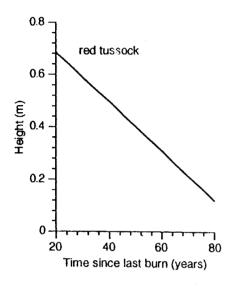
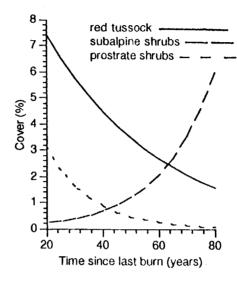


FIGURE 3. THE EFFECT OF TIME SINCE THE LAST BURN IN LOGISTIC REGRESSION MODELS ON THE HEIGHT AND COVER OF SOME MINOR SPECIES AT NORTHERN TONGARIRO NATIONAL PARK.

The graphs show changes in the estimated probability of species.





"Subalpine shrubs" are:
Dracophyllum recurvum, Epacris alpina, Hebe venustula, Olearia nummularifolia, bog pine, mountain toatoa, and pygmy pine.

"Prostrate shrubs"
are:
Coprosma
cheesemanti,
Gaultheria colensoi,
and Muehlenbeckia
axillaris

The landscapes above 1250 m are also almost all secondary, but there are two different, altitudinally separated, soil-vegetation systems. At lower altitudes heavily gleyed and often waterlogged tephra soils support tanglefern, bog pine, wirerush, pygmy pine, and scattered red tussock. Heather experiences establishment difficulties in this closed community and is at background levels only. Above this zone, frequent burning last century has induced soil erosion, exposing gravelfields and stonefields that support sparse *Racomitrium* moss with less *Dracophyllum recurvum*, *Hebe tetragona*, and hard tussock. These pavements are the main habitat of heather above 1250 m, but establishment difficulties in the free-draining scoria limit its population growth.

Genuine non-forest sites below treeline on the northern and eastern sides of the Park are confined to peat bogs between Mt Hauhungatahi and Mt Ruapehu and small areas to the north of Mt Hauhungatahi. Heather is rare on these sites and restricted to vegetation hummocks where drainage in the organic soils is improved. There are large areas of acidic-humic soils with high watertables that are, nevertheless, forest soils, but now dominated by flax, red tussock, four-square sedge, and tanglefern, with scattered manuka, inaka, silver pine, and mountain toatoa. Before forest clearance by burning, these sites supported open forest of silver pine, mountain toatoa, kaikawaka, and mountain beech, similar to the extensive forests on similar soils between Mt Hauhungatahi and Horopito. Heather is a minor and comparatively unobtrusive component of secondary vegetation today.

TABLE 5: MEAN NUMBER OF GERMINABLE SEEDS m⁻² FROM 3 SAMPLES AT EACH OF 7 SITES IN TONGARIRO NATIONAL PARK AFTER 18 MONTHS GERMINATION UNDER GREENHOUSE CONDITIONS.

LOCATION		BRUCE ROAD		MANGATE	TARANAKI FALLS	RANGIPO		
Altitude (m)		930	910	980	1080	1170	1300	860
Time since last fire (yrs)		66	37	45	37	37	35	18
Mean cover (%)	42.0	72.3	48.7	75.3	36.0	18.0	60.5
Heather	Litter Soil	3351 20893	6568 8429	11658 87895	4757 97797	2262 46104	76 0	4976 9344
Adventive grasses	Litter Soil	106 439	117 39	1561 528	878 539	178 261	50 0	408 650
Native ferns and herbs	Litter Soil	4306 4940	5646 2628	2167 2856	611 3039	2567 2317	967 0	2042 5043
Native shrubs	Litter Soil	0 33	0	100 361	56 456	56 28	0	0

4.5 SOIL CHEMISTRY

There were significant differences in soil pH, carbon and nitrogen content, and the carbon/nitrogen ratio of soils beneath red tussock grassland, manuka shrubland, and heather shrubland (Table 6). Heather soils are extremely acid, while those of manuka and red tussock are moderately to strongly acid. There are significant differences in soil carbon between manuka and heather, but not in nitrogen. All the soils had medium carbon and nitrogen contents. Manuka shrubland had a low carbon/nitrogen ratio, heather a medium value, and red tussock a high value.

TABLE 6: MEANS AND STANDARD DEVIATIONS OF SOIL CHEMICAL PROPERTIES ESTIMATED FROM THREE VEGETATION TYPES IN NORTHERN TONGARIRO NATIONAL PARK. P = SIGNIFICANCE LEVEL BETWEEN MEANS.

VEGETATION	RED TUSSOCK	MANUKA	HEATHER	P
рН	5.57 (0.21)	4.50 (0.38)	4.13 (0.21)	P<0.0001
Carbon	6.63 (1.54)	5.32 (2.45)	7.67 (1.79)	P<0.05
Nitrogen	0.30 (0.09)	0.46 (0.22)	0.48 (0.08)	P<0.01
Carbon/nitrogen	23.21 (6.86)	12.07 (3.22)	15.85 (2.08)	P<0.0001

4.6 SUCCESSIONAL ROLE OF HEATHER

Multiple regression models investigating the effects of topography, altitude, solar radiation, slope, and time since the last burn on the height and cover of species in secondary vegetation below 1300 m show a clear relationship between the important species heather, manuka, and inaka. Manuka and inaka have faster vertical growth rates than heather on all combinations of altitude and topography (Fig. 1). Manuka has the fastest vertical growth rate, and 80 years after disturbance is more or less twice as high as heather. Inaka initially grows slightly more quickly than manuka, but after 30-50 years manuka is superior. Heather has the highest stature on sideslopes by virtue of the support provided by abundant native shrubs; without support its growth form is decumbent. The emergence of manuka and inaka above heather is fastest on sideslopes and slowest at high altitudes and on hollows. Even 80 years after disturbance, shrubland dominated by all three species is still increasing in stature.

In general, the canopy cover of manuka and inaka increases rapidly from 20 to 80 years, while that of heather declines (Fig. 2). On all sites except hollows, heather has reduced to 10-30% cover after 80 years. The only exception is on frosty hollows at higher altitudes, where manuka is uncompetitive, inaka is the main native coloniser and only slowly increases, and heather continues to dominate after 80 years. The emergence of manuka and inaka over heather is fastest on sideslopes at low altitude, slower on crests and at higher altitudes, and slowest on hollows throughout. Inaka has greatest canopy cover at high altitudes and on frosty hollows, and is much less competitive on crests and sideslopes at low altitude where manuka is superior.

Other species are a minor component of the vegetation. The height and cover of red tussock decline rapidly with time (Fig. 3) as it is overtopped by invasive shrubs. On the other hand, the cover of subalpine shrubs increases, especially around the upper altitudinal limits of manuka at 1250-1300 m.

5. Interim Conclusions

5.1 HERBICIDE TRIALS

Abundant germination of heather after the initial herbicide treatment results from two factors: pioneer and building-phase stands have inherently high recruitment; and increased light levels within the stand from defoliation foster seed germination. Light limitations on seed germination appear to occur only in mature stands with very high biomass. The experiment did not assess the influence of herbicides on seed germination from litter and soil. Given the seedbank experimental results, heather will continue to germinate for a minimum of two years after the elimination of a local seed rain. The maximum period required to exhaust a seed bank is not known. Nor did the trials assess the seasonal effectiveness of different chemicals and treatments; however, convention suggests that spraying is best in December before the onset of flowering and seed-set.

A second application of chemical on selected helicopter trial plots was made in December 1992 and March 1993; these will be assessed in March 1994. Initial indications are that a very high proportion of resprouted plants and seedlings originating after the first application of chemical are now dead or dying.

Heather possesses a large capacity for vegetative resprout from both completely and partly defoliated plants, most of which is from the root crown. This may point to the biological response of plants defoliated by the heather beetle. Plants arising from basal resprout did not appear to flower at year 2, contrasting with seed set on 2-year-old plants arising from seed germination.

In Britain, herbicide trials using Cyprazine killed 50-95 % of heather plants in trials. Cyprazine is a triazine herbicide and cannot be recommended because it also kills grasses and because its residues are detectable in soil for up to 12 months.

The increased effectiveness of herbicides when applied with hand-held equipment probably arises from smaller droplets and a more direct application of chemical to target plants. Costs for retreating regenerating stands using all three application techniques will not substantially reduce, because of the expected abundant seed germination. Although helicopters provide the least successful delivery technique, they are the only feasible option for controlling extensive stands.

5.2 SOIL CHEMISTRY

There is evidence that heather and manuka acidify red tussock soils by approximately 1.5 and 1.0 pH units respectively. The pH values for heather, compared to those derived by Chapman (1984), suggest continuing acidification of soils in the last 10 years. Manuka can tolerate a soil pH of 3.6 on geothermal sites near Rotorua (B. Burns pers. comm. 1993), so acidification of red tussock soils by heather should not competitively disadvantage or exclude manuka.

Increased soil acidity is also not expected to disadvantage inaka which can tolerate quite heavily leached and waterlogged soils throughout wetter districts of the central North Island.

Carbon/nitrogen ratios are a useful indicator of the base status of litter and the rates at which organic matter breaks down in the soil. Recent volcanic ash soils generally have low nitrogen content, and consequently high carbon/nitrogen ratios. Our figures for carbon/nitrogen ratios show that red tussock vegetation has significantly slower decomposition rates of litter than manuka or heather vegetation. Despite soil acidification by heather, the carbon/nitrogen ratio suggests litter and humus are rapidly incorporated into the soil. Soil profiles show that heather strongly melanises A horizons. Colonisation of heather shrubland by manuka may slightly improve the base status of soils.

Artificially raised soil nitrogen levels in the Netherlands led to a replacement of heather by grasses. It was further hypothesised there that a heather beetle infestation alone may result in a replacement of heather by grasses. This scenario seems unlikely in New Zealand because native shrubs will eventually outcompete tussock grasses in the vacated habitats.

5.3 SEED BANKS

The dominance of heather in the soil and litter seed banks, with densities of germinable seed approaching 100 000 m², was not surprising, because studies in Britain have shown densities of viable heather seeds approaching 1 000 000 m². The heather seed was very limited above Taranaki Falls at 1300 m, probably because the coarse-grained scoria soils fail to retain the fine seed of heather. Only the discontinuous cover of a litter layer, which was dominated by *Racomitrium* moss, contained germinable seed. Despite these results, heather readily establishes in coarse-grained sand and scoria at these altitudes, and many hitherto bare pavements will soon support a low heather shrubland. The absence of native shrub seed in the Rangipo is partly due to the local absence of manuka because of repeated burning of the tussock grasslands.

Although adventive grass seed was important in the trials, grasses are unimportant in the field because they are soon suppressed by taller heather and native shrubs.

5.4 BIOMASS AND REPRODUCTIVE STRATEGY

The main influence on heather biomass is stand age. Mature-degenerate stands of heather with decumbent growth form, and 35-45 years old, generally have high biomass, but this declines with increasing age and a build-up of colonising native shrubs. Pioneer and building-phase stands have increasing biomass, tend to be less than 25 years of age, and are concentrated above 1250 m on gravelfields and stonefields and in red tussock grassland of the Rangipo.

The estimates of above ground biomass of heather presented here are substantially greater than those reported by Chapman from similar sites (1984:176). For many sites the present estimates are an order of magnitude

greater. Part of the difference may be due to heather representing a greater proportion of the total vegetation in this study than 10 years ago. But this cannot account for all the difference, because Chapman's total vegetation biomass figures are all less than one half the present estimates, and the present figures are exclusive of native plants.

The reproductive strategy of heather differs with stand age, stand growth form, and biomass. Invasive populations and those with rapid population growth have abundant recruitment by seed germination, while older, high-biomass stands regenerate vegetatively. This is a reflection of resource partitioning, as available light and soil nutrient resources alter with vegetation change. Vegetative reproduction is mostly from the root crown, and the nutrient reserves of degenerate plants are able to support extension growth of basal shoots until they reach incident light at the stand canopy. High light conditions in red tussock grassland at Rangipo and on subalpine gravelfields and stonefields permit abundant seed regeneration of heather.

5.5 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

Despite germinable seed banks of 100 000 m⁻², the number of new seedlings occurring after total harvesting and clipping of heather was low. Root competition is a major constraint on seedling recruitment in the wild.

Total removal of aerial shoots and clipping of green shoots failed to kill heather plants. Just as undisturbed stands of mature heather regenerate principally by basal resprout, fully harvested and clipped stands retain this biological response to defoliation. This is the dominant stand renewal process in clipped stands with high biomass, and points to the likely response of mature communities on the lower ringplain with predominantly decumbent growth forms and abundant woody stems. Although clipped stems in high biomass stands showed little resprout within the 18 month trial period, and woody stems are expected to decompose slowly, basal resprout is still expected to perpetuate heather within these plots. In more open vegetation both basal resprout and new seedlings are contributing to heather regeneration.

The absence of new seedlings of native shrubs in cleared and clipped plots was not unexpected in terms of the short monitoring interval. A release response of residual and colonising natives will only be detectable 3-5 years after the removal or clipping of heather, because of the relatively slow growth rates of woody species in this environment. The presence of germinable seed of native shrubs in the seed banks and abundant emergent native shrubs in heather shrubland testify to the invasive capacity of native shrubs irrespective of the stand structure and edaphic variation of heather communities. In Britain, heather shrubland hosts invasive Scot's pine, juniper, and birch among other species.

It is difficult to predict whether heather beetles will remain at a site after an initial defoliation and continue to target regenerating heather. Defoliation and regeneration could operate as a temporal and spatial patchwork in the

landscape, perhaps all the while enhancing the invasion of native shrubs and trees.

5.6 SUCCESSIONAL ROLE OF HEATHER

We can compare the present models estimating the role of heather in secondary vegetation on the northern ringplain to similar models of rates of invasion of native shrubs in red tussock grasslands without heather on the Rangipo depression (Rogers & Leathwick (in press). Heather initially colonises red tussock grassland more quickly than monoao, manuka, and kanuka. However, 40 years after burning, the cover of native shrubs is comparable in both landscapes. We conclude that while heather has a greater capacity to colonise and rapidly suppress red tussock, the medium and long-term population growth of native shrubs in these secondary landscapes is not inhibited by heather shrubland. There is a strong geographical correlation between the pattern of burning in the last 40 years and the area of red tussock grassland smothered by heather. Landscapes not burnt in the last 40-60 years now support manukainaka shrubland and, although heather has invaded this shrubland, it is slowly being suppressed with the closure of a taller native woody canopy. The timeframe for change presented here applies to topographical sideslopes and crests with freedraining soils. On frosty hollows and high-watertable sites, heather will only slowly decline, because these are suboptimal sites for heather and rates of return of poor-drainage-tolerant shrubs and trees are slow. Heather may never be competitively excluded, because a low open forest will always contain microhabitats for heather. For instance, we expect heather to remain at low levels on the poorly drained deforested sites around Mt Hauhungatahi for many decades.

Models of secondary vegetation change on the lower ringplain apply to the zone where manuka is the dominant native successional species. The subalpine zone above 1250 m has quite different soils, impacts of burning, vegetation communities, and successional changes to those of the zone below. Heather is much less important above 1250 m because:

- 1. The large areas of poorly drained and gleyed soils are edaphically suboptimal for heather.
- 2. The dense ground cover of tanglefern, wirerush, pygmy pine, and several shrubs inhibit the establishment and regeneration of heather.
- 3. Heather arrived comparatively late from its areas of original introduction lower down on the ringplain.
- 4. Winter snowlie and a generally harsher climate reduce heather productivity.
- 5. There is much less 20th century burning acting against light-requiring, pioneer species.

Nevertheless, we expect that heather will expand exponentially on the erosion pavements, and eventually produce a low, but intact, heather shrubland. In turn, heather may function as a nurse for later-successional bog pine, *Olearia nummularifolia*, and mountain toatoa.

6. Interim Recommendations

6.1 HERBICIDES

Overall, Tordon Brushkiller and Roundup produced the best results, but Hi Ester 2,4-D is the most cost effective herbicide for large stands treated by helicopter application. The three application techniques are appropriate for different-sized heather stands and different topography. Helicopter application is cost-effective against extensive stands and in difficult terrain. An example is the extensive strip of heather parallel to State Highway 1 on Army land north of Waiouru. Brushguns are suitable for outlier stands accessible by 4WD vehicles, and mistblowers are suitable for remote and small outlier stands. Helicopter application appears economical for stands greater than 0.5 ha. Total costs using Hi Ester 2,4-D are \$293/ha, comprising \$143/ha for chemical and \$150/ha for helicopter and supervision.

7. Publications or Other Significant Outputs

Expanded results, conclusions, and recommendations will be provided at a heather workshop at Turangi on 19-20 August, 1993.

8. References

Chapman, H.M. 1984: The ecology of heather, *Calluna vulgaris*, in New Zealand; with particular reference to Tongariro National Park. Unpublished Ph. D. thesis, Victoria University of Wellington.

Rogers, G.M.; Leathwick, J.R. 1994: North Island seral tussock grasslands. 2. Autogenic succession: change of tussock grassland to shrubland. New Zealand journal of botany 32: 287-303.