

Control, demography, and post-control response of heather in the central North Island: Part 2

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Abstract

The following aspects of the behaviour of heather (*Calluna vulgaris*) in Tongariro National Park have been studied: the potential for herbicidal control; likely changes in secondary vegetation if biological control is effective; some aspects of its demography; and, finally, whether heather acts to facilitate or impede rates of native shrub invasion of red tussock grassland.

The herbicides Tordon Brushkiller and Escort are effective against heather, but for eradication they must be applied at intervals of less than two years and until the soil seed bank is exhausted. Herbicidal control of heather in Moawhango Ecological District is probably no longer practical.

An outbreak of the heather beetle (*Lochmaea suturalis*) was simulated by removing all aerial tissue of heather or by clipping green foliage only, while leaving native plants untouched. However, given the virtual impossibility of accurately simulating beetle defoliation of heather and the comparatively short time frame for the experiment, the conclusions should be treated with caution. Both treatments resulted in abundant new seedlings and resprout from root crowns of heather across most communities, except those of very high biomass with dense masses of procumbent stems. Apart from small native grasses and catsear, silver tussock was the only important native species to show a growth release following removal of heather. There was also locally abundant germination of manuka, concentrated at lower altitudes, but not co-dominant inaka. These results and European experience suggest only marginal benefit to native species, particularly invasive shrubs, from beetle defoliation of heather, confined to less than three years after an outbreak of the beetle.

Vegetation change has been modelled in landscapes with and without heather. Heather does restrict the population growth of invasive native shrubs, the effect increasing from only marginal on steeper topography to dramatic on flat topography. Heather biomass is a major influence, the denser stands retarding the establishment of native shrubs. However, there are virtually no areas of heather-dominated secondary vegetation on the northern ringplain below 1200 m a.s.l. where manuka, inaka, or mountain toatoa will not increase at the expense of heather. Nevertheless, heather will remain a conspicuous component of secondary vegetation on the northwestern ringplain for at least another 50 years in the absence of burning, despite the visual balance shifting from predominantly heather to substantially native.

Recruitment of heather shifts in emphasis from seed germination to vegetative resprout with increasing stand age and biomass. Vegetative reproduction may perpetuate indefinitely the life of individual plants in dense stands, compensating for the shade intolerance of new seedlings. Stem diameter is a moderately reliable predictor of stem age for heather under 10 years of age.

Given its procumbent habit, high biomass (relative to that of red tussock grassland), and wide edaphic tolerances in Tongariro National Park, heather is possibly a major threat to the habitats of rare plants of Moawhango Ecological District. That heather may out perform the herbaceous vegetation that dominates many of these sites is clear from the dense procumbent stands at least one metre thick on damp depressions in Tongariro National Park.

1. Introduction

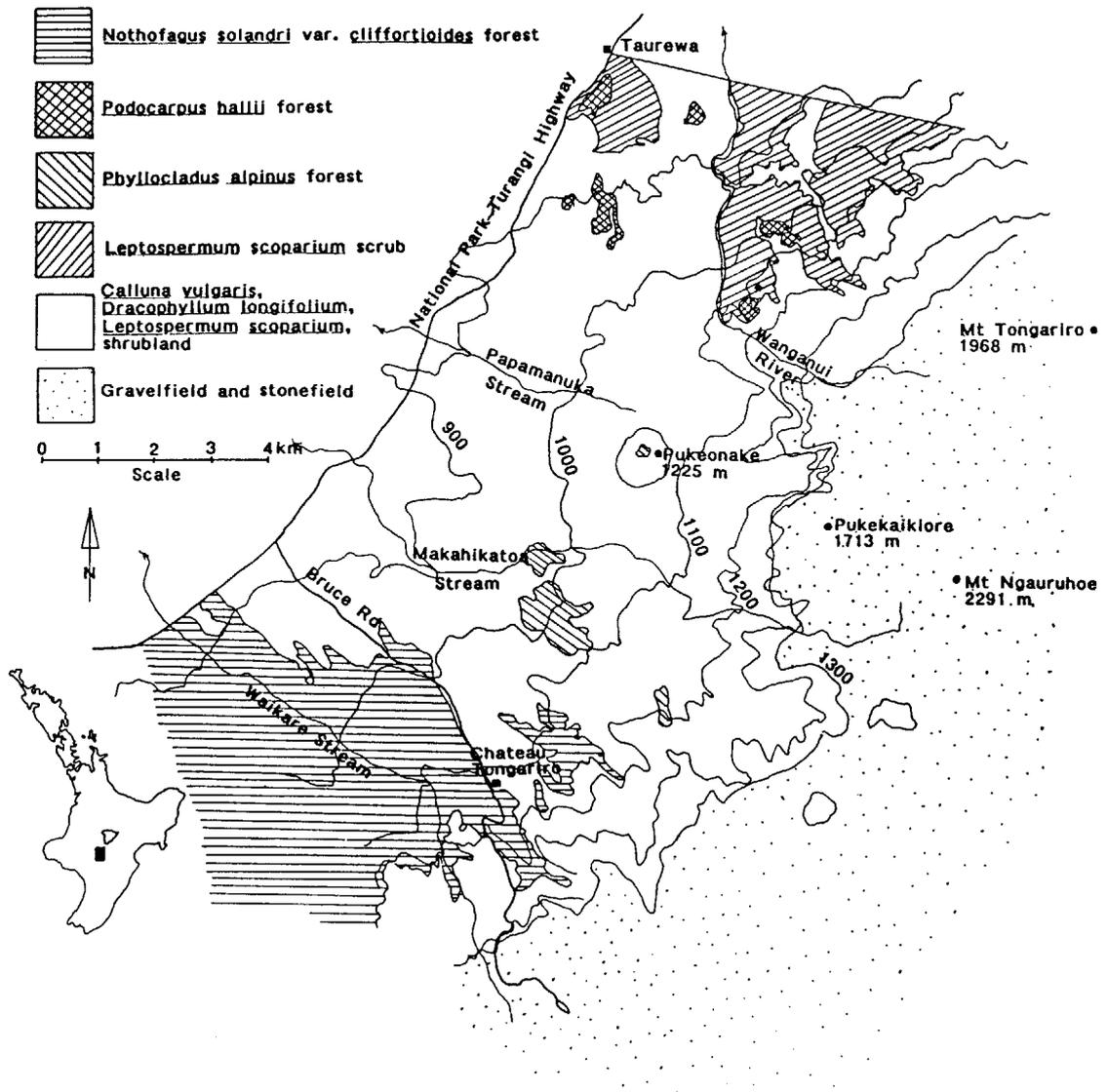
The spread of heather (*Calluna vulgaris*) through central North Island tussock grassland has reduced indigenous species dominance and diversity in both seral and steady-state communities, changed successional trends within seral vegetation, disrupted natural processes in several ecosystems, transformed the landscape of northwestern Tongariro National Park from natural to partly alien, and disrupted recreational and land use opportunities in the National Park and Desert Road area. A management strategy for heather will benefit from an understanding of its role in seral vegetation, its response to herbicides, and the plant communities' possible response to defoliation of heather by the heather beetle, (*Lochmaea suturalis*).

Today, heather is a more or less important component of 52 km² (5200 ha) of secondary shrubland below 1250-1300 m a.s.l. on the northwestern ringplain of Tongariro National Park, stretching from the Waikare Stream in the west to the Wanganui River in the east (Fig. 1). Heather has particularly high biomass on the crests of interfluves; it is less vigorous, but may persist for long periods, on small frosty hollows or damp basin floors, and is being overtopped by native shrubs on steeper sideslopes. The reproductive strategy of heather also seems to vary in response to its biomass and stature. Although most vegetation below 1250 m on the northwestern ringplain has abundant heather, it is a comparatively minor component of the subalpine vegetation above.

Chapman & Bannister (1990, 1994) studied the vulnerability of various indigenous open vegetation to the spread of heather, and demonstrated its competitive invasive properties from 850 to 1600 m in tussock grassland, shrub-tussock grassland, herbfield, open scoria slopes, and bogland. However, concerning their widespread "Calluna-dominated tussock or heathland community" they remarked "There is evidence for the invasion of this community by native shrubs such as *Leptospermum scoparium* and *Dracophyllum filifolium* (probably synonymous with *D. longifolium*), and in the absence of fire it will probably revert to native shrubland. Seedlings of manuka become established under dense *Calluna* and eventually overtop it." The influence of heather on rates of change in transitions from native tussock grassland to native shrubland requires investigation because, depending upon its performance, its status in seral vegetation could be variously viewed as disruptive, benign, or complementary.

To understand the patterns of heather in secondary vegetation, models have been prepared of the rates of heather invasion of tussock grassland, the role environmental and disturbance factors have on that process and, in turn, how heather influences the rates of invasion of native shrubs into red tussock grassland. To address the latter question, models of native shrub invasion of tussock grasslands on the northeastern ringplain at Rangipo (Rogers & Leathwick 1994), an area where heather is rare, can be compared with models from heather-rich communities on the northwestern ringplain. The Rangipo depression is the closest ecologically equivalent environment to the

FIGURE 1 LOCATION AND VEGETATION OF THE STUDY SITE ON THE NORTHERN RINGPLAIN OF TONGARIRO NATIONAL PARK, CENTRAL NORTH ISLAND. THE PRESENT VEGETATION PATTERN IS MODIFIED AFTER ATKINSON (1981).



northwestern ringplain. Landforms, altitude, and soil parent materials are similar, but Rangipo differs in having drier and sunnier summer weather.

Hand-pulling and herbicides are the traditional modes of control of heather in areas where it has recently arrived, or where it threatens special and restricted ecosystems. A lot of control work has been undertaken without any systematic evaluation of the effectiveness of various herbicides or of appropriate methods of application. In collaboration with Dow-Elanco and the Manawatu-Wanganui Regional Council, I assessed the efficiency of a range of chemicals supplied by Monsanto and Dow-Elanco, using a range of applicators.

The Department of Conservation has been investigating biological control as the most practical technique for containment of heather in Tongariro National Park (Williams & Keys 1994). Defoliation by an introduced beetle is hoped to either debilitate or kill heather plants in extensive stands, but the effect of the beetle

can not be accurately predicted. Although the beetle can disperse, it may be less effective in small isolated stands, thus favouring the competitive expression of native plants. A range of community-level responses to this induced disturbance is likely depending upon the population structure and biomass of heather, the composition and structure of the native community, and the role of environmental factors in the growth performance of both heather and natives. The possible community response to an outbreak of the heather beetle can be investigated by either completely removing or just defoliating heather in small plots, while leaving natives unaffected, and monitoring for two years, but reliable simulations of biocontrol are very difficult to achieve.

N.B. Results of work towards several of the objectives listed below were outlined in a previous report (Rogers 1995, Science for Conservation: 9) and in the proceedings of the second heather control workshop (Williams & Keys 1994).

2. Objectives

- To test the effectiveness of selective herbicides on heather.
- To predict the initial and medium-term response of heather, tussock grasses, and shrubs to biological control of heather.
- To determine whether heather inhibits or allows successional development to native shrubland and forest, and at what rate.
- To comment on the potential for managing the heather community in secondary landscapes and in non-forest sites.

3. Methods

3.1 HERBICIDE TRIALS

Herbicides for heather control were trialled 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 of the herbicides are Dow-Elanco products and selective for woody species, not grasses or forbs. The broad-spectrum herbicides Escort and Roundup, manufactured by Monsanto, were included to assess the survival of native tussocks and herbs and the non-target damage to woody natives. Three techniques for applying chemicals were trialled: helicopter, gun and hose, and mist-blower. The various techniques will each be appropriate for different-sized stands of heather and access conditions. Sizes of trial plots were: aerial, 1 ha; brushgun, 5 x 10 m; and mistblower, 5 x 5 m. The plots were monitored for a minimum of 12 months after chemical application. One hundred frequency

counts centred on a heather plant in each plot recorded 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 did not assess the seasonal effectiveness of herbicides.

Tordon Brushkiller, the most encouraging herbicide from the first trial (Rogers 1995), was reapplied by helicopter to three 1-ha plots in March 1993 to assess its effectiveness on surviving heather and on newly germinated seedlings.

3.2 SOIL AND LITTER SEED BANKS

The composition of soil and litter seed banks was assessed in germination trials of samples of litter and the top 5 cm of soil from 21 sites spanning a range of altitudes and stand ages of heather. The samples were incubated under greenhouse conditions for 18 months. Seedlings were removed at 3-month intervals and the soil was 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 biological control of heather.

3.3 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

An outbreak of heather beetle was simulated by completely removing the entire standing crop of heather from 64 1-m² plots, and by removing green shoots only of heather in another 64 plots. Resident native plants were left intact. Heather was completely harvested by clipping stems at ground level, and green shoots were removed by clipping stems just below green foliage, which is concentrated at shoot ends. The waste was removed from the site. Monitoring the response of heather involved measuring the frequency of resprout from root crowns and the germination of new seed 30 months after treatment. The foliar diameter and height of resident native plants were recorded in the 64 cleared plots and monitored 30 months after treatment. Germination of new native plants was recorded in the cleared plots, again, 30 months after treatment. Plot placement covered the key environmental gradients and differences in the demographic age, stature, biomass, and cover of heather. Of the two harvesting techniques, clipping green shoots probably offers the best simulation of a population irruption of heather beetle. The ideal simulation would be harvesting leaf tissue only and allowing decomposition of the foliage on site, but I consider clipping a good approximation within the resource limitations of the experiment.

3.4 HEATHER DEMOGRAPHY

The biomass and demographic structure of heather were also sampled from the 64 1-m² plots cleared of heather in 3.3 above. The standing crop of heather was carefully removed by clipping at ground level (whilst isolating resident native plants), oven dried for 10 days at 38°C, and weighed. The longest stems from a sample of at least seven individual plants per plot were selected for measurement of basal stem diameter, stem length, and stem age. The number of heather seedlings in each plot was also recorded. Seedlings were plants less than 30 cm long derived from seed and not those originating from root crowns as basal resprout.

3.5 SUCCESSIONAL ROLE OF HEATHER

The cover of heather and the rates of spread of native shrubs through heather were compared with the rates of spread of native shrubs through tussock grassland without heather in adjoining landscapes at Rangipo. The study sites were between the Whakapapaiti Stream and the Wanganui River on the northwestern ringplain (Fig. 1) and around the Waihohonu and Ohinepango streams at Rangipo. Transects and plots were placed subjectively to sample a range of combinations of environmental factors suspected of influencing native shrub and heather invasion of the tussock grasslands. Environmental factors investigated were time since the last burn, altitude, slope, and topographic position. The topographic classes were crest, sideslope, and basin floor, the latter characterised by frost inversion and/or poor drainage. Time since the last burn was estimated from the fire record as deduced from aerial photographs, from the oldest shrubs sampled within the vicinity of each plot, and from Tongariro National Park file records. Vegetation was sampled in 20 x 10 m plots on the northwestern ringplain from the toeslope at 850 m to upper-slopes at 1320 m a.s.l. At Rangipo, altitude was not included as an environmental factor because the entire sample space fell within 940-960 m a.s.l. There were a total of 72 plots spanning a secondary vegetation age range of 23-75 years on the northwestern ringplain, and 57 plots spanning 6-95 years at Rangipo.

The point-height intercept method of Park (1973) was used to sample vegetation. For this analysis only canopy surface intercepts of species and ground cover where arboreal vegetation was missing were used, rather than the vegetation intercepts in the vertical space of each sight. In addition, basal discs or increment cores were prepared from the range of stem sizes of the important indigenous shrubs in the vicinity of each plot to determine their age range. These discs were used to investigate the establishment ages of shrubs in different seral vegetation and to relate stem age to stem diameter.

Analyses of relationships between species canopy cover and height and environmental factors were examined using the non-parametric regression technique of Generalised Additive Models (GAMS - Hastie & Tibshirani 1990, Yee & Mitchell 1991).

The role of heather in non-forest ecosystems, both above the regional treeline and on sites with a high water table, was assessed by observation only.

The age structure of the dominant native shrubs - manuka and inaka, was sampled to assess their rate of arrival in heather-dominant shrubland on two sites. Basal discs or increment cores were prepared from the largest stem of all individuals greater than 20 cm tall of both species, in 10 randomly located 1-m² plots, on each of three topographical classes in 45-year-old seral vegetation at 900 and 1100 m a.s.l.

3.6 SOIL CHEMISTRY

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

4. Results

4.1 HERBICIDE TRIALS

Results of the trials have been reported in Rogers (1995). A re-application by helicopter of Tordon Brushkiller in March 1993 on three of the existing 1-ha plots produced almost complete control of the adult heather plants surviving the first application and the new generation of seedlings arising from the first treatment (G. Rogers unpubl. data). However, the overwhelming impression from a visual inspection in February 1995 of these re-treated plots and the remainder of the trials is of abundant germination of new seedlings from the soil seed bank in all plots. Seedling abundance appears to be unrelated to the level of herbicide control of the adult stand, and generally is sufficient to replace the original heather stands at comparable or even greater initial density.

4.2 SOIL AND LITTER SEED BANKS

Results from soil and litter seed bank trials have been reported in Rogers (1995).

TABLE 2 SIGNIFICANCE AND SIGN OF THE TREND OF LINEAR REGRESSION MODELS FOR DENSITY OF SEEDLINGS AND BASAL RESPROUT OF HEATHER (SQUARE ROOT TRANSFORMATION) AGAINST ENVIRONMENTAL FACTORS AND VEGETATION PARAMETERS 30 MONTHS AFTER CLEARANCE AND CLIPPING OF HEATHER. SIGNIFICANT P VALUES LESS THAN 0.05 ARE SHOWN; NS, NOT SIGNIFICANT,

RESPONSE VARIABLE	SLOPE	ALTITUDE	TIME SINCE LAST BURN	BIOMASS OF HEATHER
Seedlings in cleared plots	ns	ns	ns	ns
Resprout in cleared plots	ns	ns	P=0.0203, -ve	ns
Seedlings in clipped plots	ns	ns	P<0.0001, -ve	P=0.0004, -ve
Resprout in clipped plots	ns	ns	ns	P=0.011, -ve

TABLE 3 SIGNIFICANT INCREASES AND DECREASES IN MEAN FOLIAR DIAMETER AND HEIGHT OF RESIDENT NATIVE SPECIES 30 MONTHS AFTER CLEARANCE OF HEATHER. SIGNIFICANT P VALUES FROM A ONE-WAY ANOVA COMPARISON OF MEANS ARE SHOWN, WITH > DENOTING AN INCREASE AND < A DECREASE IN THE GROWTH FACTOR.

SITE	TOPOGRAPHIC POSITION	SPECIES	FOLIAR DIAMETER	FOLIAR HEIGHT
Lower Bruce Rd	sideslope	silver tussock	>0.0001	>0.0001
Lower Mangatepopo Rd	crest	inaka	>0.01	
Mid Mangatepopo Rd	crest	manuka	<0.009	
	sideslope	manuka	<0.049	
		red tussock		<0.008
	hollow	red tussock		<0.035
Upper Mangatepopo Rd	crest	manuka	<0.02	
	hollow	Dracophyllum recurvum	<0.039	>0.032
		red tussock		<0.001
		silver tussock	>0.0001	>0.0001
Rangipo	crest	hard tussock		>0.0001

TABLE 4 MEAN NUMBER OF SEEDLINGS (PER M²) IN PLOTS CLEARED AND CLIPPED (SEPARATED BY "/") OF HEATHER AT SEVEN SITES 30 MONTHS AFTER TREATMENT. ERECT SHRUBS ARE MAINLY MANUKA AND INAKA, PROSTRATE SHRUBS MAINLY COPROSMA CHEESEMANII, NATIVE GRASSES MAINLY DEYEUXIA AVENOIDES AND HIEROCHLOE REDOLENS, TUSSOCKS MAINLY SILVER AND RED TUSSOCK, AND ADVENTIVE GRASSES AND HERBS (MAINLY CATSEAR).

SITE	ERECT SHRUBS	PROSTRATE SHRUBS	NATIVE GRASSES	TUSSOCKS	ADVENTIVE GRASSES AND HERBS
Lower Bruce Rd	13.1/1.9	0.2 / -	16,4 /1.2	1.4 / 0.1	1.3 / 0.3
Lower Mangatepopo Rd	8.6 / 2.4	- / 2.0	11 / 3.5		18.8 / 3.1
Mid Mangatepopo Rd	1.4 / 0.2	- / 0.9	0.1 / -		2.0 / 0.6
Upper Mangatepopo Rd	1.3 / 0.8			1.5 / 0.05	
Pukekaikiore	- / 1.7	0.5 / -		0.2 / -	
Taranaki Falls		0.1 / -			
Rangipo				1.9 /0.1	

TABLE 5 SIGNIFICANCE OF LINEAR REGRESSION MODELS FOR DENSITY OF HEATHER SEEDLINGS AGAINST ENVIRONMENTAL FACTORS AND VEGETATION PARAMETERS.

PREDICTOR VARIABLE	SIGNIFICANCE	F-RATIO	SIGN OF COEFFICIENT
Topographic position	ns		
Solar radiation	ns		
Slope	ns		
Altitude	P=0.0101	7.03	-ve
Time since last burn	P<0.0001	41.9	-ve
Heather biomass	P<0.0001	17.1	-ve
Heather cover	P<0.0001	49.6	-ve
Heather height	P<0.0001	39.6	-ve

4.3 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

Response of heather

New seedlings and basal resprout from root crowns of heather abounded in both the cleared and clipped plots (Table 1). There were also consistently more seedlings and generally more resprouts in cleared plots than in clipped plots. However, resprouts outnumbered seedlings in the mature to degenerate stands clipped of heather foliage. The density of seedlings and of resprouted crowns declined significantly with the age of the vegetation and the biomass of heather (Table 2). The environmental variables slope and altitude (surrogates for solar radiation and temperature) are not useful predictors of the regeneration response of heather to harvesting.

Response of native species

There were few significant increases or decreases in the foliar diameter and height of resident native species 30 months after heather was cleared from the 64 plots (Table 3). On rare occasions, the foliar diameter of inaka and manuka declined, as did the foliar height of red tussock. Only silver tussock (*Poa cita*) showed a consistent positive growth response to the release treatment. However, overall, tussocks are now unimportant in established heather communities on the northwestern ringplain.

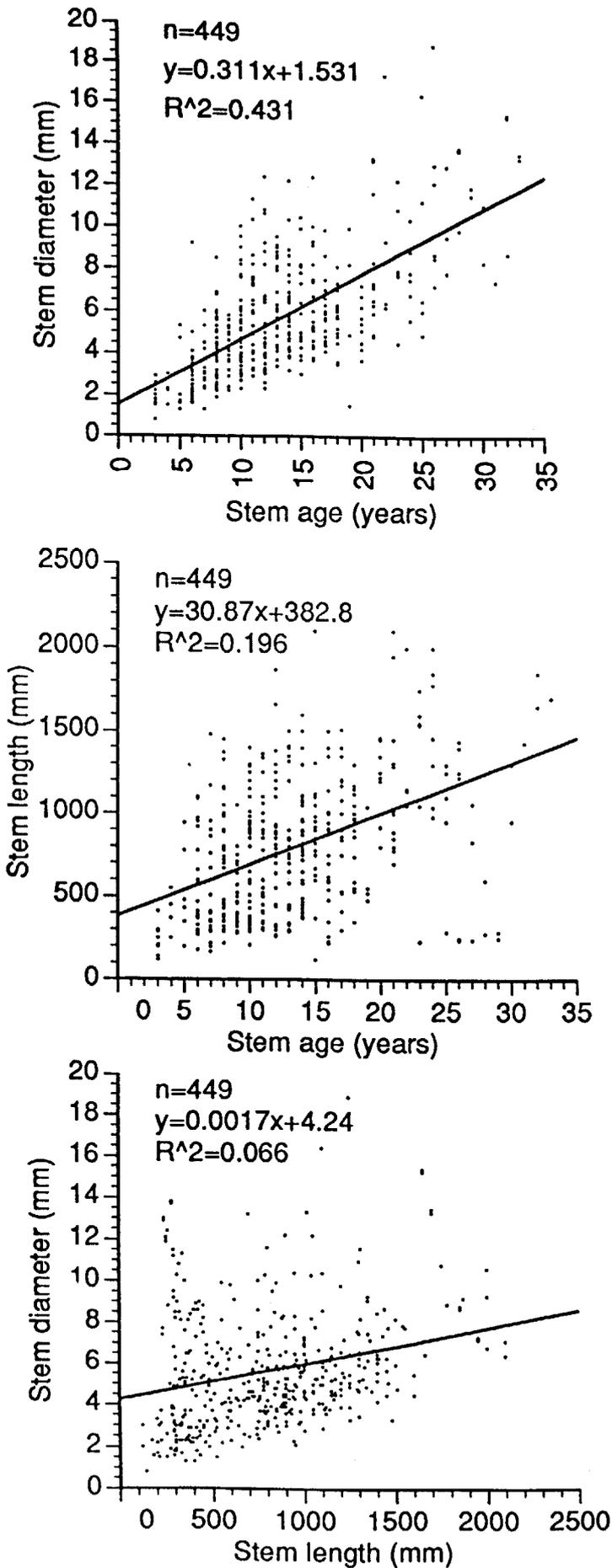
The generally limited, although varied, numbers of seedlings of native plants 30 months after clearing and clipping of heather were concentrated in the lower-altitude plots (Table 4). In general there were more seedlings of each plant class in cleared than in clipped plots. Seedlings of all plant classes were rare in plots located on basin floors, where dense layers of moss and frost inversion may have inhibited establishment. There was high inter-plot variability in seedling establishment at each site, despite a comparatively uniform distribution of seed sources and also ground establishment conditions. Manuka dominated the erect shrub class, and seedlings of inaka were rare. New seedlings of all plant classes were rare in young stands of heather above Taranaki Falls and in the Rangipo, although there appeared to be abundant local seed sources.

4.4 HEATHER DEMOGRAPHY

Reproduction

The density of heather seedlings decreased significantly with the cover, height, and biomass of heather in secondary vegetation, with altitude, and with time since the last burn (Table 5), to the point where seedlings are virtually absent in mature and degenerate stands with dense masses of procumbent stems (Table 1). Alternatively, stands in the pioneer-building phase have abundant seedlings, pointing to a shift from seed germination to vegetative resprout with increasing stand age and biomass. Vegetative reproduction may perpetuate indefinitely the life of individual plants in dense stands, compensating for the shade intolerance

FIGURE 2 SIMPLE REGRESSIONS BETWEEN STEM AGE, STEM LENGTH, AND STEM DIAMETER OF HEATHER SAMPLED IN 64 PLOTS ON THE NORTH-WESTERN RINGPLAIN OF TONGARORO NATIONAL PARK.



of new seedlings. Seedling density was generally less on sideslopes than on crests and basin floors, probably reflecting inhospitable establishment conditions beneath the dense cover of native shrubs on steep slopes.

Heather age structure

Stands of heather in the pioneer-building phase colonising at high altitude and in the Rangipo had clumped or cohort distributions of stem age, but high-biomass stands of heather had more uneven age distributions reflecting irregular gap-phase recruitment. Individual stems of heather may reach 32 years of age at Tongariro (Fig. 2), although vegetative resprout may advance the life of individual plants by several generations. Stem diameter is a moderately useful predictor of stem age for heather; the relationship is quite reliable for stems under 10 years of age, but for stems over 10 years of age the relationship deteriorates (Fig. 2). There was a poor relationship between stem age and stem length and between stem length and stem diameter (Fig. 2). This variation is not only due to plants passing through four distinct architectural phases in their lives; variations in the stature and availability of resources also elicit a highly plastic growth response. Communities of low density and low stature develop short, stout, semi-erect stems, while high-density communities develop thin, elongated, and procumbent stems. Unthrifty plants on poorly drained sites commonly develop thin, elongated stems.

4.5 SUCCESSIONAL ROLE OF HEATHER

GAM regressions

Further refinement of the logistic regression models of successional trends in heather on the northwestern ringplain reported in Rogers (1995) has been made possible with the recent development of generalised additive models (GAM). Additional sampling of seral vegetation without heather at Rangipo has also permitted comparisons between the two landscapes superior to those in Rogers (1993).

Regression fits were compiled for dominant species and species groups (Appendix) using GAM regression techniques. The factor "time since last burn" consistently provided highly significant reductions in deviance. Relationships with time since last burn are therefore presented for different combinations of altitude and topographic position for the northwestern ringplain, and for topographic position only at Rangipo, where the study area falls within one narrow altitudinal range.

Northwestern ringplain - cover

The fits for heather indicate that the species reaches its maximum cover earlier than the start of the models at 23 years on all topographical and altitudinal positions in the landscape (Fig. 3). In contrast, the dominant erect native shrubs manuka (*Leptospermum scoparium*) and inaka (*Dracophyllum longifolium*)

FIGURE 3 RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND TIME SINCE THE LAST FIRE AT 900 M A.S.L. ON THE NORTHWESTERN RINGPLAIN OF TONGARIRO NATIONAL PARK, AS FITTED BY GAM REGRESSIONS. TOPOGRAPHIC CLASSES ARE A AND D, SIDESLOPE; B AND E, CREST; C AND F, BASIN FLOOR. SPECIES ARE: CALLUNA, HEATHER; LEPTOSPERMUM, MANUKA; DRACOPHYLLUM, INAKA; CHIONOCHLOA, RED TUSSOCK.

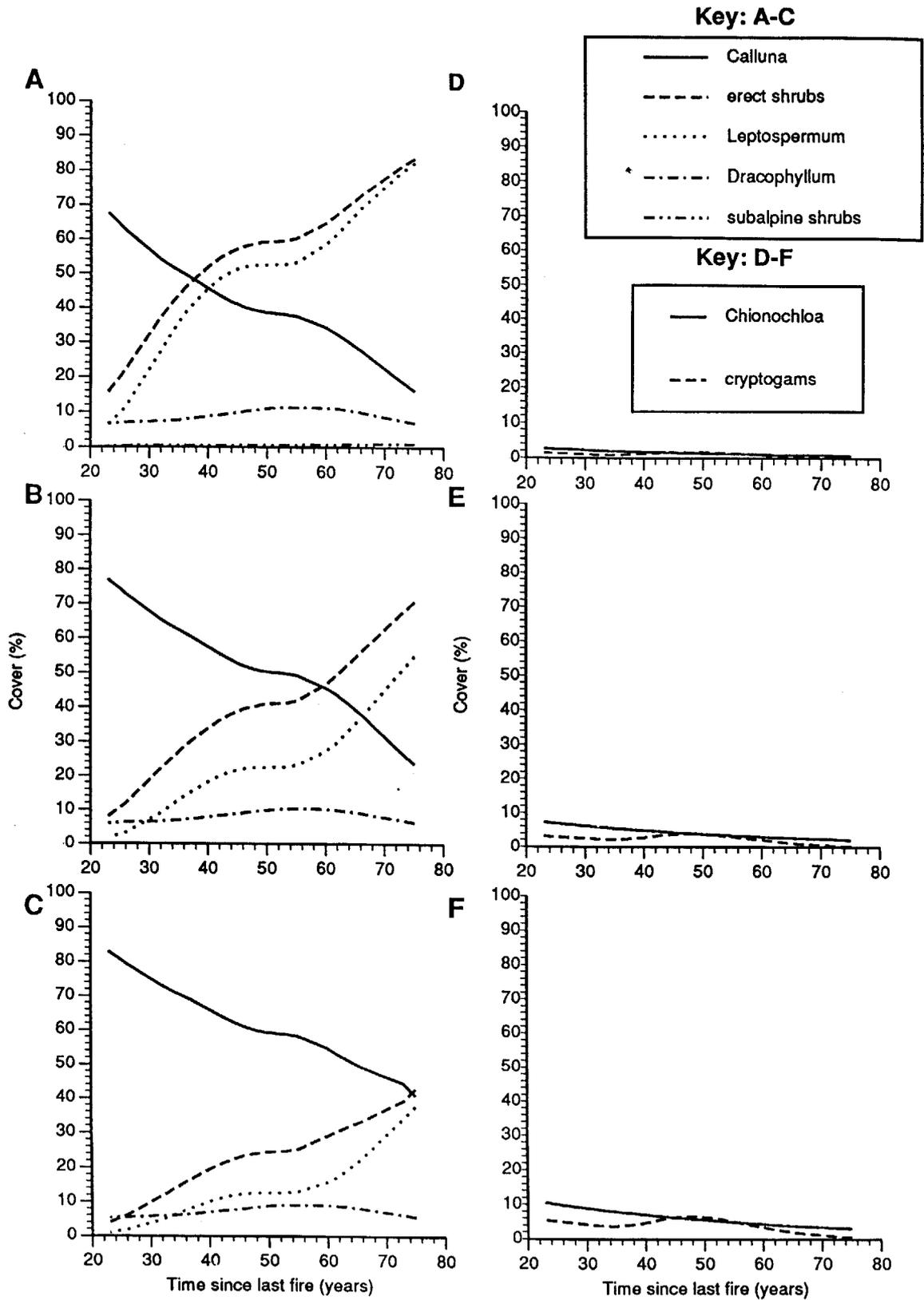
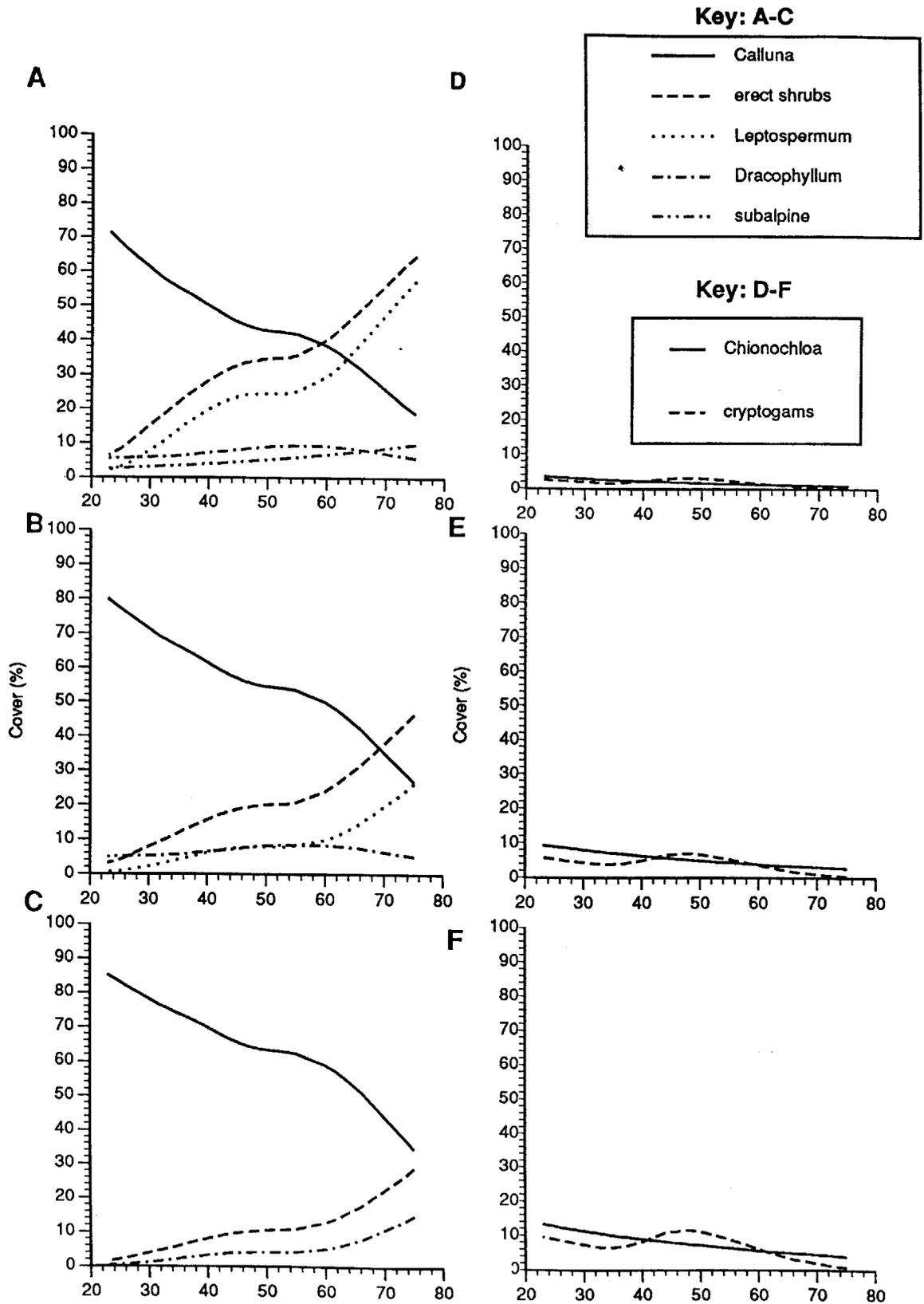


FIGURE 4 RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND TIME SINCE THE LAST FIRE AT 1100 M A.S.L. ON THE NORTHWESTERN RINGPLAIN OF TONGARIRO NATIONAL PARK, AS FITTED BY GAM REGRESSIONS. TOPOGRAPHIC CLASSES ARE A AND D, SIDESLOPE; B AND E, CREST; C AND F, BASIN FLOOR. SPECIES ARE: CALLUNA, HEATHER; LEPTOSPERMUM, MANUKA; DRACOPHYLLUM, INAKA; CHIONOCHLOA, RED TUSSOCK.



increase with time for all combinations of slope, topography, and altitude. Inaka and manuka have similar cover as invasive shrubs early in seral vegetation, but while manuka increases throughout, inaka changes little from approximately 10% cover in most landscape positions (Fig. 3). Only on basin floors at 1100 m does inaka increase (Fig. 4), reflecting its adaptation to cool, wet subalpine conditions (Rogers 1994). Plants of small stature such as cryptogams and prostrate shrubs are physiognomically unimportant at 900 m, as is red tussock (*Chionochloa rubra*), and all decline over time to less than 5% cover at 75 years. However, cryptogams and red tussock have at least 20% crown cover on basin floors at 1100 m (Fig. 4). Subalpine shrubs are unimportant in seral vegetation at 900 m, but at 1100 m (still below the regional treeline) increase to approximately 10% cover after 75 years.

The inverse relationship between heather and erect native shrubs varies with altitude, slope, and topographic position: heather declines fastest on sideslopes in competition with the native shrubs, but reaches its highest cover and persists as the dominant species on basin floors throughout the altitudinal range of the study area. On average, erect native shrubs attain the cover of heather at 37 years on sideslopes and after 60 years on crests; they just equal the cover of heather 75 years after fire on basin floors. Whereas heather has consistently high cover in early seral vegetation at all altitudes, manuka is less a generalist and is much less competitive at higher altitudes. At 1100 m, manuka exceeds heather within 75 years only on sideslopes, and on basin floors it is largely absent. Monoao (*Dracophyllum subulatum*) and *Cassinia vauvilliersii* are important invasive shrubs only very locally on basin floors, and neither is modelled.

Northwestern ringplain - height

On the lower slopes of the ringplain the dominant native shrubs are on average taller than heather on all topographical classes and at most stages of vegetation change (Fig. 5A-C). However, for the first 25 years on basin floors heather is taller than manuka, but not inaka. On sideslopes and crests manuka and inaka have similar stature until late in successions, when manuka increases sharply. On basin floors manuka is not only a minor component of vegetation but it has shorter stature than inaka throughout the succession.

The situation is somewhat different higher up on the ringplain where heather is only slightly shorter than erect native shrubs for the first 50-60 years (Fig. 5D-F). The mean height of native shrubs and heather varies little on the three topographic classes. Part of the gradual increase in height of heather results from its semi-lianoid growth form: it is supported by taller emergent native shrubs.

Rangipo - cover

Prostrate shrubs, cryptogams, and red tussock dominate early vegetation change at Rangipo, but all are exceeded by erect native shrubs within 20-25 years (Fig. 6A-C). After 50 years, red tussock is a minor component of vegetation on sideslopes and crests, but, it persists at greater levels on basin floors where it is still at 20% cover after 40 years. Cryptogams are equally important on all three

FIGURE 5 RELATIONSHIPS BETWEEN CANOPY HEIGHT AND TIME SINCE THE LAST FIRE AT TWO ALTITUDES ON THE NORTHWESTERN RINGPLAIN OF TONGARIRO NATIONAL PARK, AS FITTED BY GAM REGRESSIONS. TOPOGRAPHIC CLASSES ARE A, SIDESLOPE AT 900 M; B, CREST AT 900 M; C, BASIN FLOOR AT 900 M; D, SIDESLOPE AT 1100 M; E, CREST AT 1100 M; F, BASIN FLOOR AT 1100 M. SPECIES ARE: CALLUNA, HEATHER; LEPTOSPERMUM, MANUKA; DRACOPHYLLUM, INAKA; CHIONOCHLOA, RED TUSSOCK.

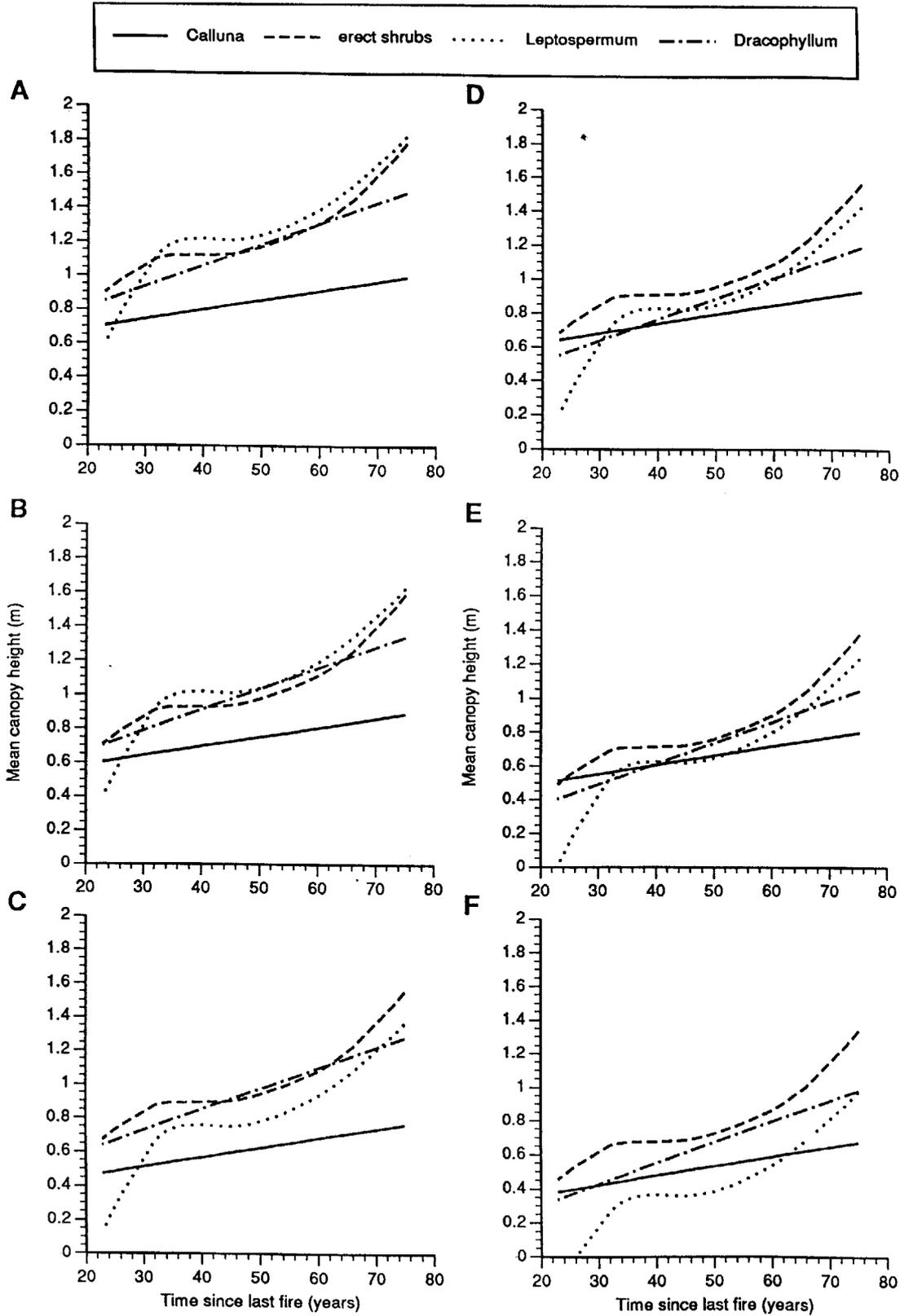
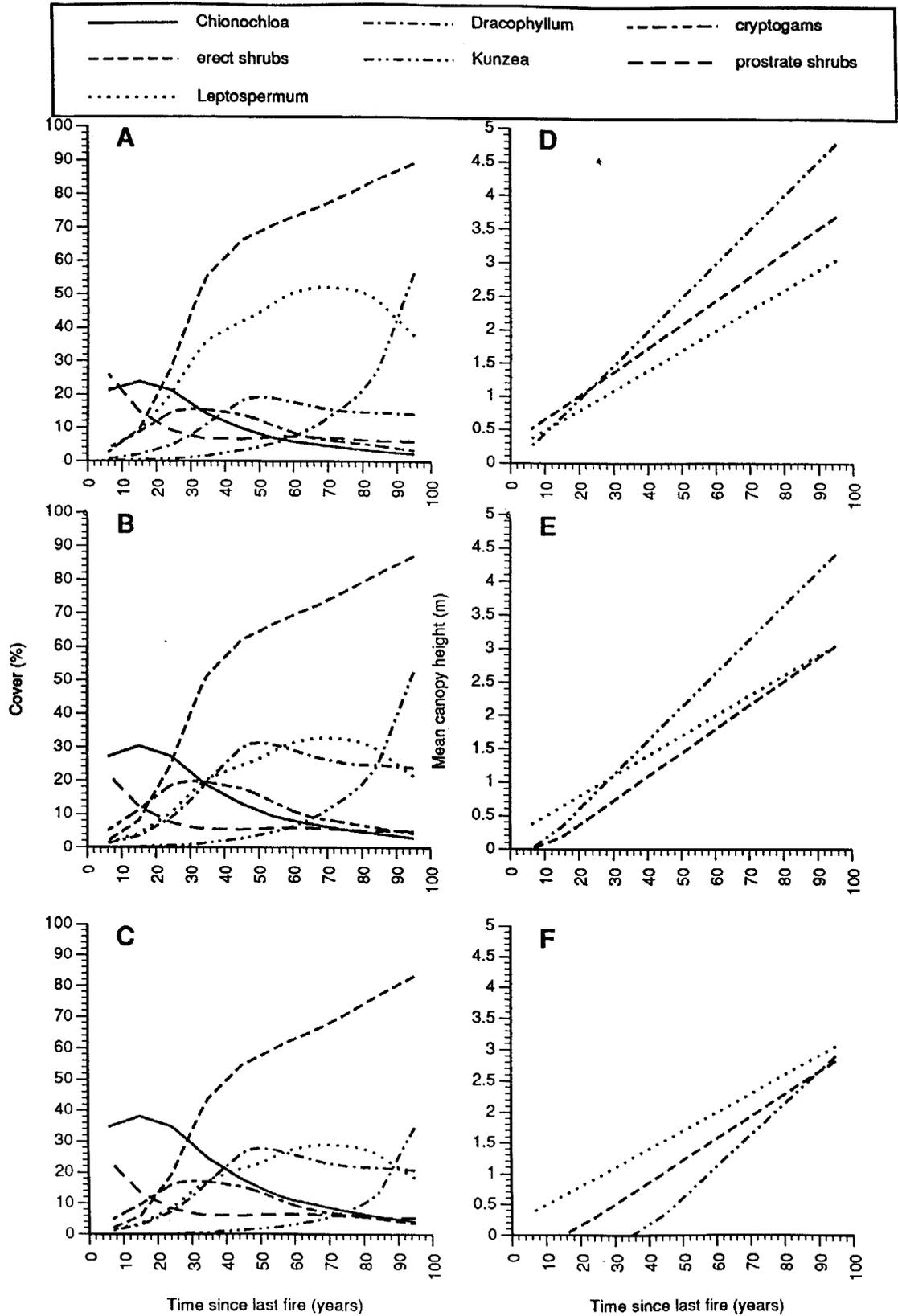


FIGURE 6 RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND CANOPY HEIGHT AND TIME SINCE THE LAST FIRE AT RANGIPO ON THE NORTHEASTERN RINGPLAIN OF TONGARIRO NATIONAL PARK, AS FITTED BY GAM REGRESSIONS. TOPOGRAPHIC CLASSES ARE A AND D, SIDESLOPE; B AND E, CREST; C AND F, BASIN FLOOR. SPECIES ARE: CHIONOCHLOA, RED TUSSOCK; LEPTOSPERMUM, MANUKA; DRACOPHYLLUM, INAKA; KUNZEA, KANUKA.



topographic classes, and on crests persist at 20% cover after 30 years. Monoao, manuka, and kanuka (*Kunzea ericoides*) dominate the erect shrubs, but with different topographical and temporal performances. Monoao and manuka dominate for the first 60 years, with manuka rapidly eclipsing monoao on sideslopes, but the two have equal performance on the gentler slopes of crests and basin floors. Kanuka is at low levels early in successions, increasing above 10% cover only after 60 years on sideslopes and crests and after 80 years on basin floors. However, within 80-90 years kanuka dominates erect shrubs on all parts of the landscape. Monoao reaches a peak within 40-50 years on all sites and then slowly declines in competition with taller manuka and kanuka. Manuka declines slightly later in successions in response to overtopping by kanuka.

Rangipo - height

At Rangipo, erect shrubs, manuka, and kanuka had linear fits for mean canopy height (Fig. 6D-F). Whereas kanuka has superior height growth to manuka on sideslopes and crests, the opposite applies on basin floors. Manuka does not show the wide variation in height growth performance on different topographies evident for kanuka. Monoao had no significant fits with the environmental or time factors.

Cover comparison

A comparison can be made between the cover of erect shrubs, manuka, and the two dracophyllums (inaka with monoao) at the two study sites (Fig. 7A-C). Sideslopes are the only topographic class on the northwestern ringplain where the cover of erect shrubs is similar to that at Rangipo at a comparable time after disturbance. On crests and basin floors of the northwestern ringplain erect shrubs have approximately 10-25% and 35% less cover respectively than at Rangipo at a similar time. The cover of manuka is similar on sideslopes and crests at both sites until about 60 years, when the species declines rapidly at Rangipo in competition with emergent kanuka. Monoao at Rangipo has substantially greater cover than inaka on the northwestern ringplain, particularly on the gentle slopes of crests and basin floors.

Height comparison

There were no significant fits for monoao at Rangipo, and height growth comparisons were restricted to erect shrubs and manuka (Fig. 7D-F). Both manuka and erect shrubs at Rangipo have height growth superior to that on all parts of the landscape on the northwestern ringplain. After 75 years this superior canopy height amounts to 0.75-1.25 m over all altitudinal and topographic classes. Faster height growth of erect shrubs at Rangipo is partly due to the rapid appearance late in successions of kanuka, and its absence on the northwestern ringplain.

Ages of invasive native shrubs

The density and ages of native shrubs provide insights into their invasive behaviour in 45-year-old heather shrubland at 900 m and 1100 m near the Mangatepopo Road. There is a short delay of 5-10 years after burning before native shrubs establish in number within heather shrubland on crests and sideslopes at both altitudes (Fig. 8). A distinct pulse of arrival occurs on sideslopes and, slightly later on crests, but there is no apparent establishment pulse on hollows. Both manuka and inaka are important on crests, but inaka is less important on sideslopes and manuka is less important on basin floors. There was no significant difference in the total density of shrubs between crests and sideslopes at both altitudes, but there was a significant difference between crests and sideslopes on the one hand and basin floors on the other at both altitudes.

4.6 SOIL CHEMISTRY

The pH, carbon and nitrogen content, and carbon/nitrogen ratio of soils beneath red tussock grassland, manuka shrubland, and heather shrubland have been reported in Rogers (1995).

5. Conclusions

5.1 HERBICIDE TRIALS

Several herbicides are effective against heather. However, the problem of enhanced germination and establishment of new generations of seedlings in response to elevated irradiance at ground level and reduced root competition presents a real management dilemma. The maximum period of seed viability within litter and soil is unclear, but seed bank germination trials indicate that it exceeds two years. Given that two-year-old plants are reproductively mature (Rogers 1995), herbicide application intervals greater than two years will not substantially reduce the regeneration potential of heather in soil and litter seed banks. The rationale for treatment intervals greater than two years would have been enhanced access and penetration of the chemical to new seedlings through the decomposing standing crop of heather, but the reproductive phenology negates this. Herbicides effective against heather and non-toxic to grasses, such as Tordon Brushkiller and Escort, can therefore be recommended only if biennial application is undertaken before seed set (preferably December), until the resident seed bank is exhausted.

The scale of heather infestation of red tussock grassland in the Army Training Group (ATG) land at Waiouru is such that conventional herbicide control now appears to be prohibitively expensive, even when restricted to outlier populations. N. Mickleson (pers. comm., 1994) estimated \$22 500 per annum using helicopter and mistblower application of Tordon Brushkiller for initial

FIGURE 7 COMPARISON OF RELATIONSHIPS BETWEEN SPECIES CANOPY COVER AND CANOPY HEIGHT AND TIME SINCE THE LAST FIRE ON THE NORTHWESTERN RINGPLAIN AND NORTHEASTERN RINGPLAIN AT TONGARIRO NATIONAL PARK, AS FITTED BY GAM REGRESSIONS. TOPOGRAPHIC COMPARISONS ARE A AND D, SIDESLOPE; B AND E, CREST; C AND F, BASIN FLOOR. SPECIES ARE: LEPTOSPERMUM, MANUKA; DRACOPHYLLUM, INAKA.

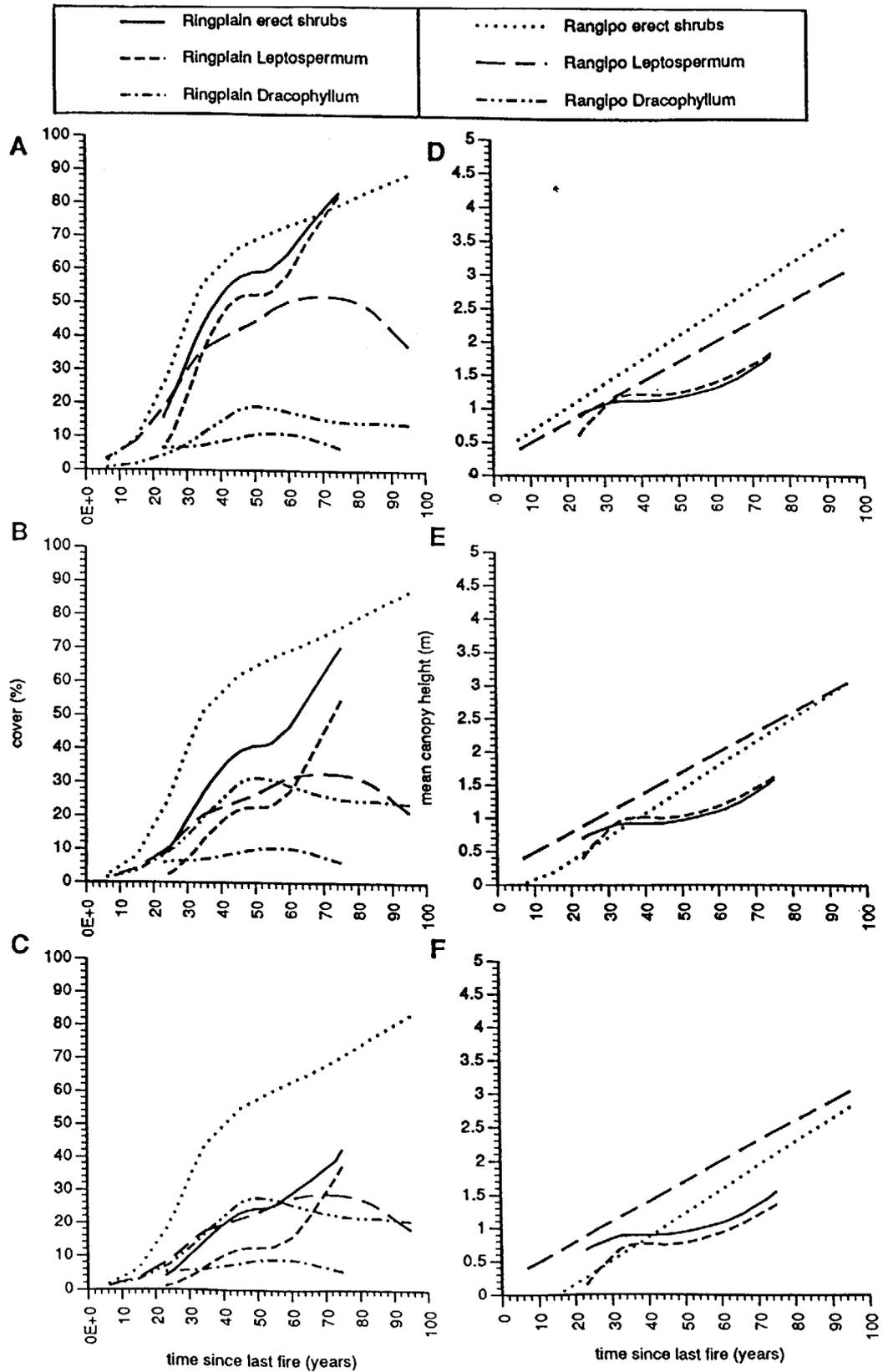
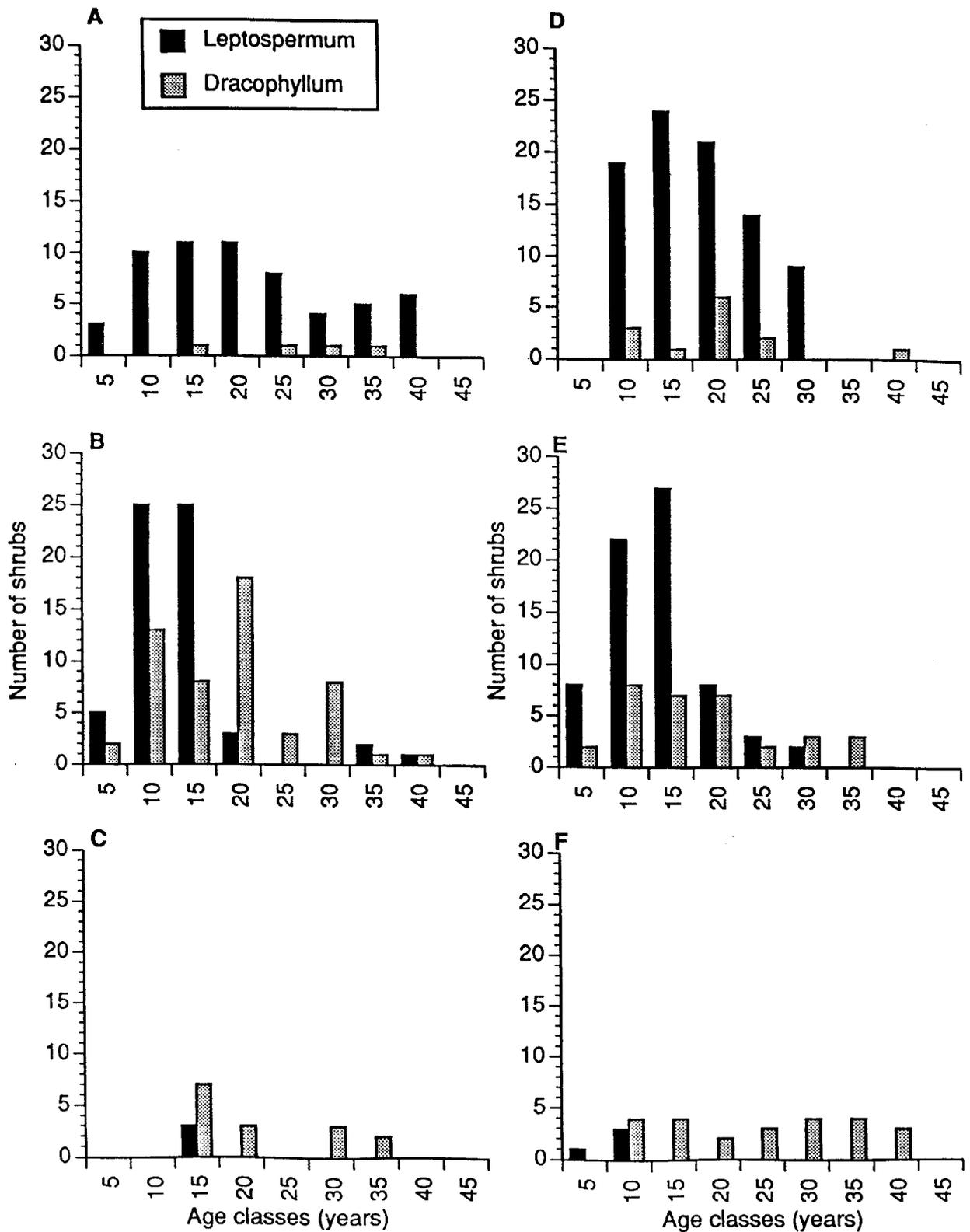


FIGURE 8 AGE CLASS DISTRIBUTIONS OF LEPTOSPERMUM (MANUKA) AND DRACOPHYLLUM (INAKA) IN 45-YEAR-OLD HEATHER-DOMINATED SHRUBLAND ON THE NORTHWESTERN RINGPLAIN OF TONGARIRO NATIONAL PARK. A, SIDESLOPE AT 900 M; B, CREST AT 900 M; C, BASIN FLOOR AT 900 M; D, SIDESLOPE AT 1100 M; E, CREST AT 1100 M; F, BASIN FLOOR AT 1100 M.



control of all outlier stands covering 1250 ha in the ATG area. The magnitude of the problem and the time commitment to address it suggest that a multiagency, co-ordinated approach is required to at least contain the spread of heather through the last extensive area of red tussock grassland in the North Island.

5.2 SIMULATION OF BIOLOGICAL CONTROL AND COMMUNITY RESPONSE

Response of heather

Simulation of an outbreak of heather beetle solicited a more sluggish response of heather seedlings and resprout than was suggested to be likely by the soil and litter seed bank experiments, which had seed density up to 100 000 m² (Rogers 1995). Root competition may be a major constraint on seedling recruitment in the wild. Seedlings and resprout were also much less in clipped plots than in cleared plots, indicating that irradiance and soil nutrients control the germination of heather. However, recruitment at even the lowest average density of 9 plants per m² is probably adequate for stand replacement at present densities of heather in most parts of the landscape. The exceptions to a high frequency of seedlings and resprout of heather were degenerate stands with dense masses of procumbent stems on poorly drained crests and basin floors. Seedlings of native plants were infrequent on these plots pointing to a possible period of plant community inertia following an outbreak of the beetle.

Prolonged presence of heather beetle in a defoliated site would act against seedling and resprout regeneration. Nevertheless, given that heather seed is viable for more than two years, delayed rejuvenation of a heather stand is likely in the short to medium term if the insect populations are resource-limited and consequently vacate the site.

Few pioneer-mature plants of heather were killed outright by either total harvesting or clipping green foliage. In Britain, older stands are the most affected by outbreaks of the beetle, and their recovery is slowest relative to either young stands or stands with an uneven age structure. Directional succession to birch woodland is accelerated in these stands. Thus, if we assume that clipping and (the more extreme) clearing are functional simulations of beetle defoliation, the results of this study agree with observations in Britain that pioneer-early mature heather is often resilient to insect herbivory. Uneven age structures characterise older, high-biomass stands, which are concentrated at lower altitudes in the zone where heather was originally liberated. More even age structures predominate in young stands where populations are increasing. The beetles are therefore likely to produce their greatest effect at low altitude, where the more vulnerable stands are concentrated.

Response of native species

Apart from small native grasses and catsear, silver tussock responded most positively to the removal of heather by abundant but patchy germination. In this regard, silver tussock parallels the behaviour of the grass *Deschampsia flexuosa* in Europe and Britain in commonly invading beetle-defoliated stands. Any

resurgence of silver tussock is expected to be shortlived, however, given the predicted rapid recruitment of heather. Other later successional species in the Northern Hemisphere benefitting from the death of heather are bracken, juniper, Scots pine, and two birch species. Enhanced invasion is mainly confined to the three years after collapse, declining as heather recovers. In Europe, outbreaks of the beetle operate over tens of square metres or more. Beetles disperse away from food-depleted areas in spring, thus producing a patch mosaic of defoliation. Increased nutrient availability through soil mineralisation of nitrogen from larval faeces and a subsequent foliar nutrient boost for heather intensifies rates of defoliation of heather. It is difficult to predict any shifts in community composition or changes in successional direction or timing with increased soil nitrogen at Tongariro without controlled experimentation. In broad terms, soil nitrogen is a limiting macroelement in leached soils in New Zealand, and this applies at Tongariro National Park. I suggest that such a eutrophication process may impact equally favourably upon the establishment and growth of native woody species and the regeneration of heather.

At Tongariro, the absence of a growth release for later successional species and only low numbers of their seedlings in cleared and clipped plots suggest that beetle-debilitated heather may only marginally, if at all, advantage invasion of native shrubs. The sluggish response and even reduced foliar profiles of native shrubs 30 months after removal of heather may result from physiological adjustment to increased exposure. It seems, even at the scale of the 1 m² plots, that closed shrubland ameliorates weather extremes. Even dead stems of heather may ameliorate ground microclimates and enhance conditions for seedling establishment. The benefits of enhanced invasion of shrubs, both native and heather, may therefore be restricted to a short period following heather defoliation and preceding the next generation of heather. Invasion by trees and shrubs in Britain does not occur in dense mature heather; rather, it is confined to bared areas and the two phases in which competition from heather is weakest - pioneer and degenerate phases. At Tongariro, gap creation by beetle defoliation in stands with dense masses of procumbent stems may not enhance invasion by native shrubs because only canopy gaps - not ground gaps - will be created. Defoliation and regeneration of heather could operate as a temporal and spatial patchwork in the landscape, perhaps all the while providing only small invasion benefits to native shrubs and trees.

Finally, in its invasive behaviour in tussock grassland and in many life history traits, heather has some equivalence to *monoa*, the dracophyllum adapted to cold, infertile, open basins of the central North Island. Both are early colonisers of tussock grassland, and in turn host taller, later successional, woody species (Rogers & Leathwick 1994). The comparison diverges in the bimodal reproductive strategy of heather as against the total reliance on seed reproduction of *monoa*. Vegetative resprout permits a more rapid recovery from disturbance, particularly burning, than recovery reliant on seed alone.

5.3 HEATHER DEMOGRAPHY

Certain biological traits have equipped heather for successful invasion of low-statured vegetation - high reproductive rates, short generation time, long-range seed dispersal, phenotypic plasticity, and wide ecological tolerance. Many of these factors are r-traits; however, a plastic reproductive strategy equips the species for k-persistence. The reproductive strategy differs with stand age, plant growth form, and biomass. Plants of invasive populations within low-statured vegetation and exposed to low within-stand competition regenerate by seed, while older, high-biomass stands regenerate vegetatively. Thus, resource partitioning alters as available light and soil nutrient resources change with vegetation development. A reproductive strategy of small, easily dispersed seed with low carbohydrate reserves assists a colonising role, but constrains a seedling's chances of attaining the canopy through a dense mass of overlying stems in mature-degenerate stands. On the other hand, the nutrient reserves of degenerate plants support prolonged extension growth of basal shoots up through compact overlying vegetation. In Europe and Britain, procumbent stems of heather commonly develop adventitious roots and epicormic shoots. In contrast, basal resprout from root crowns predominates at Tongariro.

On depressions infilled with well drained, infertile Taupo Pumice, individual heather and monoao often die without any local regeneration. The resulting clear areas beneath dead plants suggest rapid depletion of soil nutrient reserves from just one generation of woody vegetation. Damp depressions, on the other hand, promote development of sandy loams, vigorous heather with high biomass, stems up to 3 m long, and prolific regeneration.

Heather reproduces freely by seed at 1325 m a.s.l., as evidenced by concentric recruitment of seedlings around isolated plants in low herbfields, mosslands, and gravelfields. Viable seed may be produced at even higher altitudes, but this was not investigated.

5.4 SUCCESSIONAL ROLE OF HEATHER

Red tussock grassland and heather invasion

The pattern of previously dominant red tussock on the northwestern ringplain (Atkinson 1981) was largely determined by late Maori and European burning of secondary vegetation, interrupting the inexorable vegetation change from tussock grassland to shrubland as modeled elsewhere in the central North Island by Rogers & Leathwick (1994). An extensive fire on the lower ringplain c. 1959 (Sheridan 1972) was the last important influence on the pattern of red tussock grassland and, consequently, upon the susceptibility to invasion of secondary vegetation by heather. In essence, heather has colonised all early seral vegetation arising from 20th century burning on the northwestern ringplain. The vulnerability of the tussock growth form to colonisation by heather, and the benefits of fire to germination and seedling establishment of heather are evident today at Waihohonu in the Rangipo depression. For example, an invasive, pioneer population of heather within red tussock

grassland, burnt 6 years ago, has mean cover of 72% (G. Rogers, unpubl. data). Attributes of small seed size, abundant seed production, and a persistent seed bank are a highly successful strategy for at least two heath invaders in New Zealand, *Erica lusitanica* (Spanish heath) (Mather & Williams 1990) and heather. Each fire enhances the competitive advantage of established heather over tussocks and native shrubs, the former slower to recover than heather (Chapman & Bannister 1990), the latter quite unadapted to fire. Only on basin floors and the even frostier or wetter valley hollows does red tussock persist as a physiognomically important species, but at levels mostly less than 10% cover.

However, above 1200 m a.s.l. heather has yet to realise its full potential, and will continue its spread and population growth as it expands from local outliers and from its lower-altitude liberation zone. Seed and flower dispersal distances up to at least 1 km have been demonstrated for heather in Britain, and isolated outliers of heather throughout western Moawhango Ecological District point to at least these distances for wind dispersal in New Zealand. Long-distance dispersal of seed from the abundant seed source on the lower ringplain to the subalpine-alpine zone above will aid population growth there.

The susceptibility of the two soil/vegetation units of this upper montane-subalpine zone differ widely. The large areas of poorly drained and gleyed soils capping lava flows on gentler slopes, and supporting dense tanglefern, wirerush, pygmy pine, and several shrubs, are edaphically suboptimal for heather. There, heather shows limited recruitment and spread from its infrequent establishment loci, and individual plants often senesce without local recruitment. On the alternative gravelfields and stonefields (Atkinson 1981), many of which result from erosion and stripping of overlying gleyed soils, heather establishes readily and expands exponentially with little limitation from edaphic constraints or vegetation competition. On these pavements heather outperforms native plants in stabilising the coarse-textured volcanic debris.

The spread of native shrubs through heather

The models of secondary vegetation change on the lower ringplain apply to the zone below 1200 m a.s.l., that area where heather was deliberately introduced and where it now approaches its full expression in seral vegetation. This altitude is also the boundary between the more gentle topography of the lower lahar ringplain and the steeper flanks of the volcanoes above. Manuka, the co-dominant native shrub of the northwestern ringplain, also has an approximate altitudinal limit of 1200 m. The complex mosaic of seral vegetation on the lower ringplain owes most of its variation to the patterns of fires which largely ceased 35 years ago, to the influence of the environmental gradients altitude (a surrogate for temperature and rainfall variations), topography, and soil drainage, and to the relative vulnerability of native communities to colonisation by heather. Using GAMS (see p10), I have attempted to partition this landscape variation into discrete topographical and temporal units, in order to begin to understand the complex relationships between heather and the native shrubs so conspicuously invading it.

GAM regression models for red tussock, native shrubs, and heather in terms of time since the last fire, topography, and altitude are anything but uniform. On sideslopes at lower altitudes, manuka and inaka colonise heather quite rapidly,

are somewhat slower on crests, and are slowest on basin floors, particularly those with impeded drainage and cold air inversion. On sideslopes, the combined cover of manuka and inaka exceeds that of heather 38 years after burning. On the more extensive crests it takes nearly 60 years for native shrubs to dominate, and on basin floors heather will dominate for at least 75 years. At higher altitudes, the times for this transformation are nearly doubled. Manuka is excluded from frosty basins, but not so inaka, which has greater resistance to ground frosts, especially those in early summer. Although the models point to native shrubs outcompeting heather in all parts of the landscape, heather will persist as an important canopy component on all sites for at least 80 years. Vertical growth rates of manuka and inaka enable them to overtop heather early in successions at lower altitudes, but at higher altitudes they have no clear height advantage until after 40 years.

A further 50 years without burning will see the landscape character on the lower ringplain shift from heather dominance to native shrub dominance. The proportion of each topographical class in various parts of the landscape will strongly influence the visual balance between alien and indigenous vegetation. Crests and basins dominate the topography to 1100 m and, in combination with the extensive area burnt around the Mangatepopo Road in the late 1950s, will ensure that heather remains conspicuous there. One such area is the extensive depression surrounding Pukeonake Stream south of the Mangatepopo Road. There also appear to be no seed source limitations to the spread of manuka and inaka within any catchment or interfluvium, and dispersal distance does not appear to limit their establishment densities in red tussock grassland elsewhere in the central North Island (Rogers & Leathwick 1994).

Age structures of manuka and inaka within established 45-year-old heather communities indicate their ready establishment within pioneer-mature heather communities, despite inherently low irradiance levels within the understory. Heather biomass probably peaks well before 45 years, yet native shrubs have continued to establish on all three topographic classes throughout this phase. Somewhat truncated age distributions of native shrubs on crests and sideslopes probably signal the end of an establishment cohort as canopy closure of the more structurally complex community inhibits further seedling recruitment. However, a closed canopy of native shrubs has yet to develop on any basin floor previously dominated by heather.

If heather does not deflect vegetation changes away from their natural developmental pathways, does it influence the rates of change? A comparison with secondary vegetation at Rangipo suggests that, rather than demonstrating nurse-crop behaviour, heather apparently retards the population growth of native shrubs in open vegetation. This retardation amounts to only about 5 years on sideslopes for an equivalent cover of shrubs. On crests the delay extends to 25 years in intermediate stages of successions, but in the longer term there is no difference between rates of invasion of native shrubs. On basin floors the average delay extends to 40 years. Longer delays in the population growth of native shrubs occur at higher altitudes on the northwestern ringplain. Heather also appears to retard the height growth of emergent shrubs on the northwestern ringplain and, in particular, the height growth of manuka.

Heather has to a small extent invaded the understorey of established native shrubland and even scrub-low forest, but its influence on pathways to successional maturity is expected to be minor, and will decrease with increasing structural complexity of these woody communities. Its presence there is also assumed to have little affected total plant and community diversity. Several other authors have noted a decline in the susceptibility to invasion of communities with increasing successional status.

In summary, heather does restrict the population growth of invasive native shrubs, the effect increasing from only marginal on steeper topography to dramatic on the flat. In Britain and Europe it is generally accepted that invasion by trees and shrubs does not occur in dense mature heather, but rather is confined to pioneer and degenerate communities. At Tongariro, although native shrubs colonise heather on all topographies, the process of invasion is also regulated by heather biomass and form, with shrubs comparatively rare in dense procumbent stands.

Heather will remain a conspicuous component of secondary vegetation on the northwestern ringplain for at least another 50 years, despite the landscape balance shifting from predominantly heather to substantially native.

Long-term vegetation trends

Although mountain toatoa is poorly represented as an emergent tree above heather and native shrubs, long-term vegetation change will progress towards a reconstitution of mountain toatoa-dominated forest. Indications of this trend surround relict islands of forest on the lower ringplain, where the density of bird-dispersed mountain toatoa in secondary vegetation diminishes radially from its seed source. Mountain beech was largely eliminated from the northern ringplain by the Taupo Pumice eruption. Palynological evidence shows that mountain toatoa forests recolonised the study area after that eruption, with subsequent removal through burning by Maori 600 years ago. Thus, relict forests of coniferous mountain toatoa and Hall's totara in the study area (Fig. 1) successional precede mountain beech in the long-term biogeographical adjustment of vegetation to forest clearance by pyroclastic ash flow.

5.5 THREAT TO SPECIAL COMMUNITIES OF MOAWHANGO ECOLOGICAL DISTRICT

Most of the biogeographically special plants of Moawhango Ecological District occur in non-forest sites where tall forest is excluded by high watertables and frost inversion. Rare plants occur in intermontane basins and plateaux of the Moawhango and Taruarau rivers and the Mangaohane plateau. The diverse range of habitats involved primarily reflects variations in edaphic conditions, spanning the range from arid gravel levees to oligotrophic peat bogs and stream banks. Most of these sites are potential heather habitat. The question is - will heather modify the microhabitat conditions of the rare plants any differently from that of the native shrubs and low trees previously important and now reinvading after removal by anthropogenic burning? Given its procumbent habit, high biomass, and wide edaphic tolerances in Tongariro National Park, heather

will exceed the resource capture performance of native woody species that originally dominated the habitats of rare plants of Moawhango Ecological District. A detailed analysis of habitat vulnerability should be undertaken now, as heather rapidly invades the district.

6. Recommendations

Herbicide control. The two most effective herbicides against heather that are non-toxic to grasses are Tordon Brushkiller and Escort. Their use can be recommended only if: (a) biennial or even shorter treatment periods are undertaken; (b) seasonal treatment occurs before seed maturation (preferably December); and (c) the resident seed bank is exhausted. The scale of heather infestation of red tussock grassland in the Army Training Group (ATG) land at Waiouru is such that a multi-agency, coordinated approach is required to at least contain its spread through the last extensive area of red tussock grassland in the North Island.

Heather above 1200 m. Heather has high potential to dominate the unconsolidated landscapes above approximately 1200 m a.s.l. on the northwestern ringplain, and those of virtually the entire eastern ringplain to 1600 m a.s.l. The performance and persistence of heather there under different edaphic and climatic constraints is largely unknown, and requires investigation.

Moawhango Ecological District. Heather will inevitably spread through the red tussock-dominated landscapes east of the Desert Road and threaten several rare plant habitats. The vulnerability of individual rare plant habitats requires investigation.

7. Acknowledgements

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9. Appendix 1: Species included in the amalgamated cover and height classes by plant physiognomy

NORTHWESTERN RINGPLAIN

Indigenous erect shrubs: *Cassinia vauvilliersii*, *Coprosma* sp. (t) (Eagle 1982), *Dracophyllum longifolium*, *D. subulatum*, *Leptospermum scoparium*, and *Phyllocladus alpinus*.

Indigenous subalpine shrubs: *Dracophyllum recurvum*, *Epacids alpina*, *Halocarpus bidwillii*, *Hebe odora*, *H. venustula*, *Lepidothamnus laxifolius*, and *Olearia nummularifolia*.

Indigenous prostrate shrubs: *Coprosma cheesemaniae*, *Coprosma perpusilla*, *Gaultheria colensoi*, *Gaultheria depressa* var. *novae-zelandiae*, *Leucopogon fraseri*, and *Muehlenbeckia axillaris*.

RANGIPO

Indigenous erect shrubs: *Cassinia vauvilliersii*, *Coprosma* sp. (t) (Eagle 1982), *Dracophyllum subulatum*, *Hebe venustula*, *Kunzea ericoides*, *Leptospermum scoparium*, and *Phyllocladus alpinus*.

Indigenous prostrate shrubs: *Coprosma cheesemaniae*, *Coprosma perpusilla*, *Gaultheria colensoi*, *Gaultheria depressa* var. *novae-zelandiae*, *Leucopogon fraseri*, and *Muehlenbeckia axillaris*.