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## Succession after fire in alpine vegetation on Mount Wellington, Tasmania

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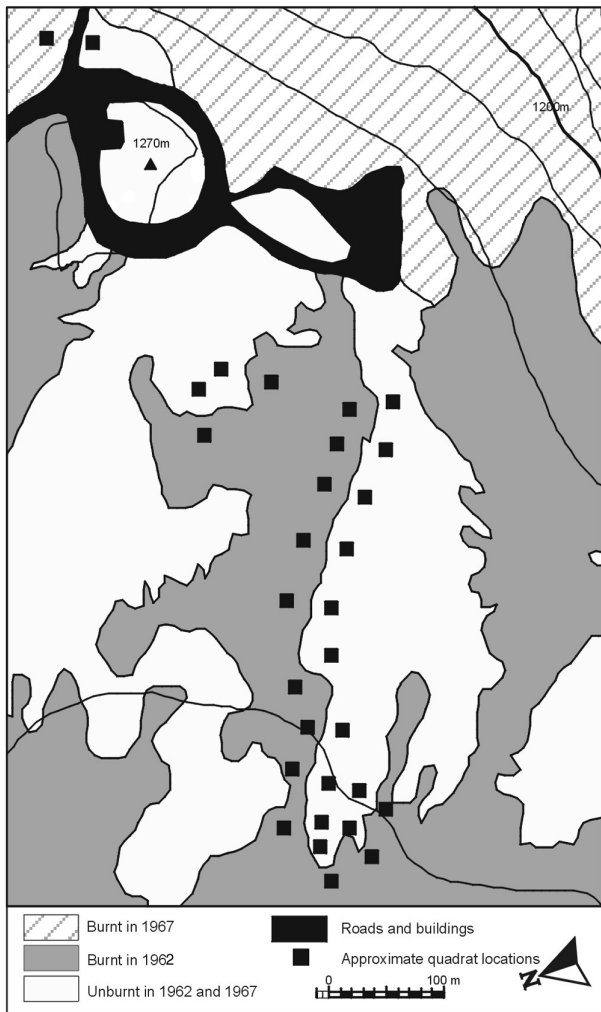
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**Abstract.** The vegetation on either side of fire boundaries in the alpine zone of Mount Wellington, Tasmania, was surveyed in 1978 and 1998. This combination of spatial and temporal sampling gave data for 16, 31, 36 and 51 years since burning. These data were used to test for convergence in vegetation characteristics through time between the areas burned in 1947 and those burned in 1962 and to determine whether lifeform is a reasonable predictor of the successional dynamics of species. While convergence largely prevailed, some lifeforms and species diverged and lifeform was generally a poor predictor of species responses. For example, size class analyses of the larger shrub species indicated a wide variety of successional responses to fire. The tall shrubs on Mt Wellington have higher percentages of tolerators and species relying on the soil seed store for postfire regeneration than physiognomically similar vegetation in more fire-prone environments. Fifty-one years after fire, there is evidence of continuing floristic and structural change in the alpine vegetation that may be partly related to recent climatic warming.

### Introduction

There are relatively few temporal studies of succession after disturbance in alpine and/or tundra vegetation. Examples of such work relate to recovery from mechanical disturbance (Bayfield 1980; Chapin and Shaver 1981; Roxburgh *et al.* 1988; Harper and Kershaw 1996) and recovery from stock grazing (Wimbush and Costin 1979; Williams and Ashton 1987; Williams 1990; Wahren *et al.* 1994; Bridle and Kirkpatrick 1999). The only temporal studies that we know of that have relevance to succession after fire in alpine vegetation are those reported by Wardle (1991) for subalpine grasslands at Arthurs Pass in New Zealand and that of Wahren and Walsh (2000) for subalpine treeless vegetation at Mount Buffalo, Victoria. There have been several spatial studies in alpine vegetation (e.g. Douglas and Ballard 1971; Kirkpatrick and Dickinson 1984). As predicted by Billings (1973), vegetation recovery after disturbance in alpine vegetation has proven to be a slow process, not least after fire. In Tasmania, areas burned 11–40 years before data collection had vegetation that bore little resemblance to adjacent unburned vegetation, with considerable bare ground and depleted surface-soil nutrient and organic-carbon stocks (Kirkpatrick and Dickinson 1984). The impacts of fires appeared greatest in the relatively infertile and highly humid western mountains of the state and least on the relatively dry and fertile Mount Wellington (Kirkpatrick and Dickinson 1984).

The alpine vegetation of Tasmania is globally unusual in that it is largely dominated by small and hard-leaved shrubs (Kirkpatrick 1997). In this physiognomic characteristic it is more akin to the Mediterranean climate heathlands and shrublands than to the normally herb- and/or grass-dominated alpine vegetation found elsewhere in the world. Fire has not been a frequent disturbance in Tasmanian alpine environments (Kirkpatrick 1997), in contrast to the high fire frequencies characteristic of Mediterranean heathlands and shrublands, such as the fynbos (van Wilgen *et al.* 1992). In these non-alpine heathlands and shrublands, the shrub species possess adaptations that promote survival after fire. A large proportion tends to be vegetative recoverers and/or have canopy-stored seed, or have persistent seed banks. Relatively few species are ‘tolerant’ or ‘requiring’ *sensu* Noble and Slatyer (1980), rather falling into the ‘intolerant’ class, establishing only after disturbance. Consequently, succession largely fits the initial floristic composition model of Egler (1954), rather than the Clementsian relay floristics model. We could expect that Tasmanian alpine shrubs would include a greater proportion of species able to establish independently of disturbance (tolerant) or requiring the establishment of other species after disturbance before being able to establish (requiring) than in the fire-prone lowland communities, as potentially very long intervals between fires would favour species not dependent on major disturbance for their establishment.



**Fig. 1.** Locations of the paired plots and areas burned at different dates on Mt Wellington.

In the present paper we present both spatial and temporal data on succession in alpine vegetation on Mt Wellington, Tasmania, comparing areas burned 16–51 years before data recording. We focus on the following hypotheses: there is a convergence in vegetation structure, species composition and relative abundance of individual taxa between areas burned in 1947 and 1962; the life history and physiognomic attributes of species influence their place in the postfire succession; tolerators and requirers are proportionately more common than in more fire-prone lowland communities dominated by small and hard-leaved shrubs. We also report on differences in soil characteristics between areas burned 51 years previously and those burned 36 years previously.

### Study area

Mount Wellington is an undulating, unglaciated, rocky, dolerite plateau which attains a maximum elevation of 1270 m. Mean annual precipitation almost certainly exceeds 1200 mm and the climatic treeline is at approximately

1160 m. For further details on the environment of the plateau see Dombrovskis *et al.* (1996).

The alpine vegetation of Mt Wellington is more prone to burning than most alpine vegetation in the state, because it lies south-east of one of the driest parts of Tasmania, experiences northwesterly föhn winds in summer and is close to the main urban centre of Tasmania. Charcoal concentrations in a core from near the summit plateau suggest that the incidence of burning of alpine vegetation has become more frequent since Hobart was established in 1802, but that, both historically and prehistorically, the frequency has been low compared with that in the drier lowland areas (Whinam and Kirkpatrick 1994). Spatially well-documented fires occurred in the alpine zone of Mt Wellington in 1962 and 1967 (Fig. 1). The 1962 fire was associated with the construction of a tower. It burned several strips of vegetation from the east to the west. The 1967 fire burned almost all of the summit plateau, the only areas escaping being those protected by the 1962 burn and those burned in 1962. Before 1967, the last extensive conflagration on Mt Wellington was in 1947 (Dombrovskis *et al.* 1996).

### Methods

#### *Selection of sample sites*

In 1978, 15  $5 \times 5$ -m plots were placed at random distances from the boundary in the areas burned in 1962 or 1967 adjacent to fire boundaries and another 15 plots were placed in adjacent vegetation with the same slope and aspect that was not burned in these years (Fig. 1). These pairs of plots were placed at roughly equal intervals along all of the available boundaries. In 1998, paired plots were placed in the same general locations as those placed in 1978, with the aid of a large-scale map, as the 1978 plots were not marked out on the ground. Random distances (up to 10 m) from the boundary were used for exact plot location. It is thus unlikely that any of the plots were exactly coincident between 1978 and 1998, although they had similar distributions.

The size of the shrubs in the area unburned in either 1962 or 1967 is consistent with a fire that burned this area in 1947, if it is assumed that the mean annual height increment of the largest bushes of *Orites acicularis* between 1978 and 1998 is applicable to the period 1947 to 1978. Henceforth, the plots in this area are therefore referred to as belonging to the 1947 burn. All except the easternmost plot in the areas burned after 1947 were burned in 1962. The easternmost plot was burned in 1967. Given the small time difference in the date of the two fires, data from this plot have been used with the rest. Henceforth, the data as a whole will be referred to as pertaining to the 1962 burn.

#### *Data collection*

The numbers, maximum heights, maximum diameters and minimum diameters of all individual shrubs rooted in each quadrat were measured at both times for the following species (nomenclature follows Kirkpatrick 1997): *Bellendena montana*, *Coprosma nitida*, *Leucopogon montanus*, *Olearia algida*, *O. ledifolia*, *Orites acicularis*, *O. revoluta*, *Ozothamnus hookeri*, *O. ledifolius*, *O. rodwayi*, *Pimelea sericea*, *Richea scoparia* and *Tasmannia lanceolata*. In 1978, the covers of other vascular plant taxa, exposed bare ground and exposed rock were measured in a  $1 \times 1$ -m quadrat located in the centre of the  $5 \times 5$ -m plots with templates of known areas. In 1998, nine  $1 \times 1$ -m plots arranged in a cross (x) within the plot were used for the same measurements. These were undertaken with 100 grid squares in each quadrat as a template for

**Table 1. Surface-soil characteristics (1998) in the areas burned in 1947 and 1962, showing probability levels for differences between means or medians**MW = Mann–Whitney *U*-test, s.e. = standard error

Characteristic	1962 burn			1947 burn			Probability
	Median	Mean	s.e.	Median	Mean	s.e.	
Organic C	16.5	16.7	1.2	18.2	18.4	1.66	0.297 ( <i>t</i> -test)
pH (Ca)	4.1	4.1	0.03	4	4.1	0.06	0.272 (MW)
Conductivity	80	76	4.76	85	86.7	8.98	0.156 ( <i>t</i> -test)
Total P	710	725	22.7	740	725	41	0.330 (MW)
Available P	14	17.8	2.34	19	17.9	1.37	0.518 (MW)
Total N	0.77	0.89	0.09	0.96	0.93	0.09	0.443 (MW)
Exchangeable N	90	115	22.9	100	133	19.8	0.290 (MW)
K	200	220	19.6	280	304	26.2	0.004 ( <i>t</i> -test)
Total Ca	570	567	53	490	664	182	0.442 (MW)
Available Ca	130	169	19.7	190	239	49.5	0.165 ( <i>t</i> -test)
Mg	64	71.6	6.9	94	102.6	12.7	0.028 (MW)
Mn	2	13.6	5.1	9	42.2	24.9	0.017 (MW)
Zn	3.9	4.4	0.44	6	6.4	0.67	0.017 ( <i>t</i> -test)
Cu	2.3	2.6	0.26	3	3.3	0.16	0.001 ( <i>t</i> -test)
Fe	500	501	46.7	610	577	67.5	0.278 ( <i>t</i> -test)

cover estimates. The cover measurements in both cases were outline covers. The grid squares were used to estimate outline cover of the most abundant taxa and/or ground-cover classes by counting the number of squares in which a particular taxon and/or ground-cover class covered more than 50% of the square. Species growing beneath shrubs were usually visible through their canopies. Where they were not, their areas were transposed to the grid. Species that were relatively rare within a 1 × 1-m quadrat were treated by adding up estimated percentages of their occurrences within the grid squares.

In 1998, a bulked sample of the upper 5 cm of the soil profile was collected from the middle of each 5 × 5-m plot and halfway to each of the four corners.

#### Data analysis

Height-class histograms were constructed for each of the 1947 and 1962 burn sets of plots for those shrub species having an average density per plot of more than two in at least one of the measurement-age–burn-age combinations. The means of maximum and minimum diameters for all the shrubs listed above were used to calculate percentage covers for these species for each quadrat. Percentage covers for other taxa, bare ground and exposed rock for each quadrat were derived by the use of the 1 × 1-m quadrat data. Percentage covers for all attributes measured were calculated for the following subsets of plots: burned 1962, measured 1978 (62.78); burned 1962, measured 1998 (62.98); burned 1947, measured 1978 (47.78); burned 1947, measured 1998 (47.98). The following ratios were calculated: 47.78/62.78; 47.98/62.98; 62.98/62.78; 47.98/47.78. In addition, a divergence index was calculated to indicate the degree to which the burned and unburned areas became more similar or dissimilar through time. The larger of the two percentages for 1978 was divided by the smaller of the two percentages. The same calculation was done for the 1998 data. As an example of this calculation, if the mean cover value for the 1947-burn paired plot for a species was 10% and the value for the 1962-burn plot was 5% the resulting ratio would be 2, as it would also be if the values were reversed. The ratio for 1998 was divided by the ratio for 1978. For example, if the ratio for 1978 were 2 and that for 1998 were 4, the divergence index would be 2. This index indicates increasing similarity (convergence) between 1947-burn and 1962-burn plots through time if values are below 1.0 and decreasing similarity (divergence) between 1962- and 1947-burn plots through time if values are greater than 1.0.

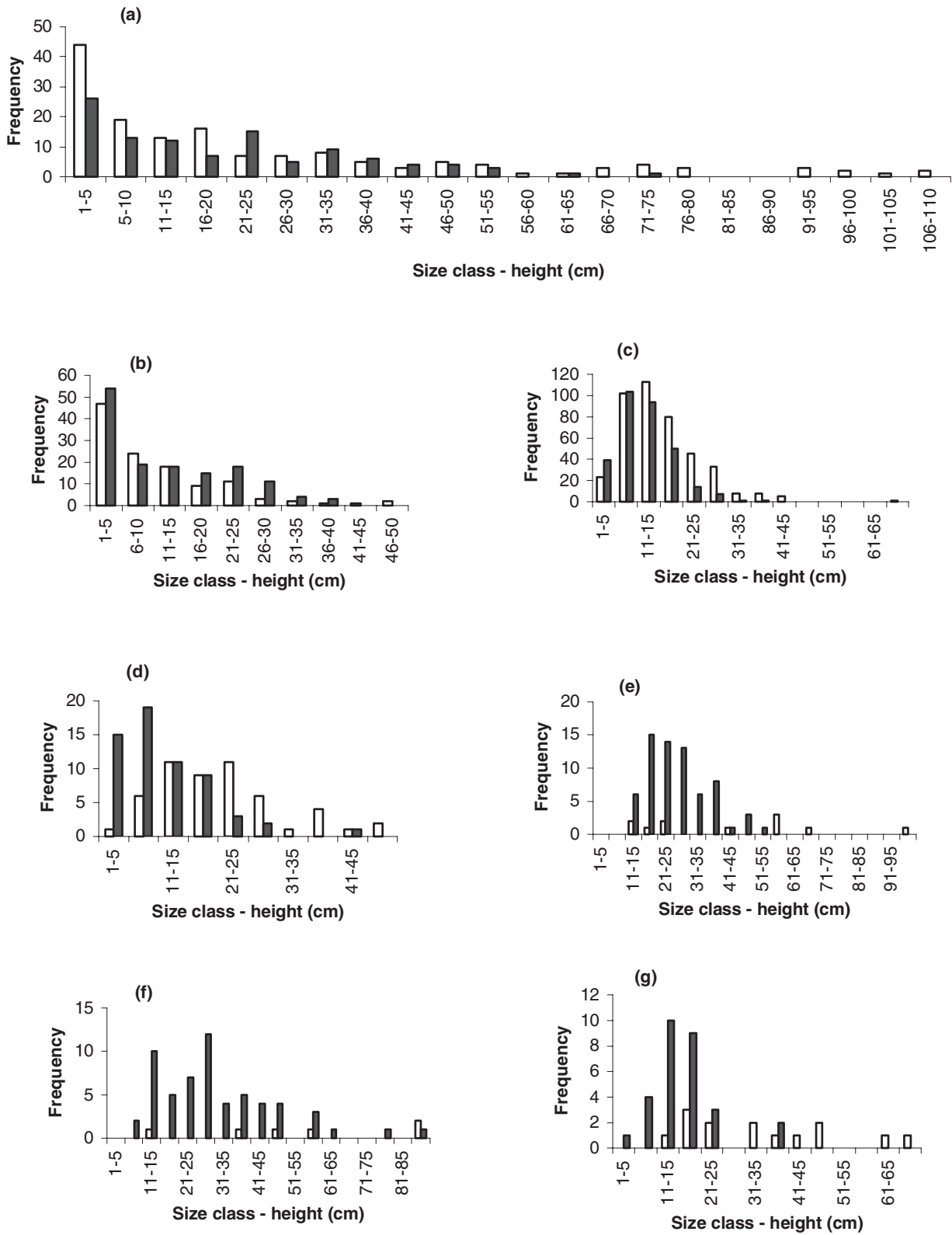
The following attributes of surface soil samples were determined in the laboratory, following the methods described in Rayment and Higginson (1992), except where indicated otherwise below by the absence of a reference number to this volume: pH, 1:5 soil:water suspension (4A1); conductivity, EC of 1:5 soil:water suspension (3A1); extractable P, bicarbonate extractable (9B2); total P, nitric-perchloric digest and inductively coupled plasma (ICP) analysis; %N, semimicro Kjeldahl with steam distillation (7A1); NO<sub>3</sub>N, KCl extract (7C2); NH<sub>4</sub>N, KCl extract (7C2); extractable K, bicarbonate extractable (18A1); total Ca, nitric-perchloric digest and ICP analysis; Cu, DTPA (12A1); Zn, DTPA (12A1); Mn, DTPA (12A1); Fe, DTPA (12A1); organic carbon, Walkley and Black (6A1).

The significance of differences between burned and unburned plots in the soil and other environmental variables, was determined by one-way ANOVA or the paired *t*-test for parametrically distributed data and the Mann–Whitney *U*-test for non-parametrically distributed data.

## Results and discussion

### *Differences in environmental attributes between areas burned during 1947 and 1962*

Between 1978 and 1998, bare ground and exposed rock cover decreased substantially in both sets of plots, with consequent substantial increases in vegetation cover (Table 3). The decreases in bare ground averaged 1.48% per year for the plots burned in 1962 and 1.05% per annum for the plots burned in 1947. These numbers are close to the 1.3% per annum bare-ground decrease recorded for plots fenced from sheep on the Central Plateau of Tasmania (Bridle and Kirkpatrick 1999) and indicate that the revegetation decreases in absolute amount as time elapses since disturbance. In 1998, bare ground did not differ significantly (ANOVA,  $F = 1.18$ ,  $P > 0.05$ ) between 1962-burn and 1947-burn plots, whereas rock cover was significantly (ANOVA,  $F = 11.1$ ,  $P < 0.01$ ) greater in the 1962-burn than in the 1947-burn plot.



**Fig. 2.** Height-class histograms for (a) *Orites acicularis*, (b) *Bellendena montana*, (c) *Ozothamnus rodwayi*, (d) *Olearia algida*, (e) *Ozothamnus hookeri*, (f) *Ozothamnus ledifolius* and (g) *Richea scoparia* in the area burned in 1962 (black bars) and in 1947 (white bars) plots.

Relatively few of the attributes of the surface soil differed significantly between plots burned in 1947 and those burned in 1962, although all had higher means and medians in the area burned less recently (Table 1). Potassium, Mg, Mn, Zn and Cu had significantly greater concentrations in the area burned in 1947 than the area burned in 1962 (Table 1). Nitrogen, P and organic C have been shown to differ significantly across younger fire boundaries at Mt Read and Mt Field in Tasmania (Kirkpatrick and Dickinson 1984), but this is not the case at Mt Wellington (Table 1). This may be explained by the fact that the less-recently burned vegetation at Mt Read and Mt Field had not been incinerated for a very long time, if ever, while at Mt Wellington the less-recently burned vegetation was incinerated only 15 years before the more-recently burned vegetation. Alpine soils in Kosciuszko National Park that had been degraded by stock-induced erosion had significantly lesser K, Mg, pH, N, P and Ca values than undisturbed soil (Johnston 1998), indicating an analogous effect to fire.

#### *Population dynamics of tall shrubs*

A variety of patterns was found in the 1998 height-class histograms (Fig. 2). *Orites acicularis* and *Bellendena montana* exhibited classical reverse J curves in both the 1947- and 1962-burned areas, with the curves being steeper in the 1962 burn. The numbers in the smallest size class were greater for the 1947 burn than the 1962 burn for *O. acicularis* and the reverse for *B. montana*. The upper half of the height-class range for *O. acicularis* was dominated by plants in the 1947-burn area. This was not the case for *B. montana*.

*Bellendena montana* dramatically increased in numbers in both the 1947- and 1962-burn plots between 1978 and 1998 (Table 2). It had a higher density in the 1947-burn plots than the 1962-burn plots in 1978 and reversed this relationship in 1998 (Table 2), indicating a requirement for vegetated ground for establishment. *Orites acicularis* more than doubled its numbers between 1978 and 1998 in both the 1947- and 1962-burn plots, while having a greater density in the 1947-burn than the 1962-burn plots at both times (Table 2).

Both *O. acicularis* and *B. montana* are obligate seed regenerators. The secondary peaks at 21–25 cm for both species in the area burned in 1962 may represent the individuals that established immediately after the 1962 fire, their reproductive maturity leading to a second regeneration surge. There seems little doubt that neither species requires the disturbance of fire for regeneration, as both have been continuously regenerating in the area burned in 1947.

The height-class distributions for *Ozothamnus rodwayi* and *Olearia algida* formed negatively skewed curves for the populations established following both the 1947 and 1962 burns (Fig. 2). For *O. rodwayi*, the curves peaked in the second-lowest class for the population in the 1962 burn and the third-lowest class for the population in the 1947 burn. For *O. algida*, the curves peaked in the second-lowest class for the 1962-burned area and the third- to fifth-lowest in the

1947-burned area. For both species, the individuals in the upper size classes were concentrated in the area burned in 1947. Substantial numbers of individuals were in the smallest height class in both areas for *O. rodwayi* and in the 1962-burned area for *O. algida*, but few individuals of *O. algida* were in the smallest class in the 1947-burned area. *Ozothamnus rodwayi* increased in density between 1978 and 1998 in both the 1947-burn plots and the 1962-burn plots, with the increase in the area burned in 1962 being greater than that in the area burned in 1947 and densities being greater in the area burned in 1947 than in the area burned in 1962 at both times (Table 2). *Olearia algida* increased its density between 1978 and 1998 in the 1947-burn plots, while remaining relatively constant in the area burned in 1962, in which it had its greater numbers in both 1978 and 1998 (Table 2).

Both *O. rodwayi* and *O. algida* resprout after fire and have wind-dispersed seed. Sufficient establishment of new seedlings appears to be taking place in the 1947-burn plots to keep both species in the community, although this is more pronounced with *O. rodwayi* than *O. algida*.

*Ozothamnus hookeri* and *O. ledifolius* had curves in the area burned in 1962 similar to that of *O. rodwayi*, but had no individuals in the smallest height class and a sporadic distribution of individuals in the area burned in 1947, which contained the tallest stems (Fig. 2).

*Ozothamnus hookeri* increased in density between 1978 and 1998 in the area burned in 1962, while remaining relatively constant in numbers in the area burned in 1947. It had much greater densities in both 1978 and 1998 in the area burned in 1962 than the area burned in 1947 (Table 2). *Ozothamnus ledifolius* decreased in density between 1978 and 1998 in both 1947-burn plots and the 1962-burn plots, the decrease being more pronounced in the area burned in 1947. Its densities were much greater in both 1978 and 1998 in the area burned in 1962 than the area burned in 1947 (Table 2).

Both *Ozothamnus hookeri* and *O. ledifolius* resprout after fire and produce large amounts of wind-dispersed seed after gaining rapid reproductive maturity. However, unlike *Ozothamnus rodwayi* and *Olearia algida*, they show no tendency to establish in long-unburned vegetation. Thus, they seem to be early successional shrubs, with *O. hookeri* being the more persistent of the two.

The populations of *R. scoparia* in the area burned in 1962 consisted largely of individuals in the second- to fifth-lowest classes, with a peak in the third-lowest class (Fig. 2). There were no individuals of *R. scoparia* in the two lowest classes in the area burned in 1947 and a sporadic distribution of individuals over the rest of the height range. Between 1978 and 1998, *R. scoparia* increased in density in the area burned in 1962, while decreasing in density in the area burned in 1947. Consequently, it was more abundant in the area burned in 1962 than the area burned in 1947 in 1998, in contrast to the reverse relationship in 1978 (Table 3). *Richea scoparia* is





**Table 3. Mean percentage covers of taxa, lifeforms, bare ground and exposed rock for quadrats burned in 1947 and 1962 and ratios between 1962-burn and 1947-burn covers, in 1978 and 1998**

See Methods for calculations of the divergence index

F = fern, h = herb, g = grass, gr = graminoid, m = mat shrub, s = upright shrub

Taxon	1978			1998			Burn-1962	Burn1947	Divergence index
	1962	1947	1947/1962	1962	1947	1947/1962	1998/burn-1962 1978 (1962 fire)	1998/burn-1947 1978 (1947 fire)	
<i>Bellendena montana</i> s	0.17	2.87	16.88	3.15	2.23	0.71	18.52	0.78	0.08
<i>Euchiton</i> spp. h	0.83	0.03	0.04	0.03	0.01	0.33	0.04	0.33	0.11
<i>Orites acicularis</i> s	0.63	14.33	22.74	6.78	27.43	4.05	10.76	1.91	0.18
<i>Pentachondra pumila</i> m	0.8	8.67	10.84	2.21	4.35	1.97	2.76	0.5	0.18
<i>Olearia ledifolia</i> s	0.1	0.9	9	0.5	0.31	0.62	5	0.34	0.18
<i>Richea scoparia</i> s	0.13	1.4	10.77	0.6	2.15	3.58	4.62	1.54	0.33
<i>Ozothamnus ledifolius</i> s	6.4	0.73	0.11	3.05	0.73	0.24	0.48	1	0.48
<i>Olearia algida</i> s	0.63	1.3	2.06	1.1	1.11	1.01	1.75	0.85	0.49
<i>Cyathodes dealbata</i> m	5.67	11.73	2.07	2.46	2.69	1.09	0.43	0.23	0.53
<i>Euphrasia</i> spp. h	2.14	0.7	0.33	0.38	0.22	0.58	0.18	0.31	0.56
<i>Epacris serpyllifolia</i> s	5.97	10.93	1.83	29.29	32.49	1.11	4.91	2.97	0.61
<i>Brachyscome</i> spp. h	0.3	0.17	0.57	0.04	0.05	1.25	0.13	0.29	0.71
<i>Monotoca empetrifolia</i> m	1.03	0.43	0.42	1.17	0.67	0.57	1.14	1.56	0.73
<i>Celmisia asteliifolia</i> h	4.1	5.57	1.36	6.74	6.84	1.01	1.64	1.23	0.74
<i>Leucopogon montanus</i> s	0.17	0.07	0.41	0.15	0.08	0.53	0.88	1.14	0.77
<i>Mitrasacme montana</i> h	0.67	0.87	1.3	0.19	0.2	1.05	0.28	0.23	0.81
<i>Poa gunnii</i> g	38.93	35	0.9	20.56	19.54	0.95	0.53	0.56	0.95
<i>Orites revoluta</i> s	2.7	3	1.11	3.85	4.98	1.29	1.43	1.66	1.16
<i>Ozothamnus rodwayi</i> s	1.3	3.73	2.87	4.04	13.41	3.32	3.11	3.6	1.16
<i>Plantago tasmanica</i> h	0.43	0.5	1.16	0.03	0.04	1.33	0.07	0.08	1.15
<i>Richea sprengelioides</i> s	5.13	6.2	1.21	6.26	9.18	1.47	1.22	1.48	1.21
<i>Acaena montana</i> h	0.47	0.33	0.7	0.55	0.3	0.55	1.12	0.91	1.29
<i>Ozothamnus hookeri</i> s	0.87	1.67	1.92	3.15	1.12	0.36	3.62	0.67	1.46
<i>Carpha alpina</i> gr	0.33	0.2	0.61	0.68	0.26	0.38	2.06	1.3	1.59
<i>Cyathodes petiolaris</i> s	1.07	1.27	1.19	1.31	2.72	2.08	1.22	2.14	1.75
<i>Luzula</i> spp. gr	0.27	0.23	0.85	0.32	0.14	0.44	1.19	0.61	1.95
<i>Lycopodium fastigiatum</i> f	0.13	0.13	1	0.11	0.01	0.09	0.85	0.08	11
Total mat shrubs	7.5	21.5	2.87	6.52	9.08	1.39	0.87	0.43	0.48
Total upright shrubs	25.34	48.47	1.92	64.47	98.2	1.52	2.54	2.03	0.79
Total herbs and ferns	10.94	9.74	0.89	8.96	7.87	0.88	0.82	0.81	1.02
Total graminoid + grass	45.56	42.83	0.94	22.62	20.28	0.9	0.5	0.47	1.06
Total overlapping cover	89.34	122.54	1.37	102.6	135.43	1.32	1.15	1.11	0.96
Total cover	47.6	66.3	1.39	77.16	87.22	1.13	1.62	1.32	0.81
Bare ground	19	12.5	0.66	2.41	1.03	0.43	0.13	0.08	1.54
Exposed rock	33.4	21.2	0.63	20.43	11.75	0.57	0.61	0.55	1.1

an obligate seed regenerator and is prominent in long-unburned vegetation in areas with more moisture than those sampled here (Kirkpatrick 1983). However, these data indicate that the species may require open ground for establishment on the drier parts of Mt Wellington.

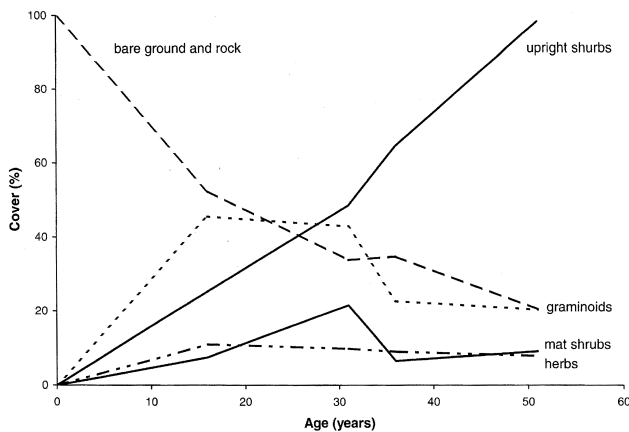
#### Vital-attribute classification of tall shrubs

The tall shrubs included in the size-class analyses varied markedly in their combinations of mechanisms of persistence and their propensity to establish at varying times after disturbance (Table 2, Fig. 2). Of the three species that are obligate regenerators from the soil seed store, *Orites acicularis* is a tolerator, *B. montana* is a requirer and *R. scoparia*, at least in the study area, is intolerant. Four

species both recover vegetatively and from wind-dispersed seed. Of these, *Ozothamnus hookeri* and *O. ledifolius* are intolerant, *Olearia algida* is intermediate between tolerant and intolerant and *Ozothamnus rodwayi* is tolerant. *Orites revoluta* is a vegetative recoverer, may have a soil seed store and is a tolerator.

#### Relative abundance of species and lifeforms

Upright shrubs, mat shrubs, total cover and total overlapping-vegetation cover converged (became more similar between the areas burned in 1947 and 1962) between 1978 and 1998, whereas herbs and ferns and grasses and graminoids diverged to a minor degree (Table 3, Fig. 3). Upright-shrub cover, total cover and total



**Fig. 3.** Changes in cover of lifeform groups and bare ground by time since last fire. Grasses are included with graminoids. Ferns are included with herbs.

overlapping-vegetation cover increased in both the areas burned in 1947 and 1962, while mat-shrub cover, fern and herb cover and grass and graminoid cover decreased in both ages of burn. In both 1978 and 1998, total cover, total overlapping-vegetation cover, upright-shrub cover and mat-shrub cover were greater in the area burned in 1947 than in the area burned in 1962. The reverse pertained for grasses and graminoids and ferns and herbs.

These data indicate a slowing of the rate of change in the course of postfire succession, so that the vegetation of the burned area is moving towards that of the unburned area and that the taller components of the vegetation are replacing the shorter as succession proceeds.

Among the more frequent upright shrubs there was considerable diversity in both temporal change and response to burning (Table 3). *Orites acicularis*, *Epacris serpyllifolia* and *R. scoparia* converged in their relative abundance in the 1947 and 1962 burns and increased their covers through time in both burn ages, while being consistently more abundant in the area burned in 1947. *Bellenden montana*, *O. ledifolia* and *O. algida* also converged, but increased in the area burned in 1962 and decreased in the area burned in 1947. *Bellenden montana* and *O. ledifolia* had greater covers in the area burned in 1947 than in the area burned in 1962 in 1978 and the reverse in 1998. *Olearia algida* had greater cover in the area burned in 1962 than the area burned in 1947 in 1978, but reversed this relationship in 1998. *Leucopogon montanus* converged, decreased in the area burned in 1962 and increased in the area burned in 1947. It had greater cover in the area burned in 1962 than in the area burned in 1947 at both times. *Ozothamnus rodwayi*, *Orites revoluta*, *Cyathodes petiolaris* and *Richea sprengelioides* diverged in their relative abundance, while increasing in both burn ages. All four species had greater cover in the area burned in 1947 than in the area burned in 1962 in both 1978 and 1998. *Ozothamnus hookeri* was the only one of the more frequent upright shrubs to diverge, increase in the area burned in 1962

and decrease in the area burned in 1947. It had greater cover in the area burned in 1962 than in the area burned in 1947 in both 1978 and 1998.

The three more-frequent mat shrubs all converged, but otherwise exhibited different responses. *Cyathodes dealbata* decreased in both the burn ages. It was more abundant in the area burned in 1947 than in the area burned in 1962 in both 1978 and 1998. *Monotoca empetrifolia* increased in both burn ages. It was more abundant in the area burned in 1962 than in the area burned in 1947 in both 1978 and 1998. *Pentachondra pumila* decreased in abundance in both burn ages. It was more abundant in the area burned in 1947 in both years.

Most of the more-frequent herb taxa converged and decreased in both fire ages (Table 3). Two of these four taxa, *Euchiton* spp. and *Euphrasia* spp., were more abundant in the area burned in 1962 than the area burned in 1947 in both 1978 and 1998. *Brachyscome* spp. were more abundant in the area burned in 1962 than in the area burned in 1947 in 1978 and the reverse in 1998. *Mitrasacme montana* was more abundant in the area burned in 1947 than in the area burned in 1962 in both 1978 and 1998. *Plantago tasmanica* diverged, decreased in both fire ages and was more abundant in the area burned in 1947 than in the area burned in 1962 in both years. *Acaena montana* diverged, increased in the area burned in 1962 and decreased in the area burned in 1947. It was more abundant in the area burned in 1962 than in the area burned in 1947 in both years. *Celmisia asteliifolia*, the most abundant of the herbs, converged and increased in both fire ages. It was more abundant in the area burned in 1947 than in the area burned in 1962 in both years. The only frequent pteridophyte, *Lycopodium fastigiatum*, diverged, increased in the area burned in 1962 and decreased in the area burned in 1947. It was equally abundant in the two fire ages in 1978, while being more abundant in the area burned in 1962 in 1998.

The three most-frequent monocotyledonous plants had varying responses (Table 3). *Carpha alpina* diverged and increased in both fire ages. It was more common in the area burned in 1962 than in the area burned in 1947 in both 1978 and 1998. *Luzula* spp. diverged, increased in the area burned in 1962 and decreased in the area burned in 1947. It was more common in the area burned in 1962 than the area burned in 1947 in both years. *Poa gunnii* converged and decreased in both fire ages. It was more abundant in the area burned in 1962 in both 1978 and 1998.

Lifeform was not generally a good predictor of a tendency towards convergence at the taxon level, with 7 of 12 upright shrubs converging, five of the eight herbs and ferns converging and one of three grasses and graminoids converging. However, all three mat shrubs converged.

Lifeform was a slightly better predictor of changes in abundance in the area burned in 1962, with 10 of 12 upright-shrub species increasing, two of three mat shrubs increasing, three of eight herbs and ferns increasing and two of three of the grasses and graminoids increasing.

### General discussion

It is clear that 51 years is an insufficient timespan after fire to achieve an equilibrium in the relative cover of lifeform guilds or a stable representation of bare ground and rock cover (Fig. 3). It also appears insufficient to achieve an equilibrium in the relative abundance of species, with several having passed over their peak, while others still expanding. A closed-heath, largely dominated by *O. acicularis*, appears to be the likely stable endpoint of the successional process, if it is not again truncated by fire, as this species is the most abundant and tallest of those that demonstrate the capacity for continuous regeneration. The high incidence of temporal convergence in the vegetation across the fire boundary indicates that the vegetation in the 1947 burn is likely to be a good predictor of the vegetation that will be found in the burned area in 15 years' time. However, this prediction needs to be subject to a proviso of climatic constancy.

Climatic constancy has not been a striking feature in Tasmania since the 1940s. Mean daily maximum temperatures have increased by more than a degree, while mean daily minimum temperatures have remained constant (Jackson 1999). Since 1978, there has been an increase in summer–autumn droughtiness in south-eastern Tasmania and a less-striking reduction in mean annual precipitation (Kirkpatrick *et al.* 2000). Both changes in daily maximum temperatures and an increase in droughtiness could be expected to have some influence on the successional process. *Orites acicularis* has suffered apparent drought mortality on the eastern Central Plateau, in areas with lower mean annual precipitation than Mt Wellington, where such mortality has not been observed. It seems likely, that the increase in mean daily maximum temperatures would have increased plant growth rates on the mountain during the time period related to our observations. However, we have no way of separating this influence from the process of succession initiated by fire. Such a separation might be partly achievable for some shrubs by the use of analyses of growth-ring widths in long-unburned vegetation. Mount Wellington is not the place to do this, having no alpine vegetation in this class. We hypothesise that the places most sensitive to the effects of a drier, warmer climate are likely to be those where snow lie has been relatively prolonged in the past and those where tall shrubs have been excluded by poor drainage. We would expect to see a decline of herbs, cushions and mat shrubs confined to such places and an increase in tall-shrub cover. Again, Mt Wellington is not the ideal place for such work, which we are undertaking elsewhere with other long-term plots.

Broad lifeform classes are poor predictors of the behaviour of individual species in the successional process, at least in this particular case. The variability in successional histories of tall shrubs is a striking case in point, with some being short-lived, fast-growing, disturbance dependents and others being slow-growing competitors and few exhibiting similar size-class distributions.

The tall shrubs in the Mt Wellington alpine zone have a proportionate distribution of vital-attribute characteristics that differs markedly from that of physiognomically similar types of vegetation from more fire-prone environments (Table 4). There are no tall shrubs on Mount Wellington that depend on canopy-stored seed for re-establishment after fire and the wind-dispersed species are all capable of vegetative recovery. While the proportion of vegetatively recovering tall shrubs on Mt Wellington is not markedly lower than that for Tasmanian lowland heath and Swartboskloof fynbos phanerophytes, most species are tolerant on Mt Wellington, while most are intolerant elsewhere and Mt Wellington has double the proportion of species depending on soil-stored seed for regeneration than either Tasmanian lowland heath or the Swartboskloof fynbos (Table 4). These data are consistent with our working hypothesis that tolerators and requirers would be proportionately more common than in more fire-prone lowland communities dominated by small and hard-leaved shrubs.

There is only one species among the frequent tall shrubs, *B. montana*, that could be classified as a requirer and this species seems not to have too delayed an access (Fig. 2). There is no indication of any species disappearing more than 50 years since the fire, although many herbs, in particular, are reducing in abundance. Given that almost all the species that are reducing in abundance through time at Mt Wellington are found in long-unburnt alpine-vegetation types elsewhere (Kirkpatrick 1997), the succession more closely resembles the

**Table 4. Percentage of phanerophyte species in simplified vital-attribute classes for abundant species in this study (MW), the Swartboskloof fynbos (SF) (van Wilgen and Forsyth 1992) and lowland Tasmanian heath (LT) (Kirkpatrick and Harris 1999)**

D = wind dispersed establishment, S = establishment from soil-stored seed, C = establishment from canopy-stored seed, V = vegetative recovery, I = establishes only after fire, T = establishes after fire and in mature vegetation, R = requires some establishment of other species for its own establishment

Vital-attribute class	LT	SF	MW
CI	12	4	0
CT	1	0	0
DI	5	12	0
DR	0	6	0
DT	0	2	0
SI	22	16	12
SR	0	0	12
ST	1	4	12
VI	55	50	25
VT	3	4	37
C	13	4	0
D	5	20	0
S	23	20	37
V	58	54	62
I	82	78	37
R	0	6	12
T	5	10	50

initial floristic composition model than relay floristics. This is not the case elsewhere in the Tasmanian alpine zone where requirers with limited dispersal ability are absent from recently burned sites, but are dominant at long-unburned sites (Kirkpatrick and Dickinson 1984). These species may have been eliminated from the alpine zone on Mt Wellington by relatively frequent, for the alpine zone, extensive fires, or Mt Wellington may be outside their climatic range.

Our data indicate that *O. ledifolius*, a Tasmanian endemic, restricted to the alpine and subalpine zones of the eastern mountains of the island, is in the process of a massive population crash on Mt Wellington. However, there is no immediate cause for concern for its future, given that it survived on the mountain through the lower fire frequencies than present that prevailed before the European invasion of Tasmania in 1802. The conclusion of Kirkpatrick and Dickinson (1984) that total fire exclusion is the best management policy for the conservation of Tasmanian alpine ecosystems is consistent with the slow process of vegetation and soil recovery that we have documented in this paper and the apparent ability of most species to persist in the absence of severe disturbance.

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