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Vegetation recovery after fire on a southern New Zealand peatland

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Abstract The effects of fires on conservation values and in determining present-day vegetation are poorly known in New Zealand. This study of vegetation recovery at Awarua Bog, Southland, began after a fire in 1985. Nine samplings were recorded over 10 years from permanent transects in six vegetation types: mixed *Baumea–Empodisma* bog, *Leptospermum* scrub, *Pteridium* fernland, *Sphagnum* bog, *Chionochloa* grassland, and *Ulex* scrub. Rapid initial vegetative regrowth was mainly by rhizomatous species. Low-growing species (herbaceous dicotyledons, grasses, bryophytes) peaked in abundance 15–22 months after fire but subsequently declined in cover or disappeared. *Leptospermum* shrubs established rapidly from seed; epacrid shrub species established later and more slowly. Former dominants (e.g., *Empodisma minus*, *Gleichenia dicarpa*, and *Chionochloa rubra*) were slow to recover. *Sphagnum* recovery was mainly by slow recolonisation of fire-bared peat, rather than regrowth of fire-damaged former cushions. Cushion bog (*Donatia novae-zelandiae*) is particularly sensitive to fire and very slow to recover. Fire provides open sites for gorse (*Ulex europaeus*) establishment, but also easy access for its eradication. Long-term fire prevention and prompt containment protect conservation values.

Keywords Awarua Bog; peatland; fire; vegetation recovery; vegetation history; seed banks; dispersal; conservation management

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INTRODUCTION

At the southern edge of New Zealand's South Island, extensive peatlands have developed in the post-glacial period upon the coastal margin of gravel outwash plains under the influence of cool prevailing winds off the southern ocean. Much of the Awarua Plain, south-east of Invercargill City, has been drained and converted to pasture, but extensive areas remain in public ownership and are being managed for biological conservation. The Waituna Wetlands Scientific Reserve (3556 ha) is classified as a wetland of international importance, particularly for its birdlife. Further peatlands, loosely known as the Awarua Bog, include the Seaward Moss Conservation Area (5604 ha) immediately to the west of Waituna Lagoon and the Toetoes Conservation Area (1648 ha) towards the Mataura River to the east.

Vegetation types over this general area include sedgeland, fernland, tussock grassland, scrub, and pockets of forest. The area is well known (e.g., Stephenson 1986; Ward 2001) for the presence, almost at sea level, of cushion bog that is elsewhere typical of montane to subalpine zones.

The peatlands have a history of repeated fires, some of accidental origin, some deliberate or vandalistic, many the result of nearby land development for agriculture over the 150 years since European settlement. A much earlier prehistory of fire is indicated by charred logs and stumps buried in the peat. Effects of fire, both in determining present-day vegetation and upon modern conservation values, are poorly known, not only for this area but for New Zealand peatlands in general.

The effects of fire generally upon vegetation, and the nature of post-fire vegetation, are dependent on numerous variables (Bond & van Wilgen 1996). Intensity of fire and flammability of plant material affect that which survives. Renewed vegetation can arise from resprouting of former plants or from "reseeders", and the location of new propagules can be within a soil seed bank, from fruits which have survived fire in charred canopies (serotinous plants), or else they must freshly disperse onto a site from

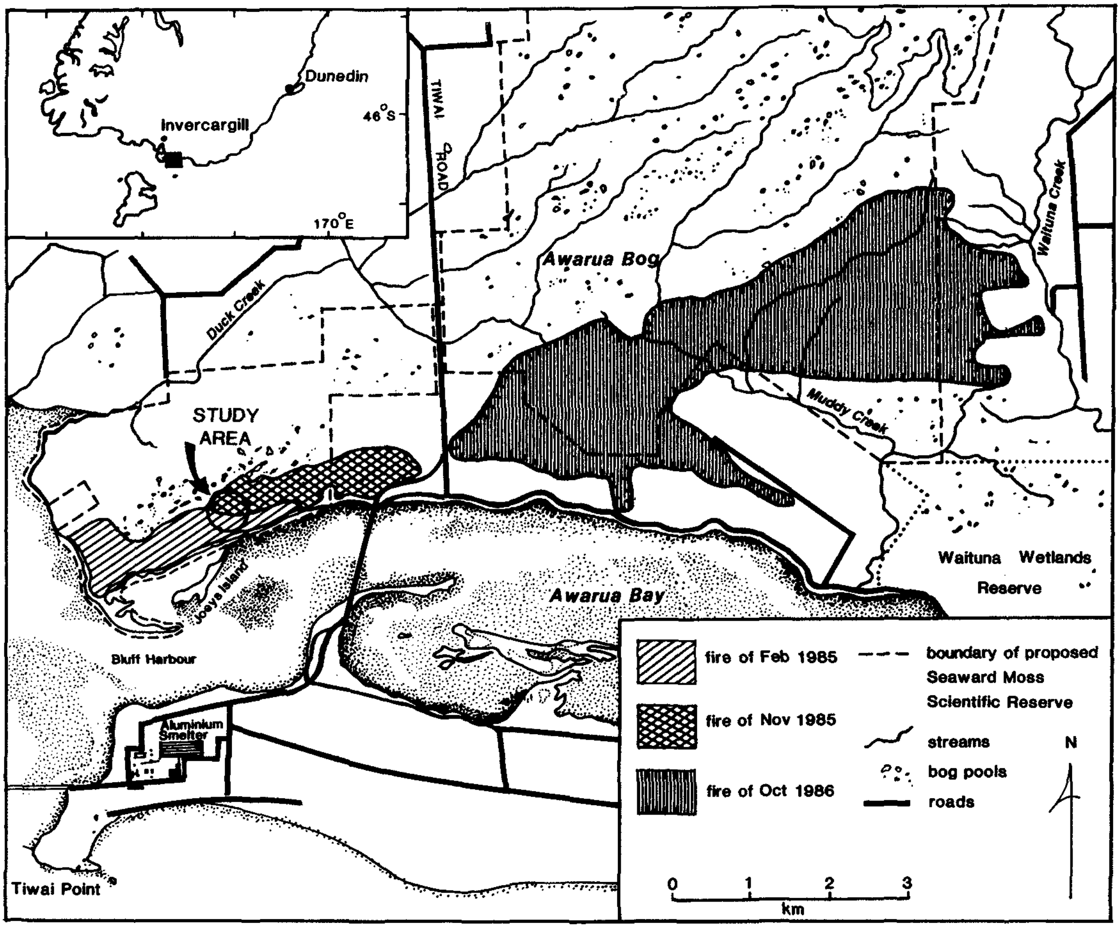


Fig. 1 Awarua Bog: study area location and extent of recent fires.

beyond the burn margin by agents such as wind or birds. Seasonality of fire can have a differential effect upon propagule survival, while frequency of fire helps to determine whether certain plants become progressively more abundant or else become locally extinct over time. Within peatland habitats fire can also burn either surface or underlying layers of peat, thereby altering the nature of the rooting zone of revegetating plants as well as interrupting the process of peat accumulation.

This study on the Awarua Bog was initiated in 1985 when a fire of accidental origin allowed an opportunity to follow the course of vegetation recovery in the principal peatland vegetation types. The aims were to document trends in regrowth and establishment, to assess effects of fire on biological conservation values, and to advise the Department of Conservation on implications for management.

THE STUDY AREA

The Awarua Bog is a gently undulating blanket bog of subdued relief upon Holocene river mouth and marine bench deposits, often quartz gravels (Watters et al. 1968). Peat depth reaches 1.5–2.5 m (Davoren et al. 1978; Campbell 1983), being the deposit laid down within the post-glacial period. The Awarua Bog was one of the peat sites sampled for the early pollen analysis study of Cranwell & von Post (1936), and their results show a three-phase post-glacial vegetation history for the region: grassland in an initially severe climate, podocarp forest during a wet and probably warm period, then *Nothofagus* forest as climate deteriorated.

Present climate for this district is characterised by strong predominant westerly winds, coolness (mean annual temperature c. 9°C), cloudy skies (c. 1600

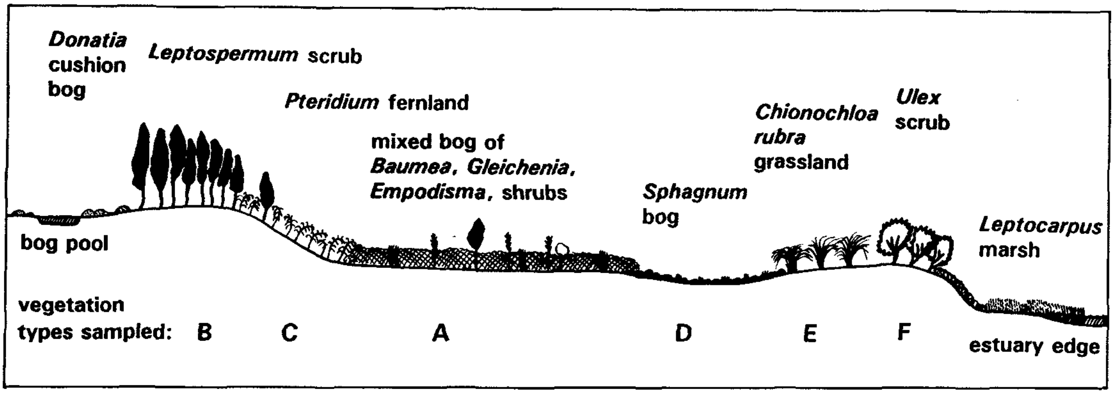


Fig. 2 Awarua Bog: a generalised profile showing topography, pre-fire vegetation, and sample sites.

sunshine hours per year), and frequent showers (c. 1000 mm mean annual rainfall, c. 150 raindays) (Wards 1976).

Vegetation and flora of various parts of the Awarua Plain peatlands have been described by Crosby Smith (1927), Martin (1960), Kelly (1968), and, in passing, by Campbell (1983). Nearby reserves (Waituna Scenic Reserve, Waituna Lagoon Wetlands Management Reserve, Joeys Island Scenic Reserve) are described in Allen et al. (1989). The general vegetation pattern (known to the author from earlier unpublished surveys) is as follows. Broad, low ridge crests hold concentrations of shallow tarns having steep sides and peat bases, surrounded by cushion bog of *Donatia novae-zelandiae** and *Oreobolus pectinatus*. Many expanses of level or very gently sloping peatland have a mixed low cover of tangle fern (*Gleichenia dicarpa*), wire rush (*Empodisma minus*), the sedge *Baumea tenax*, the fern *Blechnum minus*, bracken fern (*Pteridium esculentum*), and scattered shrubs of manuka (*Leptospermum scoparium*) and inaka (*Dracophyllum longifolium*). Where drainage is better on gentle slopes, either bracken or manuka can dominate almost alone. On parts of the peatland further inland and between 10 and 20 km to the east, tall manuka communities grade to patches of podocarp-broadleaved forest, in which the common tree species are kamahi (*Weinmannia racemosa*) and rimu (*Dacrydium cupressinum*).

Boggy grassland of red tussock (*Chionochloa rubra* subsp. *cuprea*) flanks the gentle courses of streams. The bog mosses *Sphagnum cristatum* and *S. australe* become dominant in the dampest ground of seepages and hollows. Scrub patches of gorse (*Ulex europaeus*) have invaded the peatlands, especially along low ridges or escarpments. Along the coastal margin of Awarua Bay the blanket bog grades into a saltmarsh fringe of jointed wire rush (*Leptocarpus similis*).

All the sampled vegetation types of the study area are those typical of the most infertile wetlands of cool climates in the classifications of Dobson (1979) and Thompson (1987).

The site chosen for study lies 2 km west of the causeway that crosses Awarua Bay to the gravel beach ridge landforms and the aluminium smelter of Tiwai Point (Fig. 1). This location offered examples of the main vegetation types within a few hundred metres of each other. The relationship of sampled vegetation and landforms is shown diagrammatically in Fig. 2.

Fire patterns

Limits of three recent fires, mapped in Fig. 1, are based on aerial observations and photos. These illustrate several general aspects of fire behaviour and impacts on the Awarua Bog. The fire of 31 January and 1 February 1985, its cause unknown, started 2 km west of the study area, spread east with the help of a westerly wind and was terminated after a change to a northerly wind helped firefighters to confine its northward spread.

Another fire, in mid November 1985, abutted the area burned earlier in the year, though leaving a few lone and unburned manuka shrubs scattered along the common edge-line of the two fires. Judging by the slightly greater amount of fibrous plant material left on the ground, the November fire was the less

*Authors for all plant names are included in Table 3.

intense of the two. On 28 and 29 October 1986 fire again swept across a large portion of the proposed Seaward Moss Conservation Area. This fire started when a car was driven into a power pole at the south end of Tiwai Road, collapsing the electricity lines, which in turn ignited the vegetation, which at this point was a low scrub of manuka and inaka. Pushed by westerly winds of up to 35 knots, the fire swept east across the low catchment of Muddy Creek to the far edge of the bog vegetation against pasture (Fig. 1). The extent of this fire was estimated as 1260 ha, of which 870 ha lie within the Conservation Area.

METHODS

Four months after the January 1985 fire, a total of seven permanently marked transects, each 30 m × 1 m, were sited in areas representative of six pre-fire vegetation types. For several transects located near the margin of the burn, the immediately adjacent unburnt vegetation upon comparable landforms was taken as indicative of previous cover (and might have continued to act as a benchmark except that it too was burned in the following year).

Transects were surveyed nine times: twice-yearly for a start, later about annually, and finally after a further 5-year interval. Sampling times are referred to as months after fire; the sampling dates for each of these are: 4 months after fire (May 1985), 10 months (November 1985), 15 months (April 1986), 22 months (November 1986), 28 months (May 1987), 39 months (April 1988), 54 months (July 1989), 69 months (October 1990), 120 months (February 1995).

Percent canopy cover was estimated within each 5 m × 1 m segment of each transect. Results presented in Fig. 3 are histogram representations of mean canopy cover values (from the six segments per transect; $n = 6$), except that two transects having similar plant cover and landform were combined to represent vegetation type A (mixed bog) ($n = 12$), and type F (*Ulex* scrub) is described from just the end third of a transect ($n = 2$) which best represented former *Ulex* scrub. Heights and growth forms of both resprouting and seedling plants were noted.

Samples of wood were collected from a peat profile exposed by quarrying close to the study site for identification to help interpret pre-historic vegetation of the peatland.

RESULTS

Immediate impacts of fire

When examined 4 months after the January 1985 fire, the edges of the burn were still very distinct. Within the fire boundaries a few strips of greenery up to 1 m wide were still present, probably having survived as "islands" between successive swathes of the wind-driven fire. All other above-ground vegetation had been burnt. Dead shrubs remained standing but charred; *Coprosma ciliata* skeletons retained more of their fine twigs than the more flammable shrubs of manuka and inaka.

Former dense masses of wire rush and tangle fern had been incinerated, along with their litter, to ground level. The peat itself, mostly compact and firm underfoot in this area, had not obviously ignited, and the ground surface was revealed as generally even or with scattered watery pockmarks.

Where cushions of *Sphagnum cristatum* and *S. australe* had been dominant, especially in broad puddly stream hollows, fire had removed the matrix of wire rush as well as the sides of the moss cushions, leaving pedestals 20–30 cm tall, with undercut sides. *Sphagnum* apices on top of the pedestals, although intact and not actually burned, were mostly pale and apparently dead.

Cushion bog was also burnt to steep-sided pedestals, 30–40 cm tall, with enough scorched but dead foliage of *Donatia novae-zelandiae* left on top to confirm their identification.

Along the shore of Awarua Bay, culms of *Leptocarpus* rushes were burned to their bases except for a lowermost zone which probably escaped fire because of tidal inundation.

By 35 months after fire, the limbs of former gorse bushes had rotted off. Manuka was still standing at 69 months, with aerial parts neither brittle nor soft but sufficiently rotted at ground level to break off readily when pushed. By 120 months almost all formerly standing manuka stems had fallen.

General trends in vegetation recovery

Total numbers of plant species recorded from all transects combined are listed in Table 1. Numbers of native flowering plants were highest (34 species) at 10–15 months after fire, then declined gradually to 21 species at 120 months. Naturalised plants were most numerous (14 species) at 10 months after fire, declining to just one species by 120 months. Numbers of ferns became relatively constant from 15 months. Bryophyte numbers reached a peak of 11 species at 39 months after fire, then declined as ephemeral colonists disappeared.

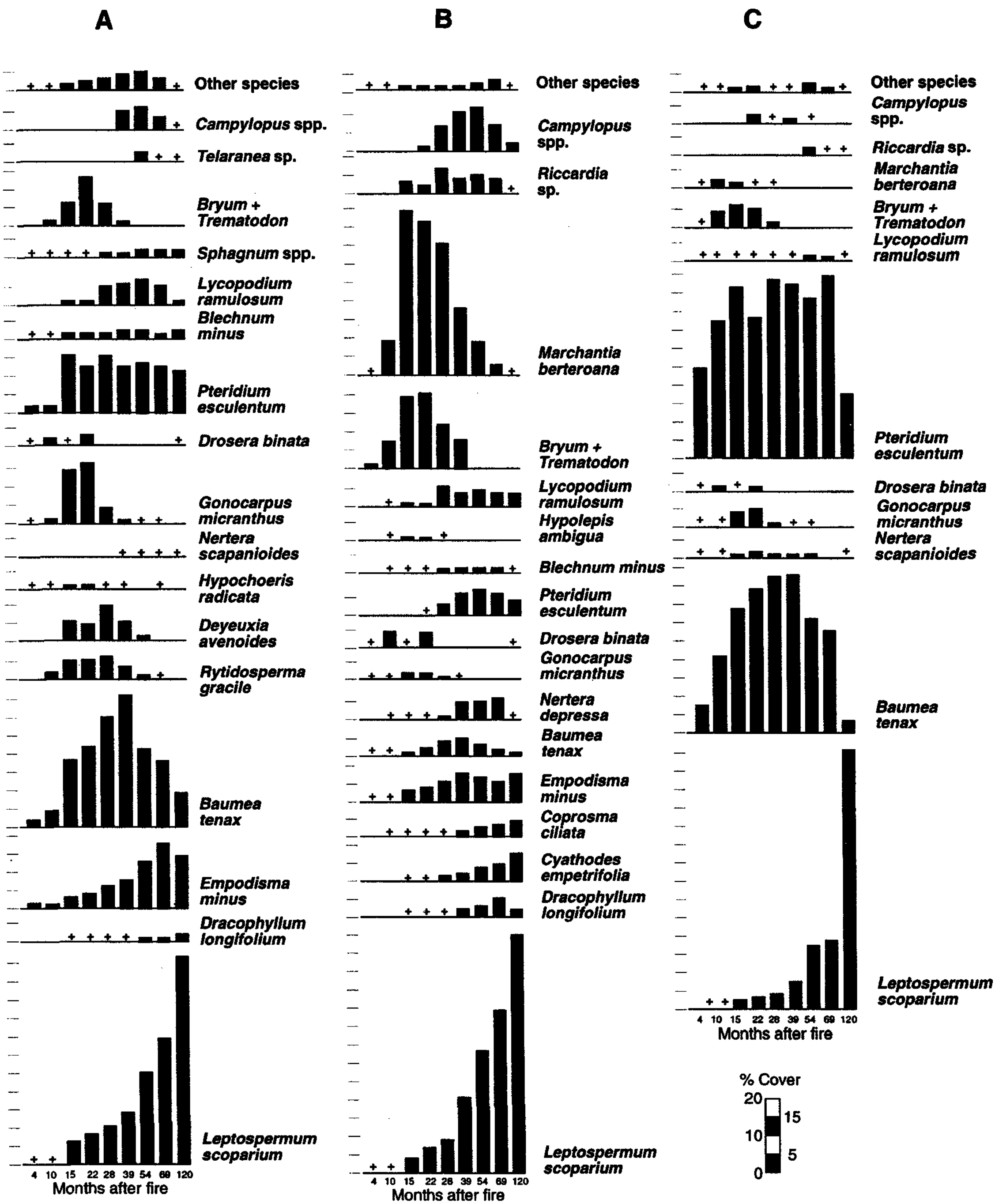
Total cover increased steadily in all vegetation types at progressive samplings (Table 1; Fig. 3). At 4 months after fire, total cover varied widely between vegetation types, from just 1% where there had previously been dense, c. 3-m-tall *Leptospermum* scrub, to 32% in *Pteridium* fernland and 56% in *Ulex* scrub, the last two largely because of rapid resprouting of bracken. By 22 months after fire most vegetation

Table 1 Mean percent canopy cover and total numbers of plant species recorded from all transects combined, at nine intervals after fire on the Awarua Bog.

	Months after fire								
	4	10	15	22	28	39	54	69	120
Mean % canopy cover	17	39	87	95	98	99	100	100	100
Native flowering plants	22	34	33	27	27	25	25	22	21
Naturalised flowering plants	5	14	9	7	6	4	2	2	1
Ferns	3	5	6	6	7	6	7	7	7
Bryophytes	5	6	6	8	8	11	8	9	9
Total no. of species	35	59	54	48	48	46	42	40	38

Table 2 Maximum plant heights (cm) of predominant colonists from all vegetation types noted at nine intervals after fire on the Awarua Bog. –, noted absence of a species; *, no measurement made at the time.

	Months after fire								
	4	10	15	22	28	39	54	69	120
Shrubs									
Coprosma ciliata									
regrowth	8	20	31	35	40	55	85	104	120
seedlings	2	9	*	*	*	*	*	*	*
Cyathodes empetrifolia	–	–	3	3	12	11	11	*	15
Cyathodes juniperina	–	–	2	*	16	*	*	*	90
Dracophyllum longifolium	–	–	4	6	20	54	79	103	190
Gaultheria macrostigma	1	4	15	*	21	35	*	*	35
Leptospermum scoparium	1	9	40	46	65	90	110	128	210
Ozothamnus leptophyllus	2	7	32	*	50	*	58	60	90
Pentachondra pumila	–	–	2	*	*	6	*	*	*
Ulex europaeus									
regrowth	2	30	90	90	120	130	140	155	210
seedlings	–	3	65	*	*	90	*	*	*
Monocots									
Astelia nervosa	30	45	*	*	*	*	*	*	*
Baumea tenax	20	25	25	40	70	80	80	105	100
Chionochloa rubra	20	80	120	120	120	140	150	205	180
Empodisma minus	8	8	18	*	22	24	43	42	120
Phormium tenax	30	50	80	*	*	105	120	125	180
Ferns									
Blechnum minus	10	10	12	*	*	*	*	*	*
Gleichenia dicarpa	–	–	–	–	–	3	10	*	40
Pteridium esculentum									
in mixed bog	10	10	15	32	50	53	62	60	60
in *Pteridium* fernland	30	45	70	80	110	120	115	125	140
Mosses									
Sphagnum australe, *S. cristatum*	0.5	1	2	*	*	3	14	18	30



types had 95% or more cover, but it was not until 39 or 54 months that new plant growth had resumed 100% canopy cover. By this stage in the recovery process vegetation structure had started to become tiered, with shade-tolerant species persisting in places as an understorey, a feature that is not fully indicated at subsequent sampling times because only canopy cover was recorded.

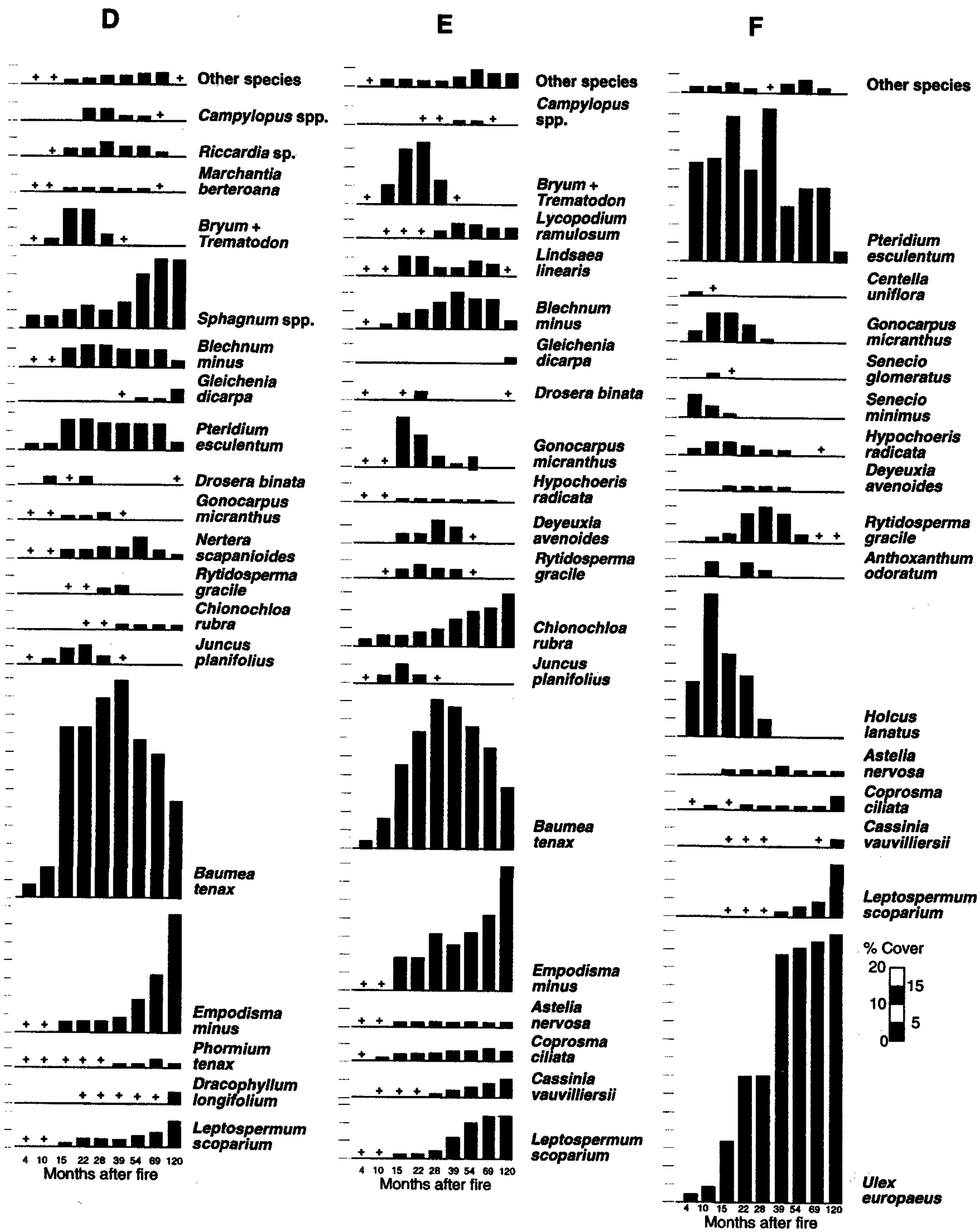


Fig. 3 Mean percent cover of plants at nine intervals after fire in six vegetation types on the Awarua Bog. **A**, mixed bog; **B**, *Leptospermum* scrub; **C**, *Pteridium* fernland; **D**, *Sphagnum* bog; **E**, *Chionochloa* grassland; **F**, *Ulex* scrub. Species included are those with mean cover of 0.5% (+ symbol) or more at one of the sampling times.

Table 3 Plant species recolonising after fire on Awarua Bog, and for vascular species their recolonising strategies and seedbank/propagule sources. *, naturalised, not native. Vegetation types: A, mixed bog; B, *Leptospermum* scrub; C, *Pteridium* fernland; D, *Sphagnum* bog; E, *Chionochloa* grassland; F, *Ulex* scrub. Ephemerals (column X): #, species with short-lived presence in transects. Recolonising strategy (column Y): P, sprouters; O, obligate seeders/sporers. Seedbank/main propagule source (column Z): S, soil; C, canopy (serotinous); W, wind-blown; B, bird-dispersed (principal seedbank listed first).

	Vegetation type						X	Y	Z
Shrubs and sub-shrubs									
Coprosma ciliata Hook.f.	A	B	C	D	E	F		P	SB
Coprosma propinqua A.Cunn.						F		O	SB
Coprosma sp. aff. *intertexta*					E			O	SB
Cyathodes empetrifolia Hook.f.	A	B	C	D	E	F		O	SB
Cyathodes juniperina (J.R. et G.Forst.) Druce			C		E			O	SB
Dracophyllum longifolium (J.R. et G.Forst.) R.Br.	A	B		D				O	WS
Gaultheria macrostigma (Col.) Middleton	A	B		D	E	F		P	SB
Leptospermum scoparium J.R. et G.Forst.	A	B	C	D	E	F		O	CW
Pentachondra pumila (J.R. et G.Forst.) R.Br.	A	B						O	SB
Ozothamnus leptophyllus (G.Forst.) Breitw. et J.M.Ward	A	B			E	F		O	SW
* *Solanum dulcamara* L.						F	#	O	B
* *Ulex europaeus* L.					E	F		P	S
Herbaceous dicots									
Acaena novae-zelandiae Kirk						F		O	BS
Centella uniflora (Col.) Nannf.	A			D	E	F		O	S
Celmisia graminifolia Hook.f.	A			D	E			O	SW
* *Cerastium fontanum* Baumg.					E	F	#	O	WS
* *Cirsium arvense* (L.) Scop.						F	#	O	W
* *Cirsium vulgare* (Savi) Ten.					E	F	#	O	W
Donatia novae-zelandiae Hook.f.		B						O	S
Drosera binata Labill.	A	B	C	D	E	F	#	O	S
Epilobium alsinoides Cunn.		B					#	O	W
Epilobium brunnescens (Cockayne) Raven et Engelhorn						F	#	O	W
* *Epilobium ciliatum* Raf.	A	B	C				#	O	W
Euchiton audax (D.G.Drury) Holub	A		C	D	E	F	#	O	W
Gonocarpus aggregatus (Buchan.) Orchard					E		#	O	S
Gonocarpus micranthus Thunb.	A	B	C	D	E	F		O	S
Hydrocotyle heteromeria A.Rich.						F	#	O	S
* *Hypochoeris radicata* L.	A	B	C	D	E	F	#	O	WS
Nertera depressa Banks et Sol. ex Gaertn.	A	B	C	D				O	SB
Nertera scapanioides Lange	A	B	C	D				O	SB
* *Parentucellia viscosa* (L.) Caruel						F	#	O	WS
Pseudognaphalium luteoalbum (L.) Hilliard et B.T.Burtt		B		D		F	#	O	W
* *Sagina procumbens* L.	A		C	D			#	O	W
Senecio biserratus Belcher				D		F	#	O	W
Senecio glomeratus Poiret	A		C	D		F	#	O	W
Senecio minimus Poiret	A	B	C	D	E	F	#	O	W
Grasses									
* *Agrostis capillaris* L.					E		#	O	WS
* *Anthoxanthum odoratum* L.						F	#	O	W
Chionochloa rubra Zotov subsp. *cuprea* Connor				D	E			P	WS
Deyeuxia avenoides (Hook.f.) Buchanan	A				E	F	#	O	W
Hierochloe redolens (Vahl) Roem. et Schult.					E			O	W
* *Holcus lanatus* L.					E	F	#	O	W
* *Poa annua* L.	A				E		#	O	W
Rytidosperma gracile (Hook.f.) Connor et Edgar	A			D	E	F	#	O	W
* *Vulpia bromoides* (L.) Gray						F	#	O	W

Table 3 *continued*

	Vegetation type						X	Y	Z
Other monocots									
Astelia nervosa Hook.f.					E	F		P	SB
Baumea rubiginosa (Spreng.) Boeck.	A							P	SW
Baumea tenax (Hook.f.) Blake	A	B	C	D	E	F		P	S
Carex gaudichaudiana Kunth					E			O	W
Empodisma minus L.Johnson et Cutler	A	B	C	D	E			P	SW
Herpolirion novae-zelandiae Hook.f.		B						P	S
Isolepis aucklandica Hook.f.	A			D			#	O	S
Isolepis nodosa (Rottb.) R.Br.						F		P	S
Juncus novae-zelandiae Hook.f.				D			#	O	S
Juncus planifolius R.Br.	A		C	D	E		#	O	W
Juncus pusillus Buch.				D	E		#	O	W
Lepidosperma australe (A. Rich.) Hook.f.	A				E			P	SW
* *Luzula congesta* (Thuill.) Lej.						F	#	O	W
Phormium tenax J.R. et G.Forst.				D	E			P	WS
Schoenus maschalinus Roem. et Schult.						F		O	S
Thelymitra longifolia J.R. et G.Forst.	A	B		D	E			P	W
Ferns and lycopod									
Blechnum minus (R.Br.) Ettingsh.	A	B		D	E	F		P	W
Gleichenia dicarpa R.Br.	A	B		D	E			O	W
Histiopteris incisa (Thunb.) J.Smith		B						O	W
Hypolepis ambigua (A.Rich.) Brownsey et Chinnock		B						P	W
Lindsaea linearis Sw.	A			D	E			O	W
Lycopodium ramulosum Kirk	A	B	C	D	E			O	W
Pteridium esculentum (Forst.f.) Cockayne	A	B	C	D		F		P	W
Schizaea australis Gaudich	A							O	W
Bryophytes									
Bryum caespiticium Hedw.	A	B	C	D	E	F	#		
Campylopus clavatus (R. Br.) Hook.f. et Wils.	A	B	C	D	E	F			
Campylopus introflexus (Hedw.) Brid.	A	B	C	D	E	F			
Dicranum billardierei Brid.			C		E				
Hypnum cupressiforme Hedw.				D	E				
Marchantia berteroana Lehm. et Lindenb.	A	B	C	D	E	F			
Polytrichum commune Hedw.	A	B							
Riccardia sp.	A	B	C	D	E				
Sphagnum australe Mitt. in Hook.f. et Wils.	A			D					
Sphagnum cristatum Hampe	A			D					
Sphagnum falcatulum Besch.				D					
Telaranea sp.	A			D	E				
Trematodon mackayi (R.Br. ter.) Broth.	A	B	C	D	E	F	#		

Plant height also increased steadily with time (Table 2). At the final sampling most shrub species were still increasing in height but *Ozothamnus leptophyllus* and the sub-shrub heaths *Cyathodes empetrifolia* and *Gaultheria macrostigma* appeared to have reached their full height for the site conditions. Height increase in *Coprosma ciliata*, although steady, was probably slowed by salt-storm damage to uppermost foliage, noted most obviously at 22 and 39 months. Similar damage to the uppermost 10 cm of most manuka shrubs was noted at 39 months. Damage to *Coprosma* shrubs by hare browsing was noted at 28 months.

Several of the non-woody dominants were still gaining height up to 69 months after fire, but the heights reached by the tallest specimens of *Baumea*

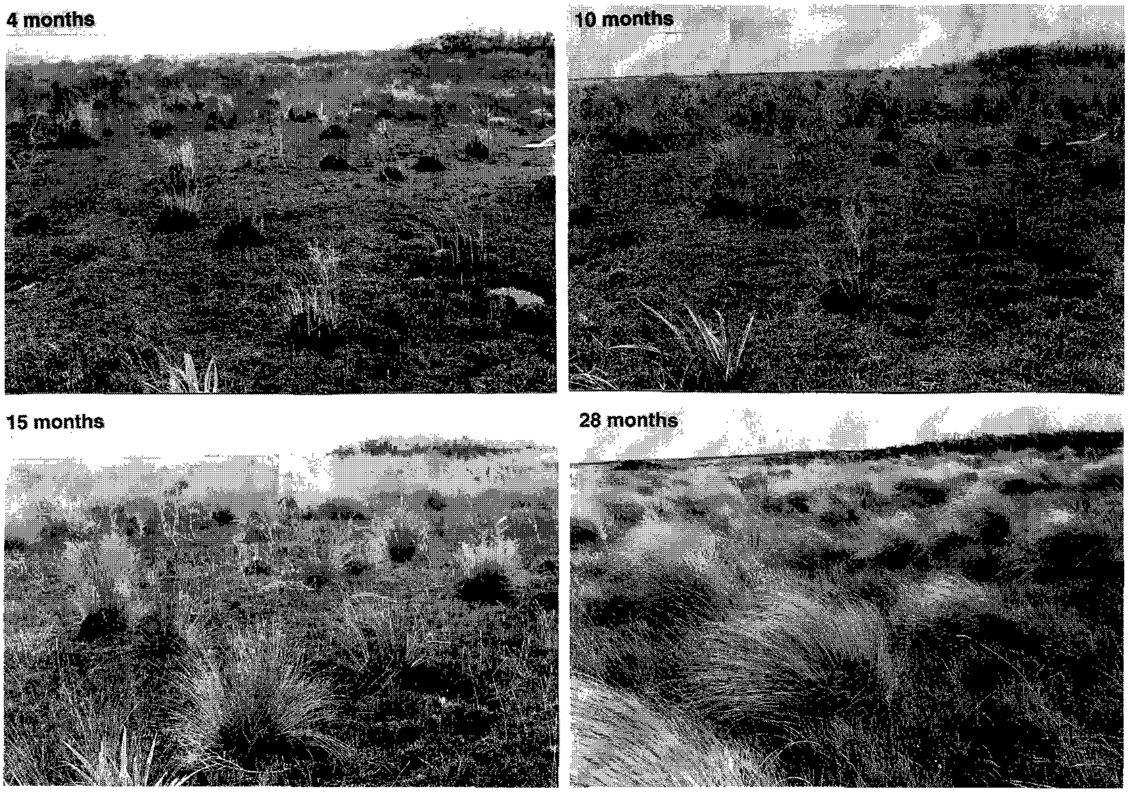


Fig. 4 Regrowth of red tussock (*Chionochloa rubra*) at 4, 10, 15, and 28 months after fire on the Awarua Bog.

tenax and red tussock would probably be about the maxima expected for the sites. The marked increase in height of wire rush between 69 and 120 months represents its ability to scramble up among shrub stems.

Maximum height of bracken is presented in Table 2 for two vegetation types: mixed bog where it is a minor component of relatively low habit, and *Pteridium* fernland where more optimal conditions, and presumably a stronger rhizome system, allowed for comparatively taller growth at every interval after fire. In both cases bracken had achieved almost its maximum height within both vegetation types just 28 months after fire.

Changes in vegetation composition over time in each of the six vegetation types are presented for predominant species in Fig. 3, while a complete list of plant species appears in Table 3, with annotations for ephemeral species and for the vascular plants showing their recolonising strategies (sprouters cf. obligate seeders) and their main propagule sources post-fire.

Vegetative regrowth

The most immediate regrowth after fire was provided by the rhizomatous plants bracken and *Baumea tenax*, which resprouted from their surviving underground parts during the autumn. A similar but more gradual contribution was made by the fern *Blechnum minus*.

Coprosma ciliata was the only native shrub species to resprout, and most former shrubs did so by new shoots arising at ground level from the base of former main stems. The height of resprouted plants consistently exceeded that of later established seedlings (Table 2). Gorse resprouted rapidly from the lower portions of old stems, and the height growth of this species likewise was more rapid on the resprout shoots than on seedlings. The sub-shrub *Gaultheria macrostigma* resprouted from former plants to a limited degree. No resprouting was observed on shrubs of *Ozothamnus leptophyllus*, or the heath shrubs inaka, *Cyathodes juniperina*, or *C. empetrifolia*.

Tall, tufted herbs that rapidly resumed leaf production from burnt basal stubbles, though with different degrees of vigour, were flax (*Phormium tenax*), *Astelia nervosa*, and red tussock. Flax in this vicinity grows to around 2 m tall, but usually with only 1–3 fans of leaves, typical of plants on infertile bog sites. Almost all flax plants appeared to survive the fire. They had produced up to 30 cm of new leaf growth after 4 months, but maximum foliage height increased only gradually by 120 months to a maximum height of 180 cm, and maximum cover (in *Sphagnum* bog) of 2%. The *Astelia* sprouted consistently from bases 20–30 cm wide, but it also made only a minor contribution to plant cover (see Fig. 4, 28 months, front left). Not all individuals of red tussock recovered after fire. Many of those which did recover resumed growth initially with only a few tillers (Fig. 4). Increase in cover was slow; by 120 months red tussock had achieved only 15% cover in what must once have been much denser *Chionochloa* grassland. At 69 months seedlings of red tussock were first recorded, as single tillers with just a few leaves, to 80 cm tall.

Other species which resprouted were wire rush (a few plants only, most re-establishment coming later from seedlings), *Baumea rubiginosa* and *Hypolepis ambigua* (both uncommon), and the tuberous orchid *Thelymitra longifolia*. Of the total flora of 69 vascular plant species, 16 of them regenerated by sprouting (Table 4).

Herbaceous plant establishment from seed

A high proportion (c. 70%) of the herbaceous dicotyledons and grasses were fire ephemerals, colonising bare ground as seedlings within a year of the fire, reaching peak cover values for brief periods, then declining or disappearing (Table 4).

Among native species one of the best examples of a rapid but ephemeral colonist was the prostrate herb *Gonocarpus micranthus*. Seedlings appeared 4 months after fire in all vegetation types, reached maximum cover (up to 17%) as circular mats to 30 cm in diameter at either 15 or 22 months, but declined rapidly so that by 69 months after fire only a minor presence remained in just one vegetation type, and by 120 months it was not recorded at any sites. Over the same time, reddish tufts of the leafy rush *Juncus planifolius* reached 5% cover in the wettest vegetation types then subsequently disappeared. Two native grasses (*Rytidosperma gracile* and *Deyeuxia avenoides*) became apparent at 10 or 15 months, reached maximum cover values (10% and 9%, respectively) at 28 months, and had virtually disappeared by 69 months.

The forked sundew, *Drosera binata*, appeared in most transects at 4 months then displayed two peaks of abundance, in the first two summers (10 and 22 months) after fire, and was not again recorded until the next summer sampling, at 120 months. For a small plant like a sundew, a maximum mean cover value of 3.5%, indicates great abundance, surprisingly so considering it would not have been at all common within the pre-fire vegetation, especially in the shade of dense scrub or bracken, other than as a large and well-distributed seed bank in the peat.

Another native mat plant, *Nertera scapanioides*, like *Gonocarpus micranthus*, began establishing on bare peat as early as 4 months after fire, but *N. scapanioides*, being more shade-tolerant, reached its greatest abundance later, at 54 months. *Nertera depressa*, typically a forest plant, was an even later colonist, and was still increasing in abundance up to 69 months in the regenerating *Leptospermum* scrub.

The herbaceous colonists include many naturalised species, which are widespread also as colonists of disturbed ground in many other New Zealand habitats, and as weeds of cultivated soils. Catsear (*Hypochoeris radicata*) had a sustained but low

Table 4 Numbers of ephemerals, sprouters and obligate seeders, and principal propagule sources after fire on Awarua Bog, categorised within five vascular plant groups (data derived from Table 3).

	Number of spp.				Propagule source			
	Total	Ephemerals	Sprouters	Seeders	Canopy	Soil	Wind	Bird
Shrubs & sub-shrubs	12	1	3	9	1	9	1	1
Herbaceous dicots	24	17		24		9	14	1
Grasses	9	7	1	8			9	
Other monocots	16	5	9	7		10	6	
Ferns and lycopod	8		3	5			8	
Totals	69	30	16	53	1	28	38	2

cover in three of the vegetation types. Table 3 includes the many ephemeral colonists of minor occurrence, which tended to occur in the driest vegetation types, especially the *Ulex* (gorse) scrub. At this site, gorse steadily resumed predominant cover (e.g., 69% after 39 months), by which time several other species had shown brief periods of abundance. Yorkshire fog (*Holcus lanatus*) was also common from 4 months, contributing 40% of the cover at 10 months, but it had dwindled to total absence before 39 months. Another naturalised grass, sweet vernal (*Anthoxanthum odoratum*), was less common but present for much the same time. Fireweed (*Senecio minimus*) had a brief presence (6% cover at 4 months) but rapid decline. Several natives were briefly present, sometimes abundantly: *Senecio glomeratus*, *S. biserratus*, *Centella uniflora*, *Gonocarpus aggregatus*, *Epilobium brunnescens*, and *Hydrocotyle heteromeria.*

Woody plant establishment from seed

Manuka was the most common and rapid of regenerating shrub species. All new growth was from seedlings, some apparent only 4 months after fire, many more by 10 months, but with few further recruits apparent at later sampling times, suggesting a single phase of almost synchronous establishment arising from one major seed dispersal event triggered by the fire itself. Manuka is the only serotinous species present at Awarua Bog. At the Kaimaumau Swamp, Northland, in November 1988, I observed fire-blackened capsules of manuka, all freshly opened and releasing their seeds, three days after a major fire (Bellamy et al. 1990, p. 139). It is likely that the January-February timing of the Awarua bog fire would have coincided with the presence of ripe but unopened capsules on the manuka.

Manuka grew rapidly as bushy shrubs (growth form shown in Fig. 5). It was a component of all the post-fire vegetation types, and at 120 months it displayed greatest cover (66%) and height (210 cm) on the site where it had also dominated the pre-fire vegetation. In the *Pteridium* fernland, manuka showed a marked increase between 69 and 120 months, from 19 to 72% cover, as it overtopped the bracken canopy and expanded its crowns above that level.

Seedlings of *Ozothamnus leptophyllus* also appeared by 4 months after fire, having germinated in autumn, while those of *Coprosma ciliata* did not appear until 10 months, suggesting that germination took place only after winter. *Ozothamnus* plants 30 cm tall were recorded in flower 15 months after fire.

Epacrid shrubs were all killed by the fire and were relatively slow to re-establish seedlings. Whereas inaka is prominent as scattered shrubs along with manuka in many established bog vegetation types in this area, its germination lags behind that of manuka. Despite this lag the subsequent rate of growth of the inaka was sufficient for it to have achieved almost the same maximum height as manuka by 120 months (Table 2). As with inaka, the seedlings of *Cyathodes empetrifolia* and *C. juniperina* were first evident 15 months after fire. With all three epacrids, young plants were initially erect and single-stemmed, but in their second season branched profusely from near ground level (Fig. 5). Inaka was flowering heavily by 69 months, when the plants would have been 3–4 years old. The dwarf heath *Pentachondra pumila*, although often abundant in long-established bog vegetation, especially among *Donatia* in cushion bogs, seemed ineffective at re-establishing after fire, only a few plants being recorded.

Gorse seed germinated in the spring after fire and seedlings were 3 cm tall at the 10-month sampling. At 15 months, seedlings of erect, unbranched form were up to 65 cm tall and obvious as scattered colonists up to 50 m from pre-fire mature bushes. At 22 months after fire, some gorse seedlings, although merely 15–20 cm tall, were producing their first flowers.

Bryophytes

The thallose liverwort *Marchantia berteroana* was a prominent colonist especially in the burnt *Leptospermum* scrub, forming ground-hugging initial thalli 1 cm across at 4 months. By 15 months those radiating thalli that were still discernible as individuals were 10 cm in diameter, and had been joined by many younger plants. Maximum cover of 45% was reached at this time, then dwindled steadily to <1% by the last sampling.

Two ephemeral, fine-leaved mosses, *Bryum caespiticium* and *Trematodon mackayi*, appeared in almost all transects by 4 months, reached peak cover values (21% in *Leptospermum* scrub) by 22 months, but declined to complete absence by 54 months. The mosses *Campylopus clavatus* and *C. introflexus* were later colonists, appearing first at 22 months, and with a correspondingly later decline. The thallose liverwort *Riccardia* sp. colonised gradually in slight shade and would be likely to persist under increasingly dense canopies.

Three species of *Sphagnum* are present in the study area: *S. falcatulum* grows in stream pools and was little affected by fire; *S. australe* and *S. cristatum*

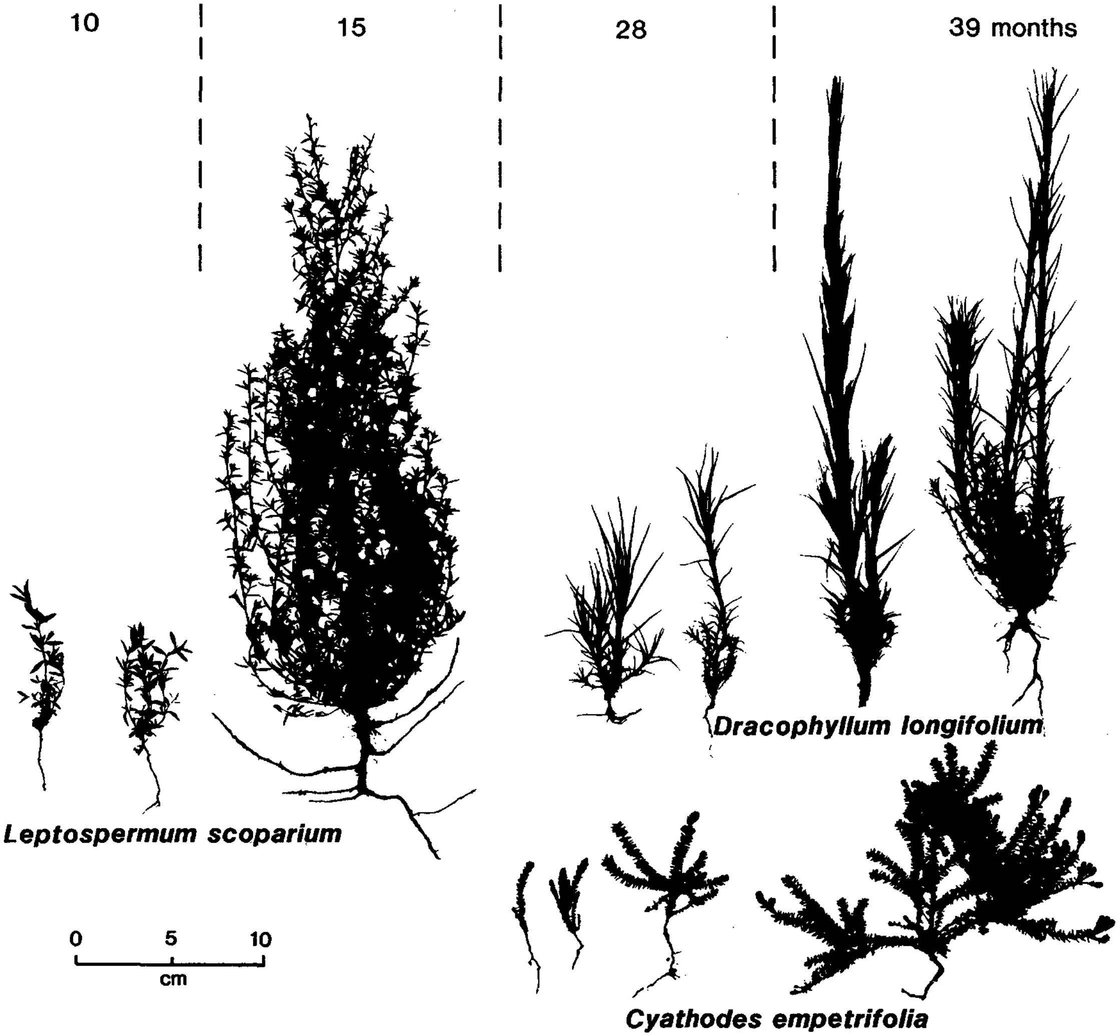


Fig. 5 Form of woody seedlings at four intervals after fire on the Awarua Bog.

occupy moist but not flooded ground, the latter species being the more common. *S. cristatum* recovered only sparingly on the crests or sides of cushions that had been damaged by fire. Most re-establishment appeared to be from spores (rather than from vegetative fragments), as small sessile recruits upon flat surfaces of bare peat, mainly in the broad wet hollow that had formerly been *Sphagnum* dominated, but also less abundantly in the mixed bog type. Initial growth was slow (Table 2), so that in the period from 4 to 15 months the largest plants grew only to 2 cm tall and were typically a single stem with a broad (2 cm diam.) head plus closely adjacent smaller stems. With later expansion and coalescence, the mutually supporting stems of *Sphagnum* plants in the most favourable sites after 39 months underwent substantial height growth, becoming cushions 18 cm tall by 69 months, and 30 cm tall at 120 months. Marked increase in cover happened between 28 and 69 months (Fig. 3D), although the 18% cover at 69 months was not exceeded by 120 months. In the mixed bog, *S. cristatum* and *S. australe* plants were still newly establishing among *Baumea* and wire rush at 69 months after fire.

Recovery of other former dominants

Although much *Baumea tenax* recovered from resprouting rhizomes, seedlings were also frequent, even at 4 months. By 10 months they were 2–7 cm tall and more clearly identifiable. *Baumea tenax* had a substantial presence in all vegetation types except the *Ulex* scrub. Peak cover values occurred at 39 months. Subsequent decline in recorded canopy cover may not be a measure of *Baumea* biomass, but corresponds with marked increases in cover of overtopping manuka in all vegetation types and with the late upsurge in cover of wire rush as this became denser among the *Baumea* culms. Wire rush recovered only to a limited extent from pre-fire plants, but at 10 months seedlings 1–2 cm in height were frequent, and by 28 months the new plants were dense tufts, to 22 cm tall. In most vegetation types, wire rush cover was still increasing its cover at 69 months, at which time many plants were flowering heavily. By 120 months wire rush had further doubled its cover within the *Sphagnum* bog and *Chionochloa* grassland vegetation types.

The clubmoss *Lycopodium ramulosum* was also slow to re-establish much cover, and it retained much of its gain up to the final sampling, even under increasing shade.

Tangle fern, although a co-dominant in pre-fire mixed bog, was slow to reappear after fire, as a few young plants at 28 and 39 months, which at 54 months had fronds only 10 cm tall. Only at the final (120-month) sampling time did it start to become at all obvious, as 4% cover and 40 cm tall, in the *Sphagnum* bog.

Donatia novae-zelandiae cushions were severely damaged by fire and did not recover within the *Leptospermum* scrub transect where they had formerly occupied open areas within the scrub. At 28 months the old cushions were disintegrating to powdery peat, one was being undermined by rabbit burrowing, and the replacement plants were mainly *Marchantia*, mosses, and manuka. Near this transect, at 69 months, regrowth was noted on some former, fire-damaged cushions, and young *Donatia* plants 12–14 cm across were seen in slight hollows of an otherwise level peat plateau.

Evidence of former forest vegetation

Of course, the "pre-fire vegetation types" are really what has survived or been induced by the many fires that have gone before. What sort of longer-lived and probably taller vegetation might have been here were it not for the frequent fires? Two clues were present close to the study area.

First, on an island within one of the many bog tarns, some 300 m NW of the study area, are tall shrubs or small trees of the following forest species, not otherwise found on the fire-prone peatland: *Coprosma foetidissima*, *C. lucida*, *Myrsine australis*, *Pseudopanax colensoi*, and kamahi. Even without a scattering of wind-shorn totara and rimu crowns overhead, it is easy to envisage a low forest, ferny inside, growing in today's climate on the same peat landform where today most people would accept the low bog and heath vegetation as the natural cover.

The second clue is a layer of wood buried about 0.5 m below the surface of the peat, where the peat profile is clearly exposed in a nearby estuary-edge quarry where quartz gravel is mined. Much of the wood is charred, and much of it comprises stem bases attached to their root plates. Manuka was recognisable and common. A selection of wood samples was identified by the late R. N. Patel (Landcare Research) as rimu (5 samples), totara (*Podocarpus hallii*/*P. totara*) (2), manuka (1), and kanuka (*Kunzea ericoides*) (1); the last identification is in some doubt because of difficulties in working with root wood compared with stem wood and because kanuka is not now found in this vicinity. Thus, within the time span of 0.5 m net peat accumulation, probably a few hundred to a few thousand years, a forest cover has been lost by fire at least once. It is probable that in the natural vegetation pattern of the study area herbaceous wetland communities would have occupied just the poorly drained hollows and level crests, as a mosaic within podocarp-broadleaved forest and scrub on the better-drained ground of gentle slopes. Such a pattern can be seen today on the relatively remote and perhaps never burned peat plateau of Ajax Hill, 60 km to the east, and at 700 m a.s.l. (Johnson et al. 1977). At that site, gently undulating peatland holds red tussock grassland and *Sphagnum cristatum* in the stream hollows, while the level crests have cushion bog with wire rush, *Donatia*, and stunted bushes of inaka and manuka. Intervening slopes have a scrub-woodland of inaka, *Coprosma foetidissima*, *C. astonii*, *Phyllocladus alpinus*, *Myrsine divaricata*, and *Libocedrus bidwillii*.

DISCUSSION

Ten years after fire, most of the vegetation types studied had an assemblage of plant species assumed to be similar to that before fire, but probably not to a point of stable composition, judging from the trend of still-changing cover of former dominants up to the last sampling time. *Baumea tenax* had reached its peak cover (60%) at 39 months, bracken (50%) at

69 months, *Sphagnum* appeared to have stabilised at 18% by 69 months, and gorse cover was increasing only gradually between 39 and 120 months. The cover of several former dominants was still increasing between the last two sampling times, especially that of manuka, wire rush, red tussock, and tangle fern.

Rapid regrowth after fire by rhizomatous species, such as *Baumea tenax* in this study, is a feature that has been noted elsewhere, e.g., by *B. tenax* at Eweburn Bog, Southland (Timmins 1992), *Baumea* spp. and *Schoenus brevifolius* in the Whangamarino wetland, Waikato (Irving et al. 1984; Clarkson 1997), *S. brevifolius* in Kaimaumau gumland, Northland (McQueen & Forester 2000), *B. teretifolia* in south Westland (Mark & Smith 1975), and by sedges in Tasmanian wetlands (Kirkpatrick & Harwood 1983).

Dobson (1979) considered that persistently burned oligotrophic mires "have a rather monotonous vegetation of *Sphagnum, Polytrichum, Empodisma, Gleichenia*, and *Drosera*". Wardle (1977) recorded fire-induced pakihi in Westland to be dominated by *Baumea teretifolia*, *Gleichenia*, and *Empodisma*. An almost sole cover of *Empodisma* was taken to indicate the most fire-modified areas of Kepler Mire by Burrows & Dobson (1972).

The abundance together of wire rush, tangle fern, and *Baumea tenax* in "mixed bog", the most widespread vegetation type of Awarua Bog, likewise suggests a history of repeated fires, but it is surprising to find that wire rush is rather slow to recover after fire, and tangle fern decidedly so, at Awarua. Mark & Smith (1975) made a similar observation in South Westland, where four years after fire these same two plant species had regained only some of their former importance. Likewise, Timmins (1992) recorded the slow reappearance of *Empodisma*, from seed, and slow recovery of *Gleichenia* at Eweburn Bog. Similar observations at Whangamarino wetland were related by Clarkson (1997) to the probable susceptibility to fire of the erect rhizome and surface roots of *Empodisma* and the slender rhizomes, at or just below ground surface, of *Gleichenia*.

Ephemeral colonists played a major part in the post-fire flora and vegetation. They included a diversity of both native and naturalised species, many of which displayed a brief period of abundance followed by a rapid and apparently complete disappearance from the vegetation. Normally minor native species of established bog communities, such as *Gonocarpus micranthus*, *Juncus planifolius*, *Nertera scapanioides*, and *Drosera binata*, demonstrated a role as fire ephemerals which must have arisen from a well-stocked and well-distributed seed bank. The two native grasses *Deyeuxia avenoides* and *Rytidosperma gracile*, which were briefly common as colonists, would not normally occur on the bog. The source of their seed, either before the fire or rapidly after it, is most likely to be from the mainly native grassland and shrubland on the Tiwai Peninsula, 2–3 km to the south across Awarua Bay.

The rapid appearance of "weedy" species, both native (e.g., *Senecio minimus*) and naturalised (e.g., Yorkshire fog) on ground where they cannot previously have had a foothold, is a measure of the extent to which this extensive peatland either holds a considerable reservoir of dormant seeds, or else receives a constant supply on the wind. Most of the ephemerals (Table 3) are daisies (8 species), grasses (7), *Epilobium* (3), or *Juncus* (3), having seeds that are light and/or specifically adapted to wind-dispersal. The possible seed sources for many of these species include disturbed ground on road margins, small open sites around the fringes of Awarua Bay, or agricultural land, though in all cases the nearest such source habitats are 1–2 km from the study site.

This phenomenon of ephemeral species, both native and naturalised, playing a brief but major role in plant cover at an early stage of recolonisation after fire has been noted also by Timmins (1992) at Eweburn Bog, by Clarkson (1997) at Whangamarino, and in a non-wetland *Chionochloa ridiga* tussock grassland (Allen & Partridge 1988).

Management implications

The post-fire perennial vegetation is composed predominantly of native plant species. Those naturalised species present are mainly ephemerals, posing few problems for conservation values in the recovering vegetation. The notable exception is gorse, assisted in its spread by fire that opens up the habitat. Gorse is capable of invading wetlands. Despite its large heavy seed gorse can make substantial invasive leaps onto any piece of raised ground, far into a wetland. Probably it is the flattened, winged pod, with its few seeds, which is picked up and spread by wind gusts. At this Awarua study site gorse seedlings were observed in the after-fire vegetation up to 50 m from the nearest parent plants. No doubt the occasional gorse seed will be carried much greater distances than this, leading to a gradual increase in the numbers of discrete infestations and to their eventual expansion and coalescence. As noted by McQueen & Forester (2000) for Kaimaumau gumland, gorse and other nitrogen-fixing shrubs have the capacity to enrich nutrient levels in low-fertility soils, and hence to favour displacement of native vegetation by faster-growing exotics.

What is the future of the Awarua peatland vegetation? With adequate long-term fire prevention and containment it should be possible to manage the area for retention of botanical diversity, wildlife habitat, and natural landscape. Given time, some of today's bracken and manuka communities might give way to a less fire-prone broadleaved-podocarp forest. With a continuing regime of fires, sensitive vegetation types such as cushion bog and red tussock grassland will dwindle further. With or without fire gorse has the potential to colonise much of the peatland. Fire does appear to encourage sudden expansion of already established gorse clumps; but the year or so after a fire also offers opportunity for easy ground access for weed control action.

Although a reserve management plan might idealistically include gorse eradication as a management aim, the more pragmatic move may soon be required of delimiting certain areas as prime conservation estate to be kept free of the weed, while accepting gorse elsewhere as an integral part of tomorrow's vegetation.

The transects remain marked as a reference point for future remeasurement at intervals of several years.

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4 months
10 months
15 months
28 months