

Successional sequences in two Tasmanian valley *Sphagnum* peatlands

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Abstract. The sequences of macrofossils in 17 cores from two Tasmanian valley *Sphagnum* peatlands reveal a wide variety of successional pathways. The most common sequence is from restiad mires to *Sphagnum* mires to heath. While it is impossible to conclusively separate allogenic and autogenic influences, it seems likely that the rapid rate of change recorded in the upper levels of the cores may, in part, reflect recent climatic change. Most other changes recorded in the core are likely to be predominantly autogenic.

Keywords: *Empodisma*; Macrofossil; Mire; Succession.

Nomenclature: Vascular species names follow Buchanan et al. (1989) and *Sphagnum* names follow Scott et al. (1976). Vegetation terminology follows Kirkpatrick (1983).

Introduction

There is a large literature on succession in *Sphagnum* peatlands (e.g. Osvald 1923; Katz 1926; Cockayne 1958; Sjörs 1980; Clymo 1983). In some peatlands there is evidence of cyclic successional change related to the development of hummocks and hollows (e.g. Walker & Walker 1961; Ashton & Hargreaves 1983; Svensson 1988). In other places there is evidence of a sere in which *Sphagnum* is eventually absent. For example, Cockayne (1958) thought that in the North Island of New Zealand the initial *Sphagnum* bog was succeeded by various related combinations of species in which *Cyperaceae* and *Gleichenia* were dominant, with this stage being followed by shrubland or low forest, which may later be replaced by tall forest. Agnew et al. (1993) suggested that *Empodisma* is the key species in ombrotrophic mire development in New Zealand, taking the functional role of *Sphagnum* in boreal systems. However, there are also places in which *Sphagnum* seems to be the final stage in a successional series. For example, Katz (1926) proposed that the 'transition bogs' of Russia formed a continuous developmental series,

with the *Sphagnum* bog complex tending to be the natural climax. These alternative patterns of temporal vegetation change can occur in close proximity (e.g. Sjörs 1980; Heinzelman 1970). Conflicting theories of cyclic change versus directional change led Walker & Walker (1961) to suggest that only an examination of the composition of the most recently formed peats can establish the successional status of any particular bog community.

Tasmania contains most of the area of *Sphagnum*-dominated vegetation in Australia (Whinam et al. 1989). The Tasmanian *Sphagnum* peatlands are largely minerotrophic valley bogs in the subalpine zone (Whinam et al. 1989). Most of these peatlands have formed on Last Glacial till or outwash deposits. While there have been studies of the palynology of this type of bog (e.g. MacPhail 1979), there have been no studies utilizing the well-preserved macrofossils, which, unlike pollen, are of undoubted local origin. While documentation of the nature of plant succession in these bogs cannot, in itself, resolve questions of process, it provides details of the patterns that need to be explained in process terms, and these patterns, if considered in combination with our perceptions of climatic history, and our knowledge of spatial patterning of species in the micro-environments of the bogs, can contribute towards hypotheses of causation. In this paper we use macrofossil and surface vegetation data from 17 cores from two subalpine valley bogs in Tasmania to determine whether there have been consistent patterns of vegetation change. We also discuss the possible causes of these patterns.

Methods

Description of the sites

The Pine Valley (41° 90' S 146° 04' E) and the Little Fisher River (41° 45' S 146° 19' E) sites were chosen because there is a mosaic of *Sphagnum* (primarily *S. cristatum*) with vascular plants and the sites are situated

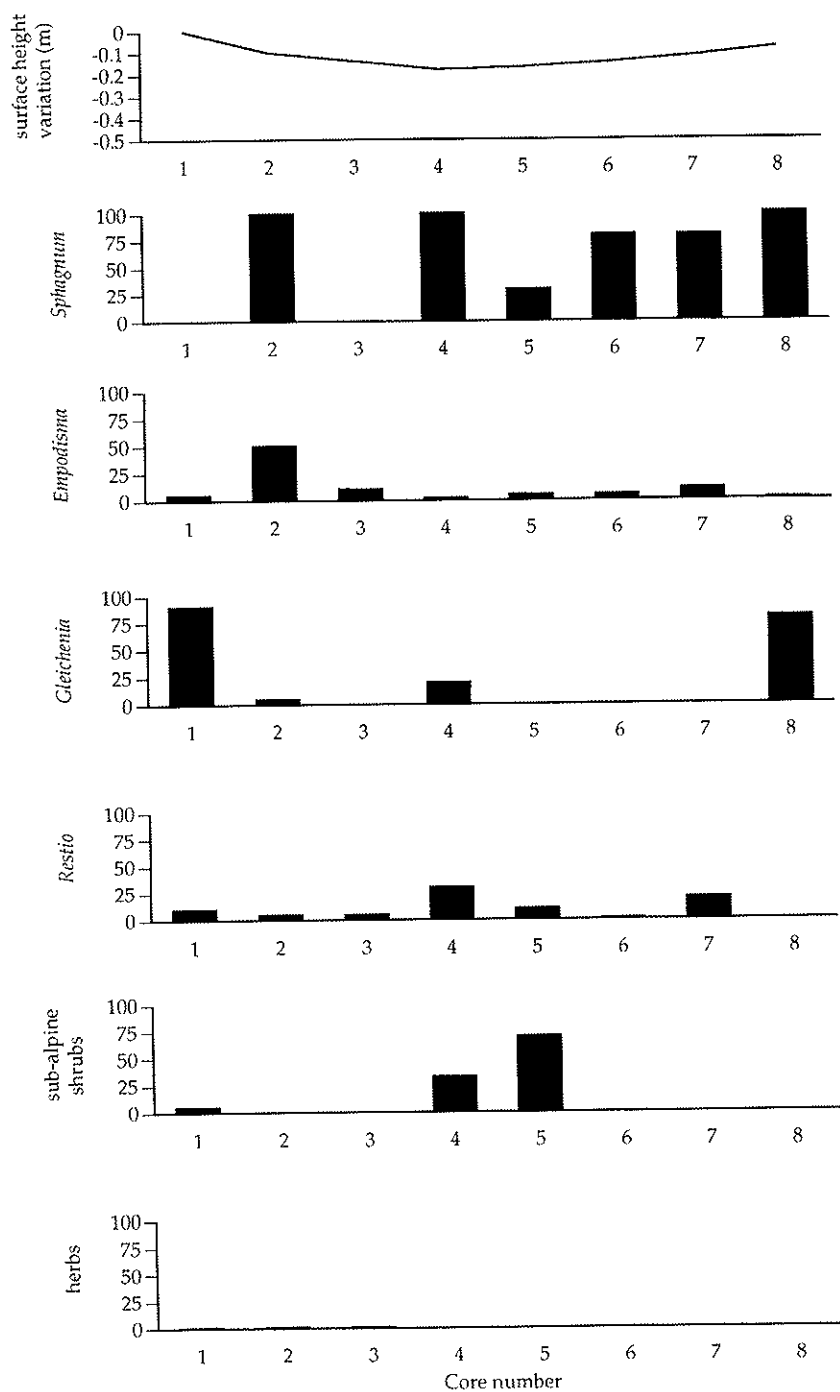


Fig. 1. Topographic cross-section of the Pine Valley mire showing the location of cores and the percentage covers of species and species groups in the present vegetation.

at different altitudes, in different biogeographic and climatically defined Nature Conservation Regions of Tasmania (Anon. 1985).

Pine Valley is a glacial valley north of Lake St. Clair at 760 m elevation, approximately 2 km long and 0.5 km wide. The vegetation is largely heath and sedgeland,

with areas of *Sphagnum* peatland, *Eucalyptus coccifera* woodland and *Athrotaxis cupressoides* forest (Kirkpatrick 1990). The valley is filled by glacial outwash deposits. The headwaters of the Little Fisher River are set in a small glacial valley at 870 m, within the Great Western Tiers. The vegetation is a mosaic dominated

variously by *Gleichenia alpina* (henceforth called *Gleichenia*), *Astelia alpina* (henceforth called *Astelia*), *Abrotanella forsteroides*, *Sphagnum cristatum* and herbs.

Collection and analysis of cores

Eight cores, 30–50 cm in depth, were extracted from each of Pine Valley and the Little Fisher River using a D-section (Russian) corer (5 cm diameter). At Pine Valley the cores were extracted at 50 m intervals on a transect running across the valley. One additional core 1.5 m in depth (core 9) was also extracted from a position approximately intermediate between cores 7 and 8. At the Little Fisher River the *Sphagnum* is confined to one side of the valley, so cores were extracted from the centre of each of the major plant communities in the peatland on that side of the valley. This peatland formed a 50 m wide band between the forests on the slopes and forest on the stream bank. It received drainage from the slope above. Samples were scattered along this linear occurrence. At both sites the water table was at or near the surface. The cores were described in the field and placed in poly-pipe for transporting. Species presence/absence and projected foliage cover were recorded in a 0.16-m² quadrat centred on each extraction hole. The cores were searched for macrofossils in the laboratory using a low magnification binocular microscope. Slices 0.1–2 cm thick were placed in the field of vision and were pulled apart to reveal the nature of the macrofossil content.

Peat depths were measured with a peat probe and surface topography was determined with a tape measure and clinometer. Loss on ignition values were calculated for the remainder of each core after macrofossils were extracted.

A change-over index was calculated by adding the numbers of species and species groups that either disappeared or became apparent between each 10 cm of the cores, and expressing this number as a percentage of the number of species and species groups that were present at both depths.

Results

The transect across Pine Valley revealed that the peatland was concave in cross-section, and that *Gleichenia* was concentrated at the higher altitudes, while shrubs were most prominent in the base of the valley (Fig. 1). There was no consistent pattern in the cover of *Sphagnum*, which was abundant in the surface vegetation of all but cores 1 and 3, from which it was absent. The abundances of *Restio australis* (henceforth called *Restio*) and *Empodisma minus* (henceforth called

Empodisma) also had no distinct relationship with topography.

Sphagnum was present at the deepest sampled level between the surface and 50 cm in all of the Pine Valley cores apart from the two at its margins (Fig. 2). In the higher altitude core 1 *Sphagnum* was absent throughout. In core 8 it was present in the top few centimetres. Between 40 and 30 cm there was only one change in macrofossil composition, with shrubs disappearing from core 2. Between 30 and 20 cm shrubs appeared in core 4 and *Empodisma* invaded core 8. Between 20 and 10 cm shrubs invaded core 7, *Empodisma* disappeared from core 8 (Fig. 2) and *Gleichenia* disappeared from core 9 (Fig. 3). Change accelerated between 10 cm and the surface in cores 1–8 (Figs. 1 and 2) with shrubs and *Gleichenia* invading core 1, *Gleichenia* and *Restio* replacing *Empodisma* in core 2, shrubs, *Gleichenia* and *Empodisma* replacing *Restio* in core 4, shrubs and *Empodisma* invading core 5, *Restio* invading core 6, *Empodisma* replacing shrubs in core 7, and *Sphagnum* replacing *Restio* in core 8.

Core 9 showed little change in the top 65 cm (Fig. 3). However, between 150 and 65 cm there was a transition from peaty clay with *Juncus* macrofossils, to a peat with charcoal from shrubs and *Juncus* remains, to a peat with *Empodisma* and *Restio* macrofossils (Fig. 3).

In the Little Fisher Valley peatlands the successional series were much more diverse (Fig. 4). The deepest sampled macrofossils included *Sphagnum* in 5 of the 8 cores, with *Restio* being the deepest macrofossil in two, and *Astelia* being the deepest in one. *Sphagnum* maintained a presence throughout cores 1 and 6 only, had a very late arrival in core 8 and a late demise in cores 2, 3, 4, 5 and 7. Herbs, subalpine shrubs, cushion plants (*Abrotanella forsteroides*) and *Astelia* variously dominated the surface where *Sphagnum* was absent (Table 1). Nevertheless, *Sphagnum* was present at one depth or another in all cores. As with the Pine Valley cores, most of the change-overs of species and species groups took place between 10 cm and the surface (22), rather than between 10 and 20 cm (5), 20 and 30 cm (8) and 30 and

Table 1. Percentage covers of species and species groups in the surface vegetation of cores from the Little Fisher River.

	Core number							
	1	2	3	4	5	6	7	8
<i>Sphagnum</i>	100	0	0	5	0	100	0	5
Herbs	5	80	75	20	5	2	80	20
<i>Abrotanella</i>	0	0	0	100	0	0	0	0
<i>Astelia</i>	0	0	0	0	2	0	0	100
Sub-alpine shrubs	70	5	10	0	0	2	5	2
<i>Gleichenia</i>	90	5	0	20	0	0	0	80
<i>Carpha</i>	0	0	5	0	0	0	5	0

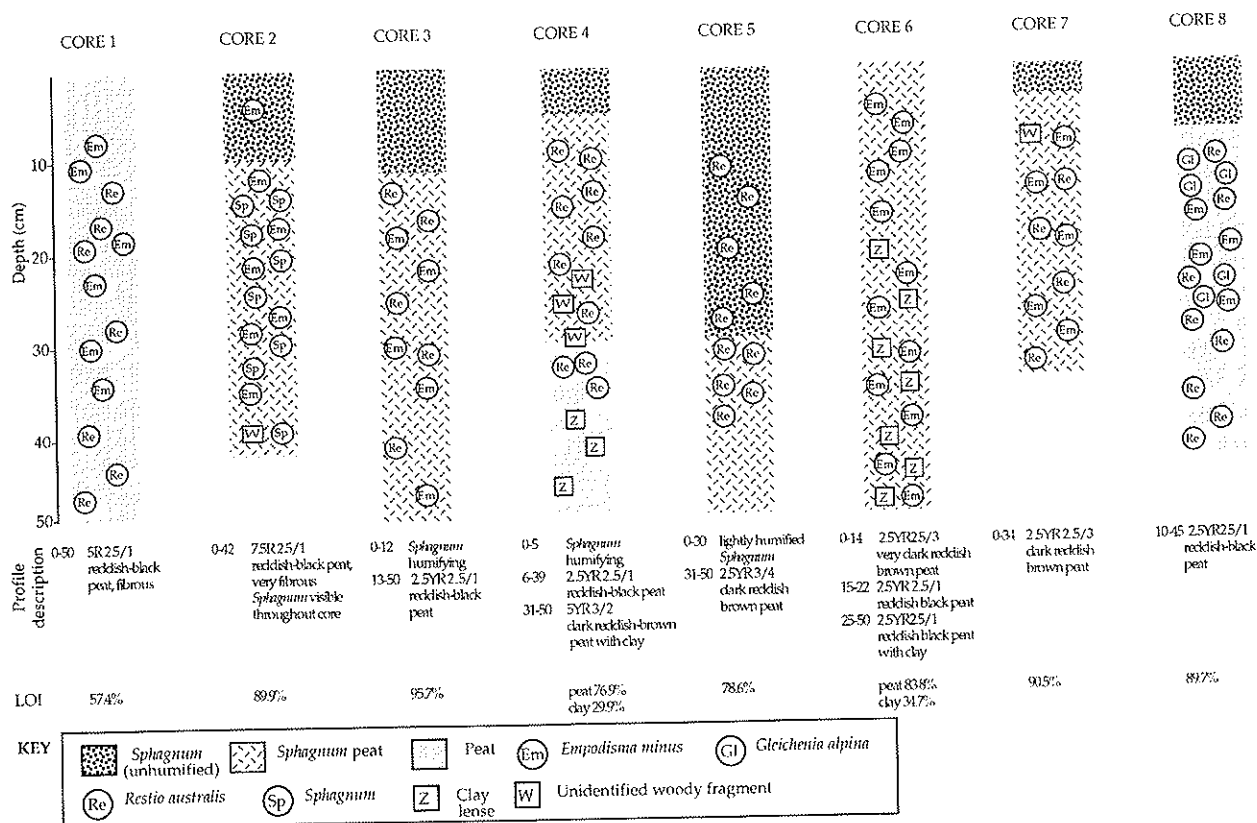


Fig. 2. Details of the Pine Valley transect cores 1 - 8. Vertical measurements are depths (cm) below the surface. Colour notations are from Munsell (1992); LOI = loss on ignition values for the whole core.

40 cm (4) (Fig. 4, Table 1).

Pooling all cores, the change-over index was 181 between 0 and 10 cm, 26 between 10 and 20 cm, 29 between 20 and 30 cm and 23 between 30 and 40 cm.

The change-overs involving *Sphagnum*, out of a possible number of transitions of 61, were: from *Restio* to *Sphagnum* (6); from *Sphagnum* to shrubs, including cushions (4); from shrubs to *Sphagnum* (3); from *Empodisma* to *Sphagnum* (3); from *Sphagnum* to herbs (2); from *Sphagnum* to *Gleichenia* (1); from *Gleichenia* to *Sphagnum* (1); from *Sphagnum* to *Restio* (1). However, in 45 cases *Sphagnum* persisted from one level to the next.

The proportions of cores occupied by *Sphagnum* increased from 67 % at 40 cm to 82 % at 10 cm, before declining to 59 % at the surface (Table 2). *Restio* attained a high proportional representation at 40, 30 and 20 cm and declined towards the surface. *Gleichenia* peaked at 40 cm and the surface. *Empodisma* peaked at 20 cm with its lowest value at the surface. Shrubs and herbs attained their highest values at the surface, with herbs being absent and shrubs infrequent below. *Astelia* was confined to the base and surface of Fisher River core 8.

Discussion

The identified presence of most of the major species that comprise the contemporary vegetation throughout the cores suggests that differential decay rates (Clymo 1987) have not biased macrofossil representation. Herbs and cushions were the only species or species groups not identified below the surface. While cushions are known to preserve well (Gibson & Kirkpatrick 1992), herbs may be absent because of poor preservation.

Radiocarbon dates are not available for any of the cores described. Peat depths cannot be directly correlated with the age of peatlands, due to variations in factors such as peat accumulation rates, peat compression, fire and other erosional events (Simmons & Cundill 1974). However, an indication of the age and general accumulation rates of *Sphagnum* mires in our study area is given by dates from a core extracted from a *Sphagnum* mire covering an area of approximately 10 ha at the nearby Walls of Jerusalem (41° 49' S 146° 19' E). The fibrous peat of this core is underlain by clays, probably lacustrine sediments. The basal radiocarbon date of the peat at 2.0 m is 8270 ± 270 yr BP (ANU 5794). Dates

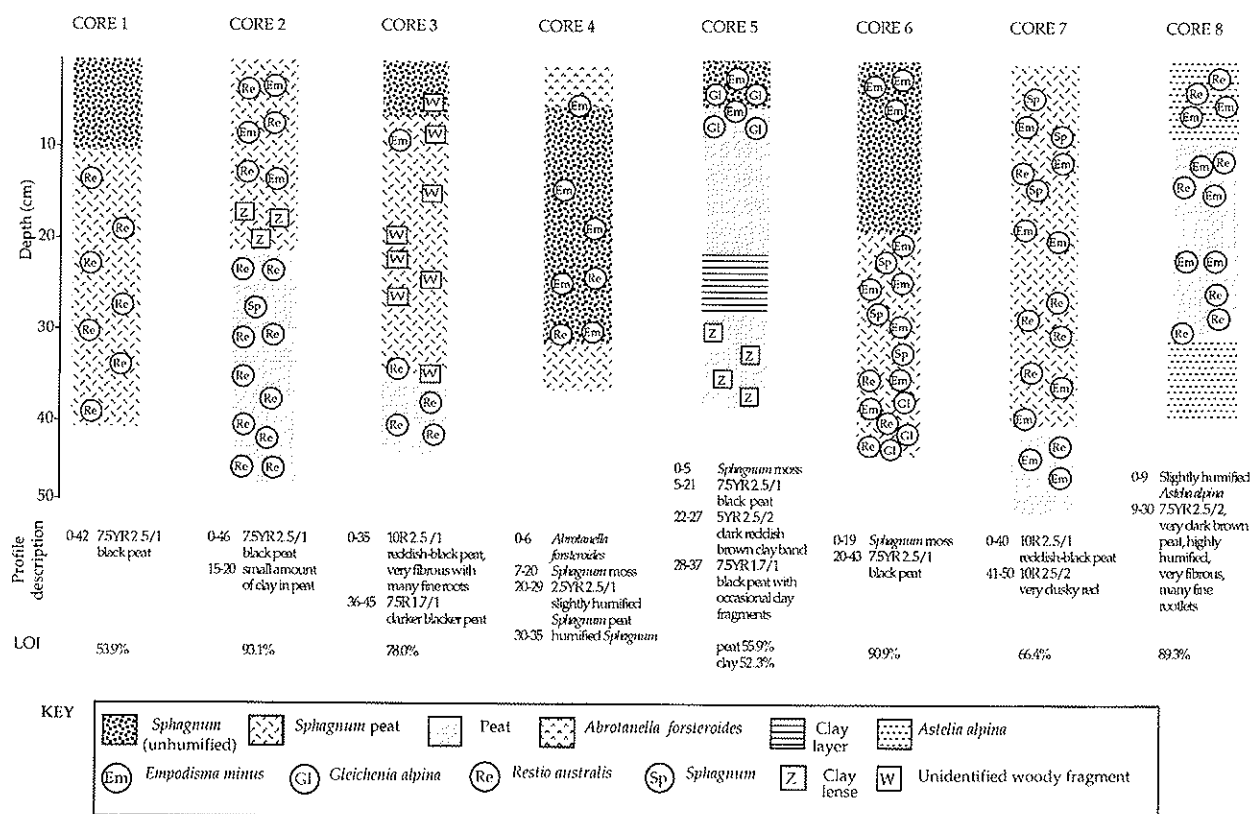


Fig. 3. Details of core 9 from Pine Valley. Vertical measurements are depths (cm) below the surface. Colour notations are from Munsell (1992).

from the same core at 1.6 m are 7350 ± 300 yr BP (ANU 5792) and at 0.7 m 5240 ± 140 yr BP (ANU 5793). One other radiocarbon date is available from a core in *Sphagnum* and sedge peats at another nearby site, Brown Marsh (750 m, $42^\circ 21' S$ $146^\circ 36' E$) on the southern Central Plateau. A sample from 30 - 50 cm of detritus mud underlying 100 cm of *Sphagnum* peat and 70 cm of sedge peat has been radiocarbon dated at 8575 ± 125 yr BP (I-9558, Macphail 1979). These data suggest a possible average peat accumulation rate in the study area of 1 - 2 cm per century, with peat deposition commencing in the early Holocene.

While our analysis of change-over rates between different depths has poor time control, it leaves little doubt that the rate of change in the mires has been greatest in the most recent years, especially considering that any given amount of time is likely to be represented by a greater depth of peat near the surface than at depth. Our subjective selection of cores to represent different end-points in the Fisher Valley may have biased these data towards greater recent change, but the systematically placed cores in Pine Valley show the same pattern, reinforcing its likely reality.

The deep core (9) at Pine Valley (Fig. 3) suggests another period of rapid change, with the colonization of glaciofluvial deposits by higher plants, first graminoids, then shrubs, before the development of *Sphagnum* dominance. Rapid change in a time of primary succession is expected. It is harder to explain the recent dynamism. Alternative hypotheses for this recent rapid change are: (1) that the ongoing accumulation of peat has changed

Table 2. The percentage representation of species and species groups with depth in the 17 cores.

Species/Group	Depth (cm)				
	0	10	20	30	40
<i>Sphagnum</i>	59	82	81	75	67
<i>Restio</i>	41	59	87	81	83
<i>Empodisma</i>	41	59	75	50	50
<i>Gleichenia</i>	35	12	12	12	25
Shrubs	35	12	6	12	8
Herbs	18	0	0	0	0
Cushions	6	0	0	0	0
<i>Astelia</i>	6	0	0	6	0

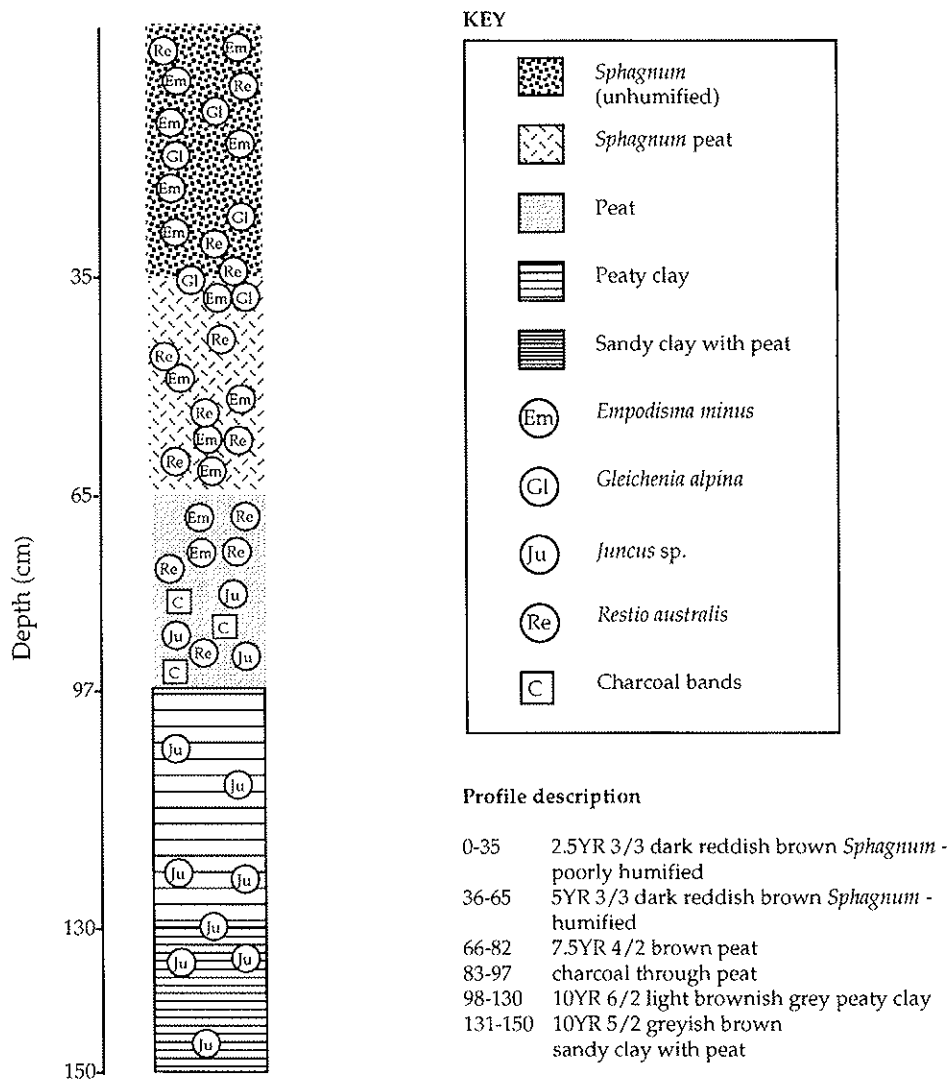


Fig. 4. Details of the cores from Little Fisher River valley. Vertical measurements are depths (cm) below the surface. Colour notations are from Anon. (1992); LOI = loss on ignition values for the whole core.

the hydrology of the bogs; (2) that climatic conditions have changed; (3) that the disturbance regime has changed.

In Pine Valley the most striking feature of the changes between 10 cm and the surface is the invasion of shrubs, and to a lesser extent, *Gleichenia*, on the north-facing slopes and base of the bog. Both the shrub species and *Gleichenia* tend to be more prominent in the drier parts of mires. This patterning suggests that they might invade as the topographic changes induced by increasing depth of peat render the surface less constantly moist. The Pine Valley mire is concave in cross-section (Fig. 1) and minerotrophic, making this hypothesis rest on either the distribution of a constant amount of incoming water into increasingly large volumes of peat and moss,

and/or an increase in the tendency of *Sphagnum* to form hummocks, thus creating local variations in drainage. Almost all bogs at this altitude and on similar underlying geology are largely dominated by shrubs. Thus, local changes in hydrology do not seem an adequate explanation for the recent rapid transformation from *Sphagnum* to shrubs. However, synchronous development of discrete bogs may have occurred, leading to a similar end-point caused by increasing peat depth.

Fire is the only major potential disturbance agent in the Pine Valley area. A change in fire regimes seems an unlikely cause of the rapid changes, as shrub charcoal precedes replacement by *Sphagnum* in the lower parts of several cores, but is absent from the upper parts of the cores. *Richea*, the dominant shrub genus in the mire,

recovers slowly from fire, while *Gleichenia* is favoured by its incidence (Kirkpatrick & Dickinson 1984).

The climatic change hypothesis is consistent with the similarities between discrete bogs. There is no doubt that recent climatic change has been in the direction of decreased moisture availability. Thus, the decline in effective precipitation in the very late Holocene in Tasmania (Goede et al. 1990) and increasing temperatures in the last century or so (Cook et al. 1991; Cook et al. 1992) may have made a strong contribution to the recent relatively rapid rate of vegetation change.

Gleichenia, *Restio* and *Empodisma* are the dominant species in a vegetation type called tall alpine herbfield by Kirkpatrick (1983), and alpine sedgeland by Kirkpatrick (1989). This vegetation type characteristically occurs on shallow peats in waterlogged areas (Kirkpatrick 1983, 1989). Although all three species are found widely in *Sphagnum* bogs (Whinam et al. 1989), their abundance tends to decline with increasing dominance of the moss, although *Gleichenia* is one of the main invaders of senescing moss cushions (Kirkpatrick & Whinam 1984). The data from the cores supports a successional pattern from alpine sedgeland to *Sphagnum* bog as the peat deepens, possibly in response to the root zone becoming independent of the underlying mineral soil and/or changing moisture relations. The successional sequence is particularly striking with *Restio*, which is a frequent precursor of *Sphagnum* in the cores. Nevertheless, with all the common taxa identified from the cores and the surface, there is at least one example of both of invasion by *Sphagnum* and displacement by *Sphagnum*. Such reversals may result from local changes in the bog morphology, or the patch dynamics of the vegetation.

While our results suggest that the most common pattern of temporal change in the two mires is from alpine sedgeland dominated by *Restio*, to *Sphagnum* bog to heath, constancy generally prevailed over change, and both cyclic change and multiple outcomes were evident. The complexity of this temporal change is comparable with that recorded by Walker & Walker (1961), Casparie (1969), Sjörs (1980), Barber (1981) and Glaser & Janssens (1986) from *Sphagnum* bogs elsewhere in the world.

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