Bryophytes of the Tasmanian buttongrass moorlands

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Declaration

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text.

Mikayla Jones

15th May, 2012

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Abstract

The aim of this study was to determine bryophyte richness and species composition in Tasmanian buttongrass moorland, and the effect of environmental variation, in particular time since fire, on bryophyte diversity. Almost nothing has been published on bryophytes in this landscape, despite buttongrass moorland covering approximately 8% of Tasmania and being a key vegetation community in the Tasmanian Wilderness World Heritage Area. Characterised by vegetation dominated by *Gymnoschoenus spaerocephalus*, a large, slow-growing, pyrogenic and tussock-forming sedge, buttongrass moorland is a highly fire-adapted ecosystem and frequently burned. Uncontrollable buttongrass fires spread into other habitats, especially on windy days or when the fuel is particularly dry. However, buttongrass moorlands are also seasonally water-logged, potentially being under water for months, and some areas are subjected to frosts and snow-cover.

This study occurred across a range of scales, from a statewide survey down to the local level. For the statewide survey of bryophytes in buttongrass moorland, 100 sites were located across Tasmania, including the far south, south-west, west, north-west, central and north-east, and across a range of altitudes (10 m - 810 m). Two-hour time sampling of bryophytes was performed at these sites. At the regional scale, two areas were used, Lake Pedder in Tasmania's south-west and Lake St. Clair in the central highlands for complementary studies; a space for time study and a before-after control-impact study. Both sought correlations between the length of time since the site was burned and bryophyte richness and composition. Two much more localised studies were established in the buttongrass moorlands surrounding Lake St. Clair, where the effects of canopy removal and grazing on bryophyte cover were examined. The effects of fire on bryophytes were investigated further by comparing changes to bryophytes after burning, which alters the soil nutrient status and light levels, and changes to bryophytes through slashing the

buttongrass canopy, which alters only light levels. This was done by comparing three recently burnt sites to three sites that had had the canopy mechanically removed through slashing. Also examined at the local level was whether bryophytes were being grazed by vertebrate herbivores after fire in the buttongrass moorlands.

On a statewide scale, overall bryophyte composition was quite uniform across the 100 buttongrass moorland sites, with no differences based on location, although altitude was found to be significantly correlated with composition. On a regional level, fire did not significantly affect bryophyte species richness or composition. In the space-for-time study, liverwort diversity was significantly related to buttongrass age, but this was due to the effects of just a few older sites with higher liverwort richness. The surprisingly poor correlation with fire was supported by the results from the sites established as a before-after control-impact study, even though these sites were not analysed collectively due to design limitations. In contrast, there was a significant difference in the vascular plant species found in the buttongrass moorlands around Lake Pedder compared to Lake St. Clair.

In the two localised studies, bryophytes were not significantly affected by an increase in light levels or found to be eaten by vertebrate herbivores. It is possible that the fruiting capsules of bryophytes were being eaten, because what appeared to be evidence of herbivory was observed on the large fruiting capsules of the moss *Pleurophascum grandiglobum* in a buttongrass moorland plain separate to this particular study. Bryophytes were not found to be significantly affected by an increase in light levels after fire or after mechanical slashing of the overstorey, although there was a significant difference in the effects on bryophytes between the two treatments during the first year.

A relatively limited suite of bryophytes may be able to deal with the challenges associated with life in the Tasmanian buttongrass moorlands. The current management regime of periodic prescribed burning in some areas would appear to be adequate to maintain bryophyte species diversity in this vegetation type, providing a variety of time since fires is retained to facilitate liverwort diversity.

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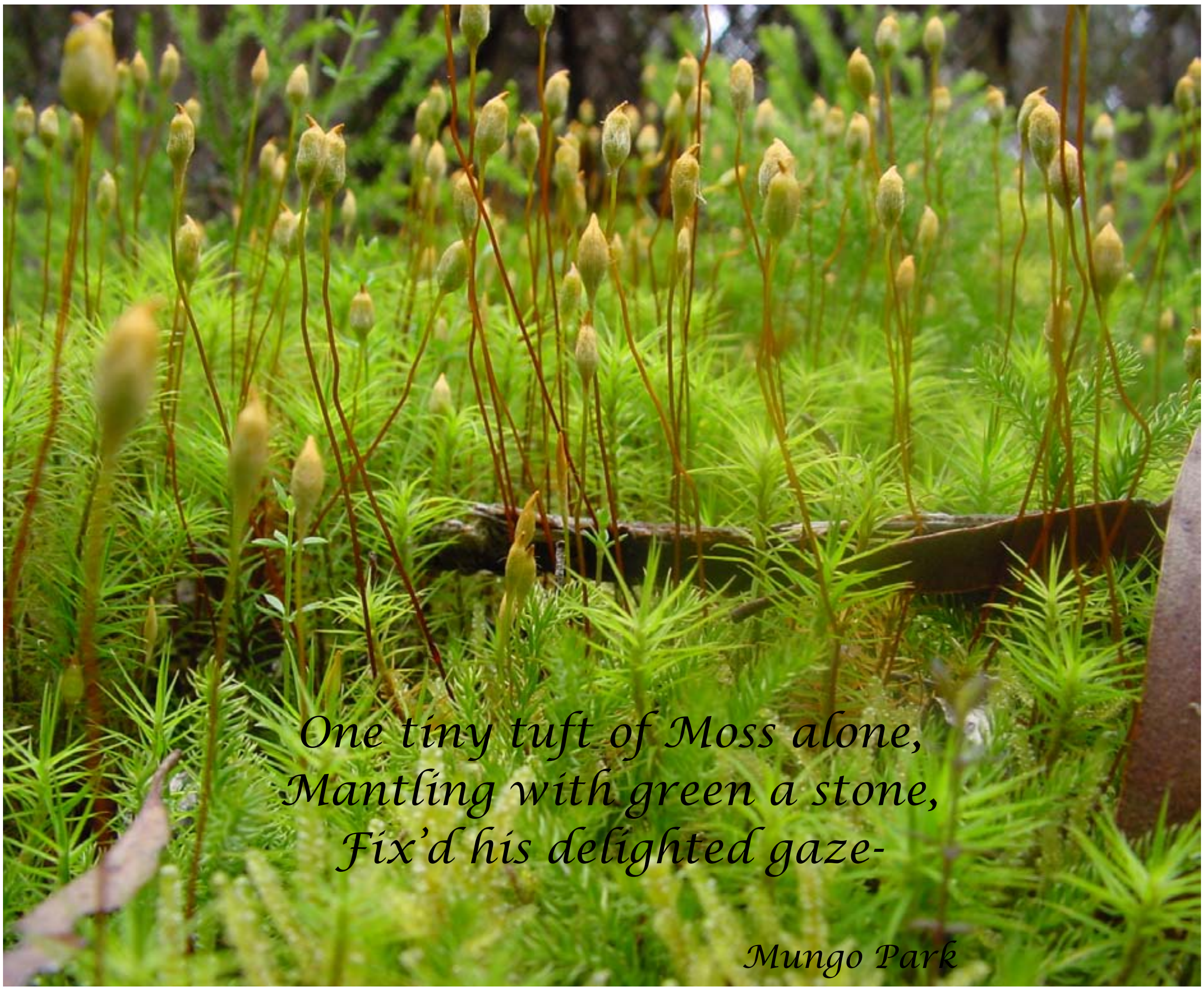
One tiny tuft of Moss alone,
Mantling with green a stone,
Fix'd his delighted gaze-
Mungo Park

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Chapter 1

Introduction

In Tasmania, the island state of Australia, approximately 8% of the land cover is buttongrass moorland (TVMMP 2005). Dominated by *Gymnoschoenus sphaerocephalus,* a large, pyrogenic tussock-forming sedge, the name 'buttongrass moorland' is derived from the round flowering heads of the dominant plant. Buttongrass moorland is a major component of the Tasmanian Wilderness World Heritage Area (WHA), which protects vast tracts of high quality wilderness and harbours a wealth of outstanding natural and cultural heritage (TWWHA Management Plan 1999). There is a high level of endemism within buttongrass moorland, with 34% of vascular plants being endemic to Tasmania, and an additional 2% being endemic to Australia (Lawrence *et al.* 2007). However, little is known about the bryophytes of this environment. This thesis is the first large scale study of bryophyte diversity and environmental correlates in Tasmanian buttongrass moorland.

Bryophytes are less conspicuous in the Australian landscape compared with many Northern hemisphere habitats. It is known from a scattering of local studies that bryophytes can be important components of the terrestrial biota in some Australian environments such as wet forests and semi-arid rangelands (Jarman & Kantvilas 1994; Pharo *et al*. 1999). However, much remains unknown about the ecology of terrestrial bryophytes in Australia.

Thesis aims and objectives

The aim of this thesis is to investigate bryophyte ecology in buttongrass moorland throughout Tasmania, exploring the relationship between bryophytes and geographical location, altitude, time since fire, soil nutrients, grazers, light and physical factors such as buttongrass height and diameter. More specifically, objectives are:

- To compare the diversity of bryophytes growing in buttongrass moorland across the state of Tasmania and to determine if location and elevation affect species composition.
- To determine if there is a relationship between time since fire in buttongrass moorland and bryophyte species richness and composition.
- To determine if bryophyte growth is affected by a change in light levels through the removal of the buttongrass canopy, by fire and by mechanical removal.
- To determine if bryophytes are grazed by vertebrate herbivores after fire in buttongrass moorland.

Buttongrass moorland: an Australian peatland

According to the definitions of the International Mire Conservation Group (IMCG) (Joosten & Clarke 2002), peat and peatland are defined as:

> Peat: "Sedentarily accumulated material consisting of at least 30% (dry mass) of dead organic material."
>
> Peatland: "An area with or without vegetation with a naturally accumulated peat layer at the surface . . . areas with a minimum peat depth of 30 cm."

While the soils underlying buttongrass moorland ecosystems in Tasmania are often described as 'peats' (Bridle & Russell 2005; Jarman *et al.* 1988a; Pemberton *et al.* 2005), analysis has shown that many buttongrass moorland soils have an organic content of less than 30% (di Folco 2007) and are shallower than 30 cm (Balmer 1991). However, these buttongrass moorland organosols cover an extensive area of Tasmania and contribute substantially to soil organic carbon stocks (di Folco 2007). While they may not classify as peatland by the IMCG definition, they are an important environment for Australia, where peatlands are unusual (Whinam *et al*. 2001).

Peatlands harbour approximately one third of the world's soil carbon and 10% of global freshwater resources (Joosten & Clarke 2002), and are recognised as important ecological communities (Joosten & Clarke 2002). In Australia, peatlands are largely in poorly drained, relatively infertile sites of montane and alpine altitudes (Whinam *et al*. 2001). Internationally, many peatland ecosystems are dominated by bryophytes, particularly *Sphagnum* (Gajewski *et al.* 2001), and lichens (Rydin *et al.* 2006). Peatlands in Australia dominated by *Sphagnum* have a restricted distribution and are usually small in area (Whinam *et al.* 2001).

Considerable attention has been paid to the peat bogs of New Zealand, with the effects of fire on vegetation being investigated (Clarkson 1997; Johnson 2001; Norton & De Lange 2003; Timmins 1992), along with the general vegetation composition of New Zealand bogs (Mark *et al.* 1979; McQueen & Bastow 2000). A wide range of topics have been researched internationally in regards to peatlands, including restoration (Sliva & Pfadenhauer 1999; Smolders *et al.* 2002; Smolders *et al.* 2003), post-fire dynamics (Benscoter 2006; Benscoter *et al.* 2005) and bryophytes (Campeau & Rocheford 1996; Duckett & Clymo 1988; Faubert & Rochford 2002; Gignac *et al.* 1991; Groeneveld & Rocheford 2005; Whinam *et al.* 2001)

An overview of buttongrass moorland

Buttongrass moorland occurs in other areas of south eastern Australia (South Australia, Victoria, New South Wales), although not as extensively as in Tasmania. Buttongrass moorland has been classified into two groups in Tasmania based on floristic and terrain factors – 'blanket moor' and 'eastern moor' (Jarman *et al.* 1998a). The majority of buttongrass moorland in Tasmania is blanket moor, occupying extensive tracts of pre-Carboniferous substrates in western and south western Tasmania (Figure 1.1). Blanket moor covers a range of landscapes, from steep slopes to flat valleys, and plateaux to ridges (Brown 1999). Eastern moor is restricted to poorly drained landscapes and is less common, dominating in eastern and north western Tasmania, notably on the Central Plateau with its boggy flats and uplands (Figure 1.2). Both blanket and eastern moor have highland and lowland forms (Jarman *et al*. 1988a). Whilst highland and lowland blanket moor share species, they contain some species which are characteristic (Table 1.1). For lowland and highland eastern moor, the dominant species or most conspicuous plants occur in both groups (Jarman *et al*. 1988a) (Table 1.1). Buttongrass moorland is formed from a mosaic of communities comprising sedgelands, heathlands, graminoid heathlands, scrub and low forests (Jarman *et al.* 1988b). However, in scrub and low forests, buttongrass moorland usually displays weak growth, suggesting that the species is approaching its ecological limit (Jarman *et al*. 1988a).

Buttongrass moorland is sparsely treed or treeless, and can include small areas of treeless vegetation that do not contain *G. sphaerocephalus* but which are surrounded by communities in which *G. sphaerocephalus* is present (Brown 1999). In spite of the challenging environment, buttongrass moorlands are floristically diverse in vascular plants, with approximately 202 species from 50 families (Jarman *et al*, 1988a), 34% of which are endemic to Tasmania (Lawrence *et al.* 2007). Present alongside the more obvious vascular plants are the less visible lichens and bryophytes, including *Sphagnum*. Although *Sphagnum* is rarely abundant in Australia, it does occur, mainly in alpine environments in south eastern Australia and in buttongrass moorlands in Tasmania where it is usually located around the perimeters of montane buttongrass plains and along drainage lines (Whinam 2007).

Figure 1.1. Blanket moor, Lake St. Clair.

Figure 1.2. Eastern moor, Ansons Bay Road.

Table 1.1. Main indicator species for lowland blanket moor, highland blanket moor and eastern moor. Table modified from Brown (1999).

Plant group	Lowland blanket moor	Highland blanket moor	Eastern moor
Shrubs	*Agastachys odorata*	*Dracophyllum milliganii*	*Baeckea gunniana*
	Baeckea leptocaulis	*Eucalyptus vernicosa*	*Callistemon viridiflorus*
	Boronia pilosa		*Epacris gunnii*
	Epacris corymbiflora		*Leucopogon pilifer*
	Eucalyptus nitida		*Pultenaea subumbellata*
	Leptospermum nitidum		*Pultenaea dentate*
	Monotoca submutica		
Forbs	*Actinotus bellioides*	*Actinotus moorei*	*Erigeron pappochroma*
	Oschatzia saxifrage	*Anemone crassifolia*	*Gonocarpus micranthus*
	Helichrysum pumilum	*Diplaspis cordifolia*	*Helichrysum japonicum*
		Erigeron stellatus	*Hydrocotyle* spp.
			Hypericum japonicum
			Mitasacme pilosa
Monocotyledons	*Calorophus* sp.nov.	*Isophysis tasmanica*	*Deyeuxia* spp.
	Restio monocephalus	*Lepidosperma lineare* var. *inops*	*Poa* spp.
	Schoenus biglumis	*Oreobolus acutifolius*	*Restio australis*
	Winifredia sola		*Thelionema caespitosum*
	Xyris marginate		
Ferns			*Gleichenia alpina*

The vascular floristics of buttongrass moorland have been well-documented by Jarman *et al*. (1988a), with some limited work on the non-vascular component of buttongrass moorlands also being carried out (Ferguson *et al.* 2009; Jarman *et al.* 1988a; Kantvilas & Jarman 1991). A more exhaustive study has occurred into the lichens of the buttongrass moorlands than the bryophytes (Kantvilas &

Jarman 1988). The flammability, fuel loads and fire management regimes of buttongrass moorlands have been extensively investigated (Marsden-Smedley & Catchpole 1995a; Marsden-Smedley & Catchpole 1995b; Marsden-Smedley & Catchpole 2001; Marsden-Smedley & Kirkpatrick 2000; Marsden-Smedley *et al.* 1999; Marsden-Smedley *et al.* 2001).

Vertebrate fauna have been well studied in the buttongrass moorlands (Driessen 2006). Most vertebrates found in the buttongrass moorlands also occur in other habitats, and buttongrass moorland is the primary habitat for only six species of vertebrate, the Broad-toothed Mouse (*Mastacomys fuscus*), the Ground Parrot (*Pezoporus wallicus*), the Striated Fieldwren (*Calamanthus fuliginosus)*, the Southern Emu-wren (*Stiputurus malachurus),* the endemic Tasmanian Tree Frog (*Litoria burrowsae)* and the endemic Swamp Galaxias (*Galaxias parvus*) (Driessen 2007). The invertebrates of buttongrass moorlands are dominated by springtails, crickets, flies, ants and soil mites (Driessen 2006; Greenslade & Smith 1999). The diversity of soil mites in relation to vegetation age has also been investigated in Tasmanian buttongrass moorlands (Green 2007). Freshwater burrowing crayfish in the three genera *Ombrastacoides, Spinastacoides* and *Engaeus* extensively colonise the buttongrass moors, and their biology, habitat requirements, distribution and feeding are well studied (Growns & Richardson 1988; Richardson & Swain 1980; Suter & Richardson 1977). These burrowing crayfish satisfy the criteria for ecological engineers because their burrows influence soil processes (Richardson 1983) and potentially plant growth (Richardson & Wong 1995). The burrows and associated pools also provide habitats for invertebrates and pygmy mountain shrimps (Richardson & Doran 2007).

The buttongrass moorlands of Tasmania offer a challenging environment for biota. Buttongrass moorlands are seasonally waterlogged, potentially under water for months. Buttongrass moorland is generally a low nutrient environment, located on a range of substrates but with the greatest extent on low-fertility quartzite, conglomerate, granite or derived gravels (Jarman *et al.* 1988a). As a consequence, a high degree of scleromorphy is found in the buttongrass moorland vegetation (Pemberton *et al.* 2005). Scleromorphy increases the flammability of the vascular vegetation, and during warmer months buttongrass moorlands can become extremely dry and prone to fire, although they can still burn when fuel moisture is high (Marsden-Smedley & Catchpole 1995b).

Fire and buttongrass moorlands

Australian plant communities have evolved to survive in the face of a fire-prone environment (Attiwill & Wilson 2003). Buttongrass moorland is a highly fire-adapted ecosystem and frequently burned, both naturally (lightning strikes) and by humans. Buttongrass moorland is a key vegetation community in the Tasmanian World Heritage Area, and presents a special challenge to land managers given the pyrogenic nature of *G. sphaerocephalus* and the need to protect contiguous vegetation communities such as wet forest and alpine vegetation from fire. Uncontrollable buttongrass fires can spread into neighbouring habitats, especially on windy days or when the fuel is particularly dry (Marsden-Smedley *et al*. 1999). Some areas of buttongrass moorland have been subjected to fuel reduction burns for many years in an attempt to protect nearby forests from unplanned fires (Jarman *et al*. 1988a). In recent years, land managers have increased the frequency of planned burning in some buttongrass areas (J.B. Marsden-Smedley pers. comm.). Following burning, most of the herbs and graminoids recover quickly, taking advantage of the temporary increase in nutrients and light available between charred buttongrass tussocks, whilst shrubs recover more slowly, usually by seed (Corbett & Balmer 2007). The recovery patterns of non-vascular species, the lichens and bryophytes, have only been investigated in one localised study (Ferguson *et al.* 2009).

Bryophyte biology: features for survival in harsh environments

Mosses, hornworts and liverworts, together known as 'bryophytes', are small non-vascular plants that lack the elaborate internal water conduction system of vascular plants. Having only a fraction of the diversity of vascular plants, bryophytes number as many as 20,000 species worldwide. They are more flexible than vascular plants, inhabiting nearly every ecosystem on Earth including the most hostile environments with few vascular plant species (Scott 1994). Like vascular plants, the abundance and distribution of bryophytes is driven by a variety of physiological and environmental factors (Aude & Ejrnæs 2005; Dzwonko & Gawroński 2002; Morgan 2004; Proctor 2000; Smith Merrill 1991; van der Wal & Booker 2004). Some features of bryophytes give them particular resilience in harsh environments such as buttongrass moorlands, and these features represent significant differences to the ways in which vascular plants are adapted to harsh environments. First, bryophytes are 'poikilohydric', which means that their cells are not damaged by drying (Proctor & Tuba 2002) resulting in many bryophytes being able to wait out unfavourable conditions, such as exposed soil baked by the summer sun in recently burnt buttongrass moorlands. Second, bryophytes exhibit 'totipotency', which means they can regenerate from small fragments, including just individual cells, without any apparent special conditions (Scott 1994). In such a disturbance-prone environment as buttongrass moorland, this could prove a distinct advantage. Third, the majority of bryophytes can absorb water, mineral salts and gases over much of their surface and substances can move adequately directly from cell to cell (Proctor 2000). This enables many bryophytes to survive in microhabitats not commonly inhabited by vascular plants, such as on trees, branches, dead wood, and rocks (Pharo & Blanks 2000), or growing in the tussock base of buttongrass tussocks.

Bryophytes and ecosystem function

In order to set the scene for this investigation of terrestrial bryophytes and their response to the changes associated with fire, in particular, changes in light and nutrient status, the literature was surveyed to determine what is already known about terrestrial bryophytes and their role in ecosystem function. Little work has been published on Australian bryophytes and nutrient relations, with the only published studies being the post-fire work of Brasell and colleagues (Brasell & Mattay 1984; Brasell *et al.* 1986) and Bridle and Kirkpatrick (2003), which focused on the impact of nutrient additions on plants, including moss. However, in some overseas work, bryophytes emerge as a major factor influencing nutrient dynamics in some environments (Binkley & Graham 1981; Carr *et al.* 1980; Chapin *et al.* 1987; Clark *et al.* 2005; Hsu *et al.* 2002; Li & Vitt 1997; Rieley *et al.* 1979; Weber & van Cleve 1984;).

Whilst no work into the functional role of bryophytes in buttongrass moorland has been carried out, some of the functional roles terrestrial bryophytes have been found to play in other environments, which may also be at play in buttongrass moorlands, include:

1. Acting as reservoirs of macronutrients, such as nitrogen and phosphorus (Carr *et al.* 1980; Chapin *et al.* 1987; Clark *et al.* 2005; Hsu *et al.* 2002; Li & Vitt 1997; Rieley *et al.* 1979; Weber & van Cleve 1984). Binkley and Graham (1981) found that ground-layer mosses in an old-growth Douglas-fir forest accounted for only 0.13% of the aboveground biomass, yet they added 10% to estimates of forest uptake of nitrogen and phosphorous. In Australia, there is no equivalent environment of the *Pleurozium, Hylocomium,* and *Ptilium* feather moss carpets of the northern hemisphere. The most similar environment would be our rainforests where bryophyte abundance is high and vascular understorey vegetation is sparse (Jarman *et al.* 1991).

2. Trapping airborne silts and clays amongst their stems in dry environments such as deserts (Danin & Ganor 1991) and rangelands (Eldridge & Greene 1994; Eldridge & Tozer 1996; Eldridge *et al.* 2000). Work in the arid rangelands of Australia has shown that bryophytes in soil crusts are acting to stabilise soil and reduce erosion and enhance infiltration (Eldridge & Greene 1994; Eldridge *et al.* 2000). Even when dead, the soil crust was found to help stabilise the soil surface. The roughened surface of soil crusts or bryophyte mats also allow small amounts of water to accumulate on the soil surface (Eldridge *et al.* 2000). Given the exposed soil conditions of the buttongrass moorlands post-fire, this may be a role bryophytes are playing in this environment. Experiments outside of Australia have shown that bryophyte cover can also drastically reduce the amount of frost heave experienced by soils (Groeneveld & Rochefort 2005), thereby stabilising the soil surface, reducing erosion and aiding the establishment and survival of other plant species. In winter the buttongrass moorlands are commonly exposed to severe frosts, therefore the reduction of frost heave may be another potential role of bryophytes in the buttongrass moorland environment.

3. Influencing the germination, establishment and survival of vascular plants, thereby playing a role in their distribution (Sedia & Ehrenfeld 2003). In the northern hemisphere, bryophytes have been found to both prevent (Densmore 1992; Harmon & Franklin 1989; Hörnberg *et al.* 1997), and assist (Bell & Bliss 1980; Cross 1981; Delach & Kimmerer 2002; Sedia & Ehrenfeld 2003) vascular plant establishment and survival depending on the environment, community involved, and even the year, with variation in climate having an effect on the outcome. Very thick moss mats can inhibit the germination of vascular plant seeds that require a high red/far red ratio (Zamfir 2000). Thick moss mates can also prevent germination because vascular seedlings can simply be too short to reach

the soil beneath them and also the light above them (Cross 1981; Harmon & Franklin 1989; St. Hilaire & Leopold 1995). In Australia, Eldridge *et al.* (1991) examined cryptogamic crusts (which included bryophytes) and a range of other substrates (e.g. litter, scalds, bare ground) in terms of the number of *Atriplex vesicaria* seedlings each supported and found no particular microsite supported greater seedling survival. Morgan (2006) found that bryophyte mats carpeting intertussock spaces in temperate native grassland remnants in western Victoria prevented the establishment of non-native species.

It may be possible that vascular plant development in some Tasmanian environments is inhibited by the secondary compounds found in bryophytes (Asakawa 1990; Matsuo & Nadaya 1987). Extracts from *Sphagnum capillaceum* plants were found to inhibit the germination of *Pinus banksiana* in laboratory trials (Brown 1967). However, this needs to be balanced against the potential improvement in moisture conditions for seeds and seedlings by landing on bryophyte mats rather than bare ground (Hörnberg *et al.* 1997; Kinnaird 1974; Sohlberg & Bliss 1987). In the highly disturbed ecosystem of milled peatlands in Québec, *Polytrichum strictum* reduced frost heave and prevented seedlings being ejected from the ground (Groeneveld & Rochefort 2005).

Bryophytes in the post-fire Tasmanian environment

In Tasmanian wet forest, bryophytes can dominate the post-fire ground cover during the first five to ten years after fire (Cremer & Mount 1965), with the main cover on burnt ground being *Marchantia berteroania* and *Funaria hygrometrica* rather than vascular plants (Duncan & Dalton 1982). Brasell and Mattay (1984) found that this dense covering was maintained for 14 to 38 months after burning. The effect of the bryophyte cover had been to harness some of the mineral nutrients and release them to the rest of the ecosystem directly by decomposing after a relatively short life span (Brasell & Mattay 1984). Different species of bryophyte absorbed different mineral elements, with 'high concentrations' of nitrogen (Brasell & Mattay 1984). This effect may be short-lived given that a Spanish study in burnt Mediterranean forests found that once perennial species removed pioneer and competing bryophyte species, the nitrogen content under those turfs was similar to that of unburnt sites (de las Heras *et al.* 1996).

A more significant functional role for bryophytes post-fire may be in soil stabilisation, although there have been fewer studies published on this topic (Figure 1.3). Although not post-fire, the soil crust work of Eldridge and Tozer (1996) in Eastern Australia shows that bryophytes (as part of the soil crust) contribute to soil surface stability by reducing raindrop energy.

Figure 1.3. The moss *Campylopus* sp. present in a recently burnt buttongrass moorland (burnt six months previously).

It is possible that some of the mechanisms outlined above are at work in Tasmanian buttongrass moorland, in particular trapping sediments by bryophytes following disturbance and the severity of frost heave being softened by a groundcover of bryophytes. However, Tasmania lacks the thick carpets of bryophytes found across the boreal forest floor. The only terrestrial bryophyte cover in Australia that is as thick and expansive as in some of the northern hemisphere studies are some *Sphagnum* mats. This thesis establishes the ground work for understanding bryophytes in buttongrass moorland by documenting response to changes in vascular plant structure and composition, change in light and nutrient status, and following the exclusion of grazers. However, there is still much to be done to develop our functional understanding of bryophytes in buttongrass moorland that could not be included in this thesis.

Bryophytes and grazing

Internationally, bryophytes are an important food-source for some animals, such as lemmings and reindeer (van der Wal & Brooker 2004; Virtanen *et al.* 1997), particularly when resources are scarce. It is not known to what extent bryophytes are utilised as a food source for native Australian animals in a post-fire environment, although Cremer and Mount (1965) observed that the fruiting bodies of mosses and the thallose liverwort *Marchantia* were browsed by native animals following fire in Tasmania. A study in the United States documented slugs consuming both immature fruiting bodies and protonema of bryophytes, but reported that neither vertebrate nor invertebrate herbivores freely consume bryophytes (Davidson *et al.* 1990). They reported negligible consumption of mature moss leaves by slugs, even after seven days of starvation! This suggests that even invertebrate herbivory of bryophytes may be minimal in post-fire environments. However, without documented studies, no supportable conclusions can be drawn. It may be that, in the harsh environment of recently burnt buttongrass moorlands, bryophytes are a valued food source.

Thesis structure

Chapter 2 provides an inventory of the bryophytes found on the ground in buttongrass moorlands across Tasmania, ranging from the far southwest to the northwest, from the west coast to the east coast. The differences in location and altitude are compared to the bryophyte species found.

In Chapter 3, the influence of time since fire and soil nutrient status on bryophyte and vascular plant richness and diversity is investigated. The effect of the physical structure of the overstorey (buttongrass characteristics) on bryophytes is also addressed.

Using sites previously established for a before-after control-impact study in buttongrass moorland in southwest Tasmania, Chapter 4 explores the relationship between time since fire and bryophyte composition and biomass in more detail.

Chapter 5 presents a comparison of the response of bryophyte cover to light through two treatments: mechanical removal of the overstorey through slashing and fire.

The purpose of Chapter 6 is to report on whether vertebrate herbivores are eating the moss patches that survived a recent fire in buttongrass moorland. This chapter was published in the December 2007 - February 2008 issue of The Tasmanian Naturalist. Minor alternations have been made to this published and peer-reviewed paper for inclusion in this thesis.

Finally, Chapter 7 consolidates the various themes of this thesis together by discussing the significance of fire, nutrients, geography and altitude on bryophytes of the buttongrass moorlands and the implications for management and conservation. Recommendations for future research are made.

Each chapter has been written in the format of a journal article, therefore some repetition has been unavoidable. Referral to a previous chapter for information is made where appropriate.

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Chapter 2

A statewide survey of bryophytes in Tasmanian buttongrass moorlands

Abstract

In Tasmania, buttongrass moorland is a common feature, covering approximately 8% of the state. Buttongrass moorland can dominate the landscape, being present as continuous moorlands in wetter north western, western and south western areas, but it occurs as smaller isolated plains in the drier north east and east. This is the first comprehensive survey of bryophytes in buttongrass moorland. One hundred, two hour searches were undertaken in buttongrass moorland sites from a range of different landscapes across Tasmania. Bryophyte diversity was low, with a total of 62 bryophyte species being collected and an average of 7.4 species per site. Bryophyte composition was found to be significantly correlated with altitude but not to geographical location. Buttongrass moorland is environmentally extreme in terms of soil moisture conditions, soil acidity and frequency of disturbance in the form of fire. These factors, in combination with the relatively homogeneous array of vascular species, appear to support a subset of bryophytes adapted to such extreme conditions.

Introduction

Buttongrass moorland is a vegetation type unique to Australia. Its name is derived from the sedge, *Gymnoschoenus sphaerocephalus*, which has round flowering heads ('buttons'). It is present in South Australia, Victoria and New South Wales, but it is most widespread in Tasmania. In Tasmania, buttongrass moorland can dominate the landscape in wetter north western, western and south western areas, occupying large continuous moorlands as well as smaller isolated pockets in the drier north east and east. Buttongrass moorland is a highly variable environment, varying from extremely dry in summer to seasonally inundated in winter and is subjected to frost and periodic snow cover.

Buttongrass moorland has been classified by Jarman *et al.* (1988) into two groups based on floristic and landscape characters, blanket moor and eastern moor. Blanket moor is found in the western part of the state where rainfall is high, extending over a range of topographies – poorly drained flats to well drained slopes, steep ridges to hilltops, with uninterrupted tracts of buttongrass occurring over a broad altitudinal range (Jarman *et al.* 1988). Eastern moor occurs as more isolated patches mainly in northern, central and eastern Tasmania, in poorly-drained depressions, gullies or flats, with no extensive plains covering a range of altitudes (Jarman *et al.* 1988). Buttongrass moorland occurs on nutrient-poor soils (Brown 1993), eastern moor developing on alluviums or associated with basalt, dolerite, granite, conglomerate or quartzite rocks, whilst blanket moor occurs over infertile rock types, mainly quartzite, conglomerate or granite (Jarman *et al*. 1988).

Buttongrass moorland is highly pyrogenic, containing many vascular plant species able to survive or regenerate after fire (Brown 1999). Buttongrass itself is highly sclerophyllous, with resinous leaves which burn at a higher moisture content and higher relative humidity than other monocotyledons such as grasses (Brown 1999). Buttongrass moorland is burnt through hazard-reduction burns, habitat-management burns and wildfires and will burn over a wide range of moisture conditions (Marsden-Smedley *et al*. 1999).

The vascular flora of the buttongrass moorlands is diverse, with more than 272 species from more than 50 families (Lawrence *et al*. 2007). Much less is known about the non-vascular flora. A preliminary survey of the bryophytes (mosses and liverworts) in buttongrass moorland was published by Jarman (1988), and consisted of eight moss species and seven liverwort species. The bryophytes found in buttongrass moorland on Mt Sprent in the state's southwest have been documented (Kantvilas & Jarman 1991), as have those found in the buttongrass moorland at localised spots on Mathinna Plains, in north eastern Tasmania (Ferguson *et al.* 2009). A comprehensive list surveying the buttongrass moorlands in all major regions of the state has not been undertaken despite the importance of this unique community of international conservation significance. This study aimed to provide such a comprehensive list of bryophytes for buttongrass moorland. The effect of geology, area and altitude on buttongrass moorland bryophytes throughout Tasmania was examined.

Method

One hundred buttongrass moorland sites throughout mainland Tasmania were surveyed for bryophytes, from the far southwest of Tasmania to the far northwest, and in Tasmania's east (Figure 2.1). Sites were selected to ensure sampling over all environmental ranges over which buttongrass occurs, e.g. both lowland and highland, alpine limits, geographical ranges from far east to far west. Sites ranged from 10m – 810m above sea level, and across a range of substrates. Vegetation officers with extensive experience in surveying the Tasmanian buttongrass moorlands were consulted to determine an appropriate range of sites. 1:25000 maps showing altitude and geology and cross-referenced with vegetation maps in the presence of highly experienced vegetation officers to determine an all-encompassing selection of sites. Three 'sandy pans' consisting of white, fine-grained, quartzitic sand were also surveyed for bryophytes as part of this study (Figure 2.2). These sandy pans in south western Tasmanian are outwashes where the typical moorland peat layer never formed or has been removed, but are classified as a buttongrass environment (Jarman *et al.* 1988). *Gymnoschoenus sphaerocephalus* is present as inconspicuous dwarfed rosettes (Jarman *et al.* 1988; Figure 2.3), and surrounds the sandy pans as standard blanket moor (Johnson *et al.* 2008). Data from the sandy pan sites were included with the nearby buttongrass moorland site for analysis.

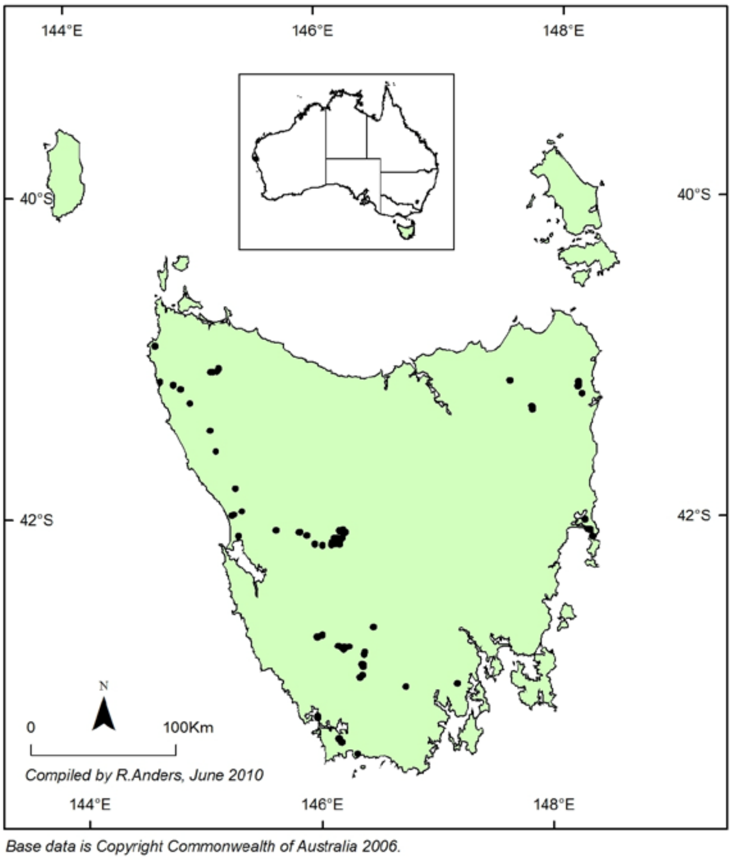

Figure 2.1. Distribution of the 100 study sites across the Tasmanian mainland.

A two-hour timed bryophyte survey was conducted at each site (Newmaster *et al*. 2005). Samples were collected and labelled for identification in the laboratory. Nomenclature followed McCarthy (2003) for liverworts and Streimann and Klazenga (2002) for all mosses except Bryaceae (Spence & Ramsay 2006) and the genus *Campylopus* (Klazenga pers. comm.). Any rocks or logs present were checked for bryophytes. The buttongrass tussock height, diameter and tussock interspace were also measured. At each site, ten measurements were taken of tussock height, diameter, and tussock interspace and then averaged. Tussock height was measured from ground level to top of vegetation, tussock diameter was taken from the widest point on the tussock, and tussock interspace was measured from base of one tussock to the base of the closest neighbouring tussock.

Site environmental variables that were measured included: location, tussock height, average tussock diameter, average tussock interspace, geology and altitude. Location was divided into five different regions for analysis: west, south, southwest, central and east. Geology and altitude was determined from plotting GPS coordinates on 1:25000 maps. Sites were then divided into six broad geological classes: mudstone/pelite, granite, quartzite, siltstone, sediments, and glacial.

Bryophyte species data from wet forest, heathy woodland, grassy woodland and alpine heath previously collected by another researcher was used for comparison to buttongrass moorland (McMullan-Fisher 2008; McMullan-Fisher *et al.* 2010). McMullan-Fisher (2008) surveyed 32 sites (heathy woodland, alpine heath, grassy woodland, wet forest) for bryophytes on all substrates by walking along a 30 m x 2 m belt transect. Bryophytes were also collected more intensively by surveying ten 1 m x 5 m strip plots within each of the 32 sites for bryophytes on all substrates.

Figure 2.2. A sandy pan in the buttongrass moorland at Wallaby Creek, Southwest Tasmania.

Figure 2.3. Sandy pan showing the dwarfed version of *G. sphaerocephalus*. Area shown approximately 1.5 m x 1 m.

Data analysis

The suitability of bryophyte sampling size was tested in EstimateS 7.5 (Colwell 2005), using incidence-based coverage estimator (ICE) of species richness to show expected species accumulation (Lee & Chao 1994). Differences in species richness (number of bryophytes, mosses or liverworts per site) that possibly could be attributed to the variables of the site were determined using simple regression (Minitab 2000). Non-metric multi-dimensional scaling was performed to produce ordinations of species richness, and bryophyte and vascular species compositions (PRIMER 5, Bray-Curtis dissimilarity coefficient, 25 restarts; Clarke & Gorley 2001). The first three ordination axes (stress < 0.2) of bryophyte and vascular species composition were then imported to Minitab (2000) for regression against site variables (significance taken at $P < 0.05$). Cluster analysis was also performed to determine if any patterns were found in bryophyte species distribution in relation to geology and altitude (PRIMER 5, Bray-Curtis dissimilarity coefficient, 25 restarts; Clark & Gorley 2001).

Results

From the 100 sites surveyed across Tasmania (Appendix 1), a total of 62 bryophyte species were collected (Table 2.1). The only species that occurred exclusively in the three sandy pans was *Ambuchanania leucobryoides,* and these three sites were combined with nearby buttongrass moorland sites for analysis purposes (Table 2.2). Bryophyte species were almost equally divided between mosses and liverworts, with 29 moss species and 33 liverwort species, with an average of 7.4 bryophyte species per site. Six species (9.7% of total species found) occurred at only one site; three liverworts (*Acromastigum mooreanum, Isotachis intortifolia, Saccogynidium decurvum*) and three mosses (*Bryum caespiticium, Distichophyllum crispulum, Rosulabryum microrhodon*). Half of all species recorded occurred in five or fewer sites. Only four species were found in over half the sites, the liverworts *Geobelobryum unguiculatum, Kurzia hippurioides* and *Riccardia aequicellularis* and the moss *Campylopus chilensis*.

Species accumulation curves forecasted that 65.6 species would be found if sampling were to continue indefinitely. An incidence-based coverage estimator of species richness predicted that when 25% of sites had been sampled, 97% of the estimated bryophyte species already had been collected (Appendix 2).

Variation in substrate was low. Eight rocks were found in the buttongrass plains, and only one rotting log. Bryophyte species found on the rocks and log did not differ from those found on the ground (Table 2.2).

Table 2.1. Bryophyte species recorded for buttongrass moorland and frequency of occurrence.

Bryophyte species	Number of occurrences	Bryophyte species	Number of occurrences
Campylopus chilensis	73	*Heteroscyphus conjugatus*	4
Kurzia hippurioides	65	*Hypnum cupressiforme var. tectorum*	4
Goebelobryum unguiculatum	55	*Jackiella curvata*	4
Riccardia aequicellularis	53	*Lepidozia ulothrix*	4
Riccardia crassa	44	*Ditrichum difficile*	3
Campylopus kirkii	40	*Fossombronia sp.*	3
Hyalolepidozia longiscypha	40	*Gackstroemia weindorferi*	3
Dicranaloma billarderi	38	*Heteroscyphus fissitipus*	3
Dicranaloma eucamptodontoides	34	*Heteroscyphus knightii*	3
Pleurophascum grandiglobum subsp. grandiglobum	30	*Marsupidium surculosum*	3
Campylopus torquatus	25	*Tayloria octoblepharum*	3
Acromastigum anistostomum	23	*Acromastigum colensoanum*	2
Chiloscyphus semiteres	11	*Gemmabryum australe*	2
Dicranaloma robustum	11	*Heteroscyphus argutus*	2
Campylopus bicolor var. bicolor	10	*Heteroscyphus varians*	2
Campylopus introflexus	10	*Pohlia nutans*	2
Balantiopsis diplophylla	9	*Polytrichum juniperinum*	2
Breutelia affinis	9	*Ptychomion aciculare*	2
Campylopus insititius	9	*Sphagnum australe*	2
Heterscyphus billarderi	9	*Sphagnum falcatulum*	2
Riccardia cochleata	9	*Teleranea mooreana*	2
Rosulabryum billarderi	8	*Temnoma townrowii*	2
Sphagnum cristatum	8	*Wijkia extenuata*	2
Frullania falciloba	6	*Acromastigum mooreanum*	1
Jamesoniella colorata	6	*Ambuchanania leucobryoides*	1
Kurzia compacta	6	*Bryum spp.*	1
Sphagnum novozelandicum	6	*Bryum caespiticium*	1
Symphyogyna podophylla	6	*Distichophyllum crispulum*	1
Heteroscyphus coalitus	5	*Isotachis intortifolia*	1
Podomitrium phyllanthus	5	*Rosulabryum microrhodon*	1
Chaetophyllopsis whiteleggei	4	*Saccogynidium decurvum*	1

Table 2.2. Bryophytes found on substrates other than soil.

Sandy pans	Rock	Log
Acromastigum anistostomum	*Campylopus bicolor*	*Campylopus chilensis*
Ambuchanania leucobryoides	*Campylopus chilensis*	*Dicranaloma billarderi*
Campylopus chilensis	*Campylopus insititius*	*Kurzia hippurioides*
Campylopus introflexus	*Campylopus introflexus*	
Campylopus kirkii	*Campylopus kirkii*	
Dicranaloma billarderi	*Campylopus torquatus*	
Dicranaloma eucamptodontoides	*Dicranaloma eucamptodontoides*	
Dicranaloma robustum	*Dicranaloma robustum*	
Geobelobryum unguiculatum	*Jamesoniella colorata*	
Heteroscyphus conjugatus	*Kurzia hippurioides*	
Hyalolepidozia longiscypha	*Polytrichum juniperinum*	
Jamesoniella colorata	*Ptychostomum augustifolium*	
Kurzia hippurioides	*Riccardia aequicellularis*	
Podomitrium phyllanthus	*Riccardia crassa*	
Riccardia aequicellularis		

Bryophyte richness did not correlate with locality, geology, altitude or the buttongrass characteristics of tussock height, average tussock diameter or average tussock interspace (Table 2.3). Ordination of bryophyte composition labelled by bryophyte richness of each site showed no clustering of sites with similar levels of species richness (Figure 2.4). Cluster analysis of bryophyte species and geology (Figure 2.5) and bryophyte species and altitude (Figure 2.6) also supported the lack of correlation. But when mosses and liverworts were analysed separately, moss richness was found to be significantly influenced by the height of the buttongrass tussocks, although this appeared to be caused by a couple of outliers (Figure 2.7).

Table 2.3. Relationship between species richness and buttongrass site characteristics. Significant correlations presented in bold.

	Bryophytes		Moss		Liverworts	
	r^2 %	P	r^2 %	P	r^2 %	P
Locality	1.9	0.171	1.5	0.227	1.1	0.308
Geology	0.3	0.622	1.0	0.318	0.02	0.895
Altitude	0.1	0.748	0.5	0.489	0.001	0.902
Tussock height	2.6	0.115	**7.7**	**0.006**	0.001	0.993
Average tussock diameter	0.001	0.870	0.7	0.428	0.9	0.340
Average tussock interspace	0.4	0.551	0.8	0.371	0.001	0.902

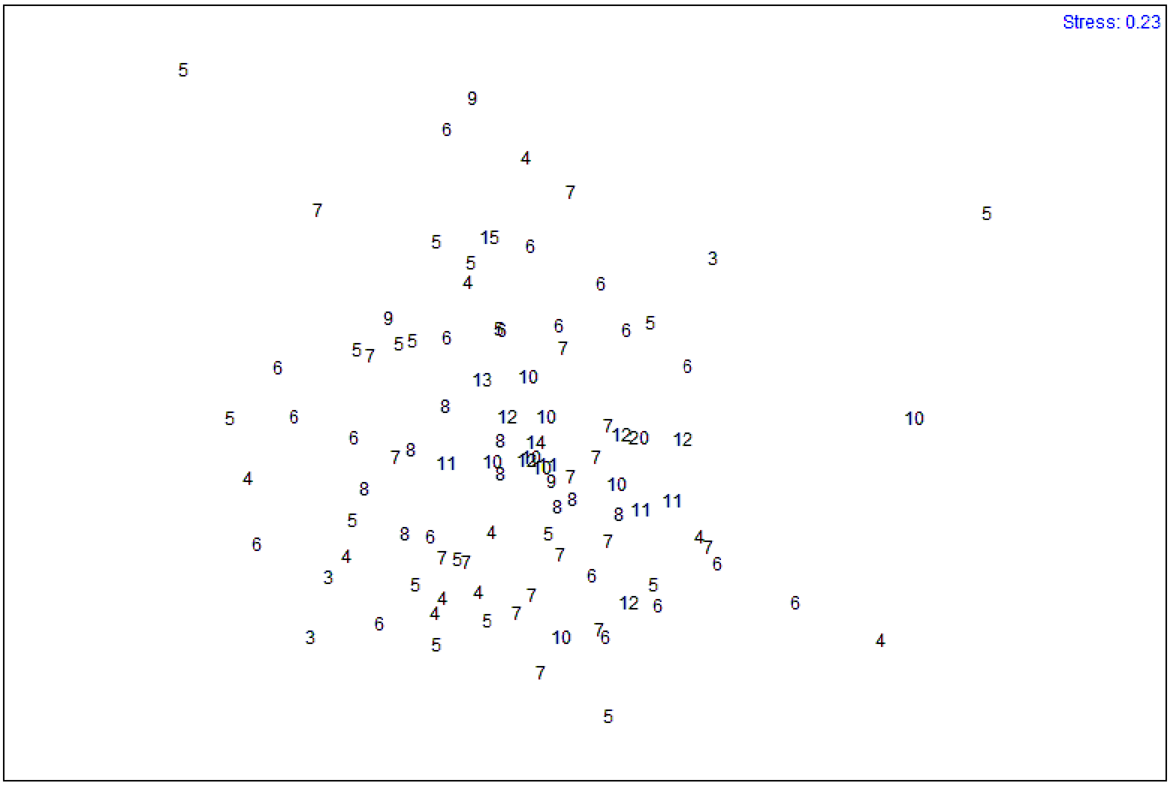

Figure 2.4. Ordination of bryophyte composition coded with bryophyte species richness.

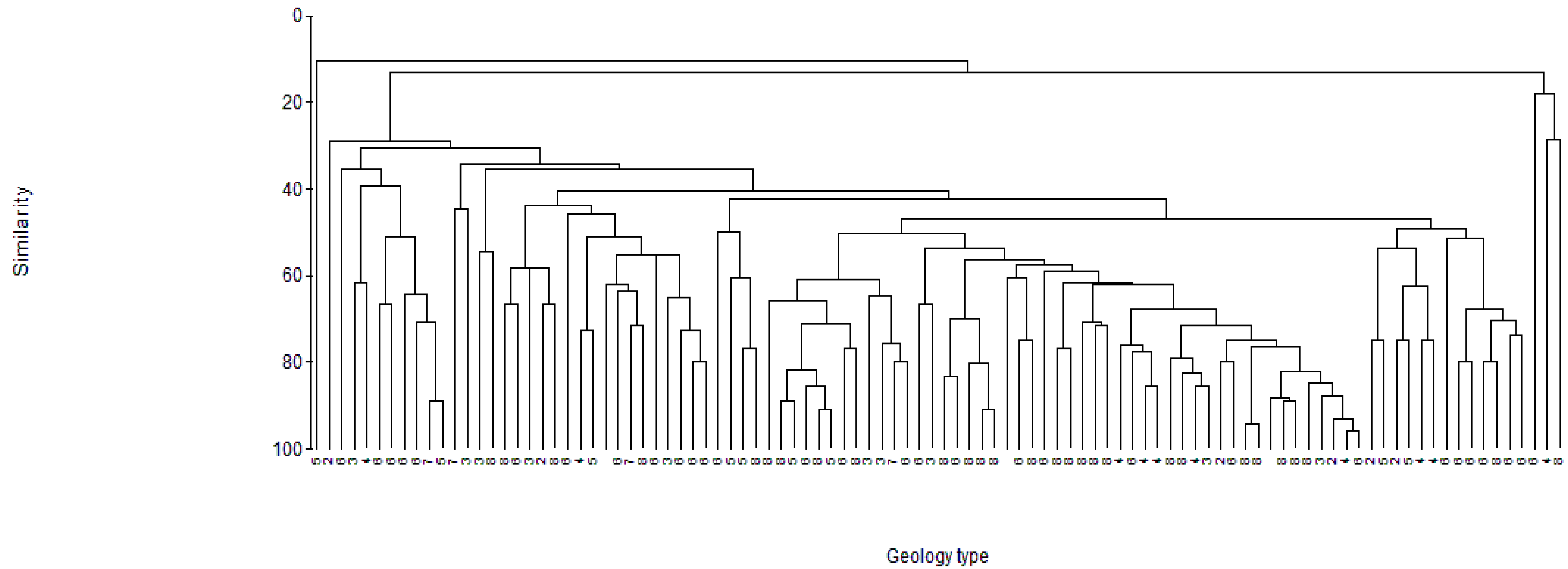

Figure 2.5. Cluster analysis of bryophyte species in relation to geology type. 2 = granite, 3 = siltstone, 4 = quartz, 5 = alluvial, 6 = glacial, 7 = schist, 8 = Quaternary sediments.

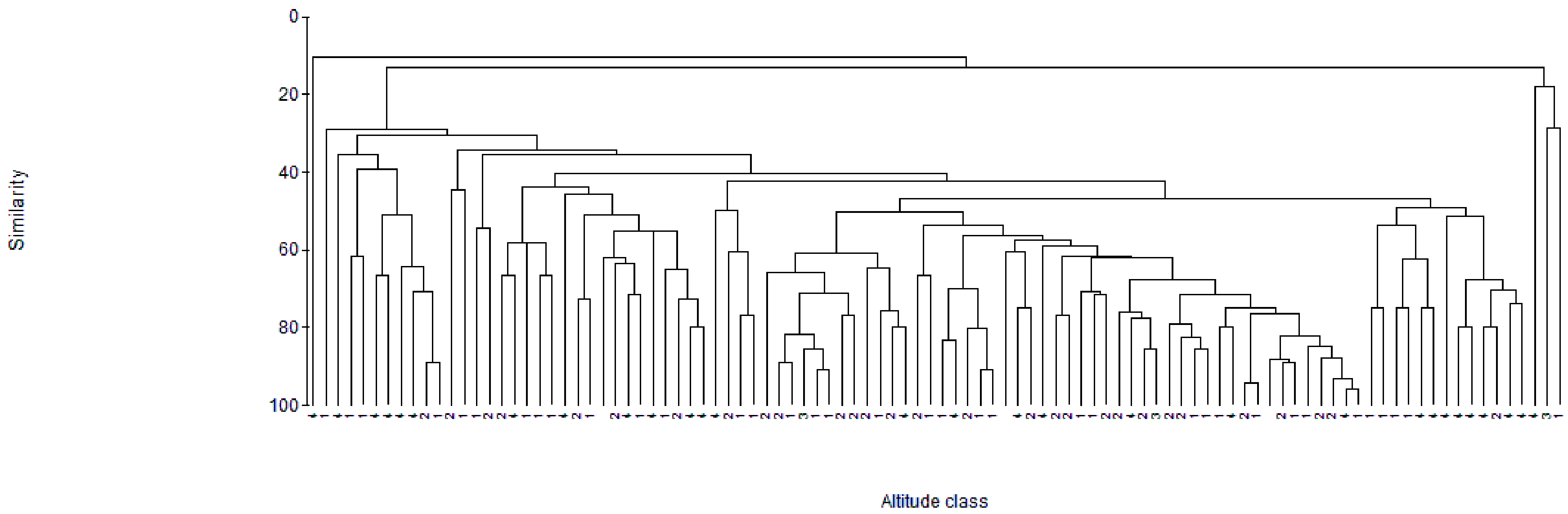

Figure 2.6. Cluster analysis of bryophyte species in relation to altitude class. 1 = 0m – 199m a.s.l., 2 = 200 – 499m a.s.l., 3 = 500m – 699m a.s.l., 4 = 700+ a.s.l.

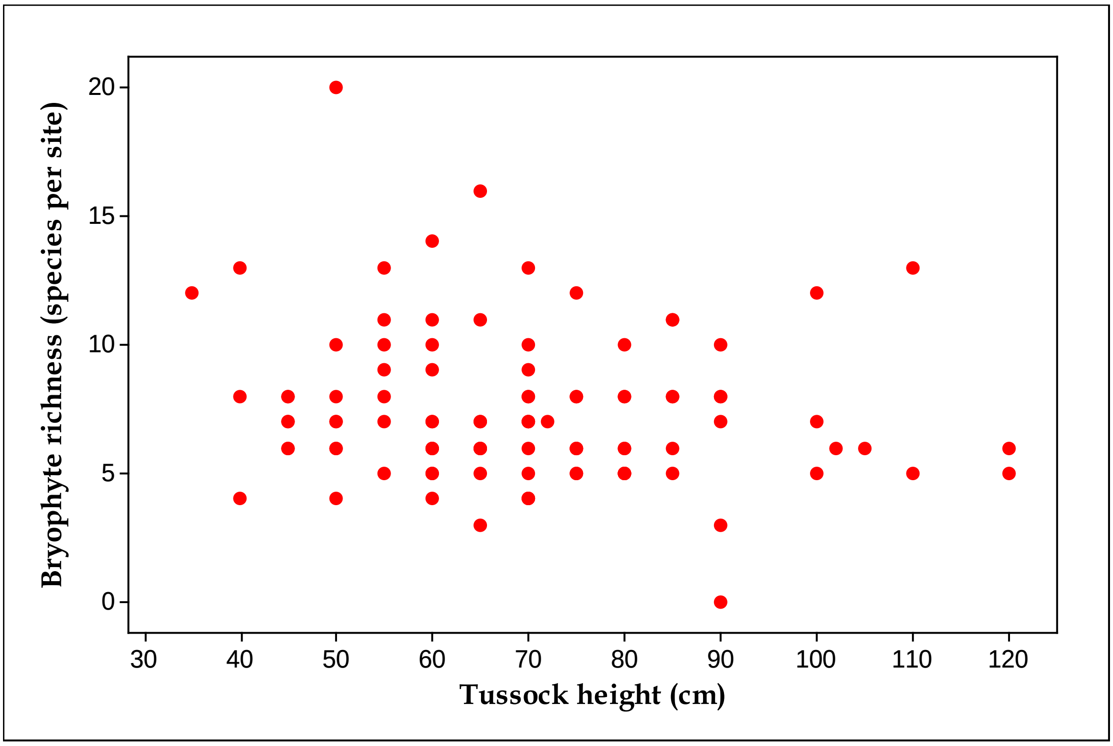

Figure 2.7. Moss species richness compared to tussock height.

All three ordination axes of the MDS analysis indicated that bryophyte composition was significantly related to altitude (Table 2.4; Figure 2.8). Because two-dimensional stress was greater than 0.2, a three dimensional analysis was used and identified. A significant relationship between bryophyte composition and tussock height was seen, although this was not strong (Figure 2.9). Similarly, a weak but significant relationship was seen between bryophyte composition and tussock diameter.

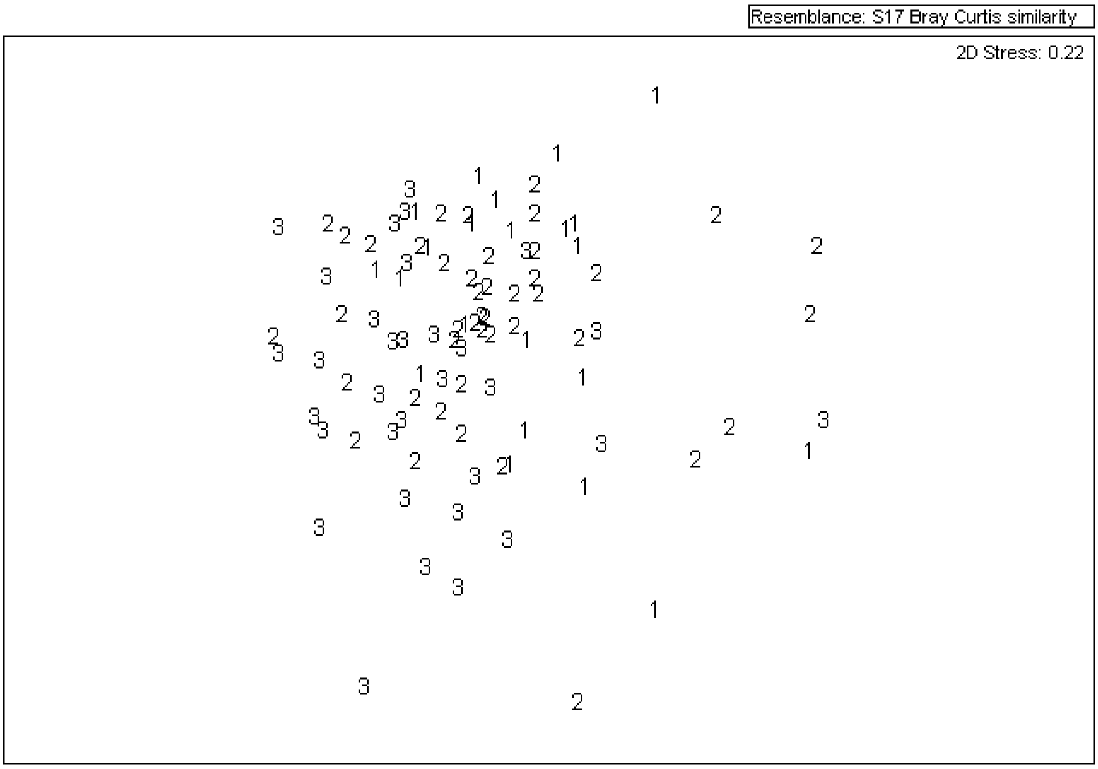

Figure 2.8. Ordination of bryophyte composition coded with altitude classes. 1 = < 100 metres above sealevel (a.s.l.), 2 = 100 m – 600 m a.s.l., 3 = > 600 m a.s.l. Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

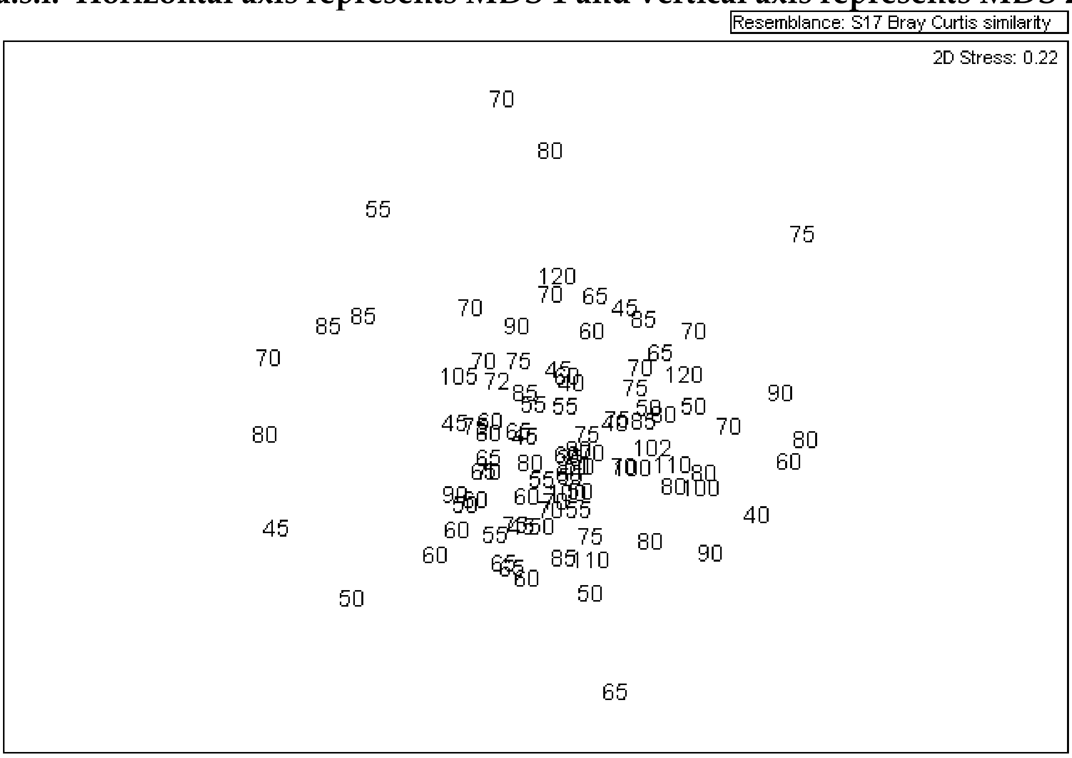

Figure 2.9. Ordination of bryophyte composition coded with tussock height (cm). Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

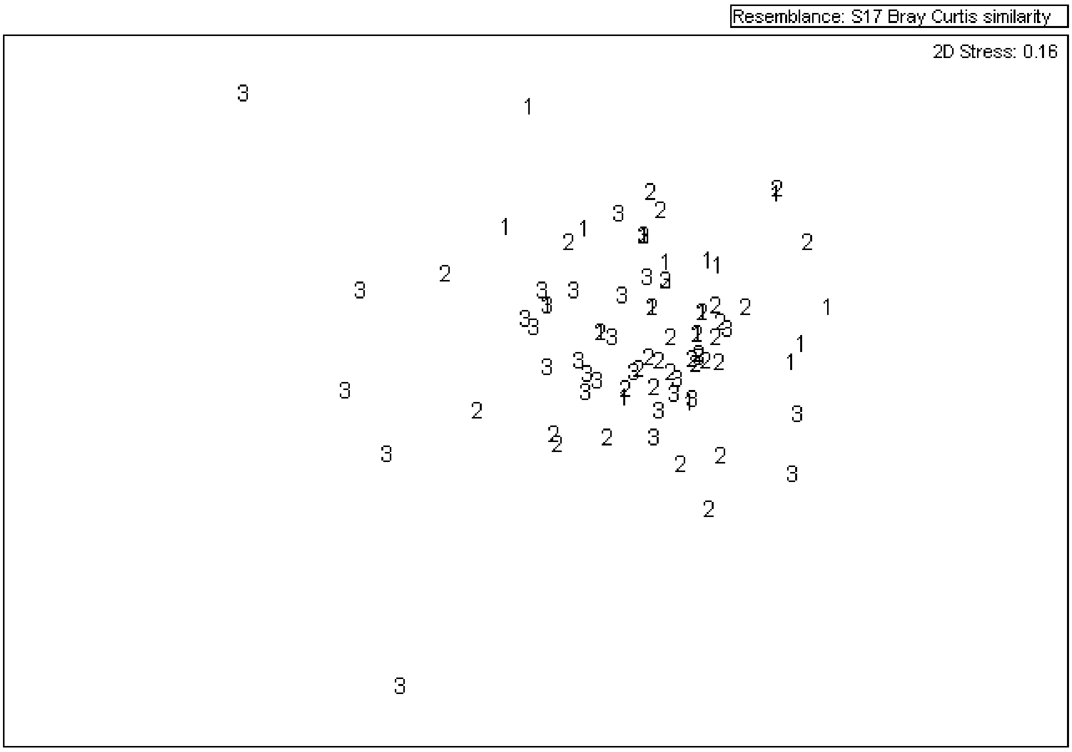

Figure 2.10. Ordination of moss composition coded with altitude classes. 1 = < 100 metres above sealevel (a.s.l.), 2 = 100 m – 600 m a.s.l., 3 = > 600 m a.s.l.. Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

Table 2.4. Analysis of moss composition correlated with environmental variables. Significant correlations presented in bold.

	MDS 1		MDS 2	
	r^2 %	P	r^2 %	P
Location	0.1	0.743	**4.8**	**0.033**
Geology	0.8	0.40	**11.1**	0.**001**
Altitude	**13.2**	**<0.001**	**8.2**	**0.005**
Tussock height	1.9	0.188	1.2	0.296
Average tussock diameter	3.1	0.091	0.1	0.820
Average tussock interspace	0.5	0.514	3.1	0.091

Table 2.5. Analysis of moss composition correlated with environmental variables. Significant correlations presented in bold.

	MDS 1		MDS 2	
	r^2 %	P	r^2 %	P
Location	0.2	0.676	1.1	0.310
Geology	3.0	0.090	2.8	0.099
Altitude	0.1	0.77	**9.9**	**0.002**
Tussock height	1.1	0.320	0.2	0.691
Average tussock diameter	2.9	0.097	0.001	0.854
Average tussock interspace	0.1	0.811	0.2	0.655

When analysed separately, moss and liverwort composition was also significantly correlated with altitude (Tables 2.5 & 2.6, Figures 2.10 & 2.11), with some change in moss composition also attributable to location (Table 2.5), although graphical representation showed this was not a strong correlation (Figure 2.12).

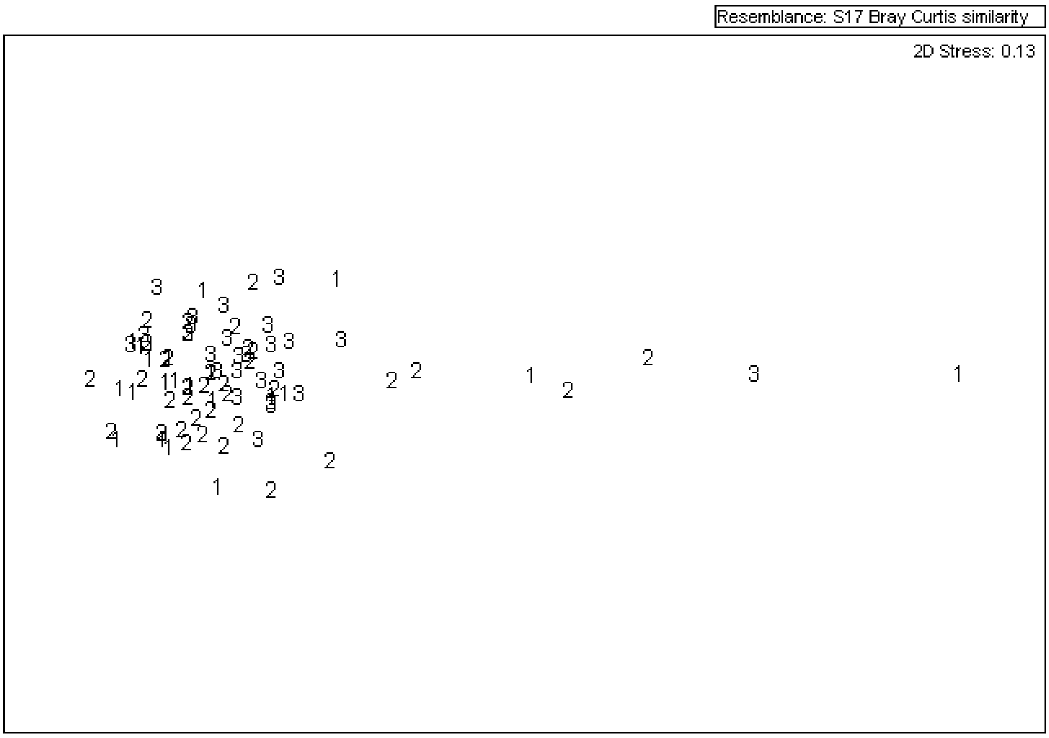

Figure 2.11. Ordination of liverwort composition coded with altitude classes. 1 = < 100 metres above sealevel (a.s.l.), 2 = 100 m – 600 m a.s.l., 3 = > 600 m a.s.l.. Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

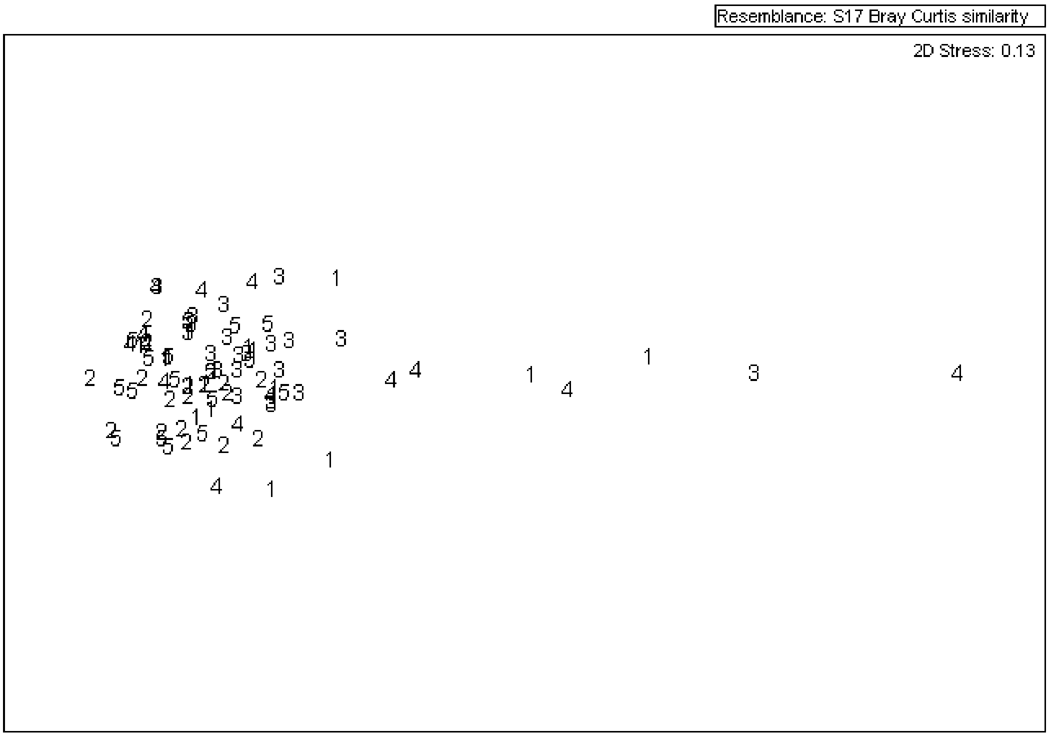

Figure 2.12. Ordination of moss composition coded with location. 1 = West, 2 = Southwest, 3 = Central, 4 = East, 5 = South.
Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

Comparison of the bryophyte species composition found in wet forest, heathy woodland, grassy woodland and alpine heath (McMullan-Fisher 2008) to the species found in the buttongrass moorland sites from this study shows that 66% of the 62 species found were not present in the other environments (Table 2.7). Thirty of these species not found in the other habitats were liverworts.

Table 2.6. Species found in Tasmanian buttongrass moorland, wet forest, heathy woodland, alpine heath and grassy woodland.

Species	Buttongrass moorland	Wet forest*	Heathy woodland*	Alpine heath*	Grassy woodland*
Acrocladium chlamydophyllum	1	1	0	0	1
Acromastigum anistostomum	1	0	0	0	0
Acromastigum colensoanum	1	0	0	0	0
Acromastigum mooreanum	1	0	0	0	0
Ambuchanania leucobryoides	1	0	0	0	0
Balantiopsis diplophylla	1	0	0	0	0
Breutelia affinis	1	1	1	0	1
Bryum spp.	1	1	1	1	1

Species	Buttongrass moorland	Wet forest*	Heathy woodland*	Alpine heath*	Grassy woodland*
Campylopus spp.	1	1	1	1	1
Chaetophyllopsis whiteleggei	1	0	0	0	0
Chiloscyphus semiteres	1	0	0	0	0
Dicranaloma billarderi	1	1	0	0	0
Dicranaloma eucamptodontoides	1	0	0	0	0
Dicranaloma robustum	1	1	0	1	0
Distichophyllum crispulum	1	0	0	0	0
Ditrichaceae spp.	1	1	0	1	0
Fossombronia spp.	1	0	0	0	0
Frullania falciloba	1	0	0	0	0
Gackstroemia weindorferi	1	0	0	0	0
Gemmabryum australe	1	0	0	0	0
Goebelobryum unguiculatum	1	0	0	0	0
Heteroscyphus argutus	1	0	0	0	0
Heteroscyphus coalitus	1	0	0	0	0
Heteroscyphus conjugatus	1	0	0	0	0
Heteroscyphus fissitipus	1	0	0	0	0
Heteroscyphus knightii	1	0	0	0	0
Heteroscyphus limosus	1	0	0	0	0
Heteroscyphus varians	1	0	0	0	0
Heterscyphus billarderi	1	0	0	0	0
Hyalolepidozia longiscypha	1	0	0	0	0
Hypnum cupressiforme	1	1	0	1	0
Isotachis intortifolia	1	0	0	0	0
Jackiella curvata	1	0	0	0	0
Jamesoniella colorata	1	0	0	0	0
Kurzia compacta	1	0	0	0	0
Kurzia hippurioides	1	0	0	0	0
Lepidozia ulothrix	1	0	0	0	0
Leucobryum candidum	1	1	0	0	0
Marsupidium surculosum	1	0	0	0	0
Pleurophascum grandiglobum	1	0	0	0	0
Podomitrium phyllanthus	1	0	0	0	0
Pohlia nutans	1	0	0	0	0
Polytrichum juniperinum	1	1	1	1	1
Ptychomnion aciculare	1	1	0	1	0
Riccardia aequicellularis	1	0	0	0	0
Riccardia cochleate	1	0	0	0	0
Riccardia crassa	1	0	0	0	0
Rosulabryum spp.	1	1	1	1	1
Saccogynidium decurvum	1	0	0	0	0
Sphagnum spp.	1	0	0	1	0
Symphyogyna podophylla	1	0	0	0	0
Tayloria octoblepharum	1	0	0	0	0
Teleranea mooreana	1	0	0	0	0
Temnoma townrowii	1	0	0	0	0
Wijkia extenuate	1	1	0	1	0

Species	Buttongrass moorland	Wet forest*	Heathy woodland*	Alpine heath*	Grassy woodland*
Acaulon sp.	0	0	0	0	1
Andreaea sp.	0	0	0	1	0
Barbula calycina	0	0	1	0	0
Barbula torquate	0	0	0	0	1
Bartramia ithyphylla	0	0	1	1	0
Blindia robusta	0	0	0	1	0
Brachythecium rutabulum/salebrosum	0	1	0	0	0
Breutelia elongata/pendula	0	0	0	1	0
Bryoerythrophyllum binnsii	0	0	0	0	1
Calyptopogon mnioides	0	1	0	0	0
Calyptrochaeta apiculata	0	1	0	0	0
Calyptrochaeta otwayensis	0	1	0	0	0
Camptochaete arbuscula	0	1	0	0	0
Camptochaete deflexa	0	1	0	0	0
Ceratodon purpureus	0	1	1	1	1
Conostomum pusillum	0	0	0	1	0
Dicranoloma menziesii	0	1	0	0	0
Didymodon australasiae	0	1	1	0	0
Fissidens curvatus	0	1	0	0	1
Fissidens leptocladus	0	1	0	0	1
Fissidens taylorii	0	1	1	0	1
Fissidens tenellus	0	1	1	0	1
Grimmia spp.	0	1	0	1	0
Hypnodendron sp.	0	1	0	0	0
Hypopterygium didictyon	0	1	0	1	0
Hypopterygium sp.	0	1	0	0	0
Isopterygium aff. Minutirameum	0	1	0	0	0
Kindbergia praelonga	0	1	0	0	0
Lembophyllum clandestinum	0	1	0	0	0
Lembophyllum divulsum	0	1	0	0	0
Leptotheca gaudichaudii	0	1	0	1	0
Notoligotrichum aff. Australe	0	0	0	1	0
Orthodontium lineare	0	1	0	0	0
Orthotrichum tasmanicum	0	1	0	1	0
Philonotis australiensis	0	0	0	0	1
Philonotis sp.	0	0	0	0	1
Polytrichum commune	0	0	0	1	0
Pottiaceae spp.	0	0	0	0	1
Pseudoleskea imbricata	0	0	1	0	0
Racocarpus spp.	0	0	0	1	0
Racomitrium spp.	0	0	0	1	0
Racopilum cuspidigerum	0	1	0	0	1
Rhizogonium distichum	0	1	0	0	0
Rhizogonium novaehollandiae	0	1	0	0	0
Rhynchostegiella muriculata	0	1	0	0	0
Sematophyllaceae spp.	0	1	0	1	0

Species	Buttongrass moorland	Wet forest*	Heathy woodland*	Alpine heath*	Grassy woodland*
Telaranea patentissima	0	0	0	0	0
Thamnobryum pumilum	0	1	0	0	0
Thuidium sparsum	0	1	0	0	0
Tortula calycina/truncata	0	0	0	0	1
Tortula muralis	0	0	0	0	1
Tortula rubra	0	0	1	0	1
Weissia controversa	0	1	1	0	0
Total species	**55**	**29**	**14**	**25**	**21**

Discussion

Previous Tasmanian bryophyte work focused mainly on bryophyte species-rich wet forests and rainforests (Jarman & Kantvilas 1995; Kantvilas & Jarman 2004; Pharo & Blanks 2000; Roberts *et al.* 2005; Turner & Pharo 2005; Turner *et al.* 2006). In comparison to these bryophyte-rich wet habitats, a total of 62 species from a statewide survey of the buttongrass habitat seems low. For example, 53 bryophyte species were collected from a rainforest fragment 0.5 hectares in area on the Yarlington Tier (Kantvilas & Jarman 1993). In a larger study comprising 33 sites in Tasmanian old growth mixed eucalypt forest, 202 bryophyte taxa were recorded (Turner *et al*. 2006) – more than three times the number found in the 100 sites of this study. Tree-ferns (*Dicksonia antarctica*) surveyed at 10 sites supported an epiphytic bryophyte flora of 81 species (Roberts *et al.* 2005). Possibly the most startling comparison is that a single old Huon Pine tree (*Lagarostrobos franklini)* in a rainforest in western Tasmania had a total of 55 bryophyte species (Jarman & Kantvilas 1995)! One tree held 89% of the total bryophyte species richness found across the Tasmanian buttongrass plains.

Two other studies recorded bryophyte species composition in Tasmanian buttongrass moorlands. Ferguson *et al*. (2009) looked at the disturbance response of bryophytes in one buttongrass plain, whilst Kantvilas and Jarman (1991) included buttongrass moorland in a study of Mt Sprent. A total of 19 bryophytes were recorded. Twelve of these 19 species were found during this study into the statewide bryophytes of buttongrass moorland. Kantvilas and

Jarman (1991) and the statewide survey also shared a further four genera in common, although different species were found in each study. Ferguson *et al.* (2009) found 18 bryophyte species at a single buttongrass plain at Mathinna Plains in the state's east. Fourteen of these species were recorded in this statewide study, and different species of two genus were also seen. Ferguson *et al.* (2009) found *Heteroscyphus limosus* and Kantvilas and Jarman (1991) found *H. decipiens* in buttongrass moorlands. This study did not, but seven other *Heteroscyphus* species were found: *H. argutus, H. billarderi, H. coalitus, H. conjugatus, H. knightii* and *H. varians.*

Only two of the bryophyte species found in this study were habitat-specific to the buttongrass moorlands. *Pleurophascum grandiglobum* subsp. *grandiglobum* is endemic to the Tasmanian buttongrass moorlands, and, when fruiting, is a spectacular plant with spherical pale green (Figure 2.13) to orange capsules (Meagher & Fuhrer 2003). *Ambuchanania leucobryoides* is a moss listed as rare under the Tasmanian *Threatened Species Protection Act 1995* due to its small population size and limited distribution (Tasmanian Threatened Species Scientific Advisory Committee 2008; Figure 2.11). It is known only from Precambrian quartzite sandy washes, known as 'sandy pans' from three sites in far southwest Tasmania (Johnson *et al.* 2008). It is not endemic to the buttongrass moorlands, but to the sandy pans which occur in the buttongrass moors and is classified as a buttongrass environment (Jarman *et al.* 1988).

Buttongrass moorland is subject to extremes of weather, from drought and fire in summer to winter frosts, snow and flooding (Jarman *et al.* 1988). Only a small suite of bryophytes may be able to deal with the multiple challenges associated with living in buttongrass moorland. Only thirty-four percent of taxa found also occurred in the four habitat types surveyed by McMullan-Fisher (2008). The four most common bryophyte species in the buttongrass moorlands, the liverworts *Geobelobryum unguiculatum, Kurzia hippurioides* and *Riccardia aequicellularis* all occur in a range of moist habitats (Meagher & Fuhrer

2003) and the common buttongrass moorland moss *Campylopus chilensis* occurs on peaty soils in buttongrass moorland and heaths (Klazenga pers. comm.).

Figure 2.13. ***Pleurophascum grandiglobum*, showing capsules.**

Figure 2.14. ***Ambuchanania leucobryoides* demonstrating its habitual growth pattern of only the tips of the plant being present above the sandy surface.**

Altitude was the key factor found to influence distribution of bryophytes, although other factors played a minor role (Table 2.4; Table 2.5). This was not unexpected as both international and Australian studies previously have found correlations between bryophyte composition and altitude. In Fennoscandia, Bruun *et al.* (2006) found bryophyte composition was significantly related to altitude, as did Andrew *et al.* (2003) with bryophytes from Mt. Field and Mt. Rufus in Tasmania and Otira Valley and Seaward Kaikoura Mountains, South Island, New Zealand. Numerous environmental constraints occur at high altitudes, causing slow growth and reduced size in plants (Kiirner 1989). These include lower soil temperatures (Bliss 1971), reduced microbial activity (Holzmann & Haselwandter 1988) and more limited nutrient availability (Kiirner 1989).

Bryophyte richness and composition is low in buttongrass moorlands across the state of Tasmania, particularly when this habitat type is compared to the species-rich wet forests and rainforests, iconic environments for bryophytes in

Tasmania. The lack of species diversity may be attributed to the particularly challenging environment buttongrass moorland offers as habitat. Surveys are needed in the buttongrass moorlands of mainland Australia, to determine if low species diversity is a trait common to this ecosystem regardless of geographical location. Further work could be conducted at buttongrass ecotones to determine whether species nearby are within dispersal distance of buttongrass moorland but unable to establish. Also, the effects of fire regimes are unknown and may affect bryodiversity.

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Chapter 3

Bryophyte diversity in buttongrass moorland with differing fire histories, southwest Tasmania

Abstract

Bryophytes sometimes occur as ground cover following fire in buttongrass moorland, but little is known about their response to this common form of disturbance in buttongrass moorlands. Richness and composition of bryophytes was examined at sites that ranged from 6 months to 67 years since the last fire occurrence. A similar suite of bryophytes was found, regardless of time since fire, although sites more than three decades since last fire occurrence were slightly more species rich. When examined separately to mosses, liverwort richness correlated with time since fire, although this was due to a slightly higher richness at older sites. As fire did not appear to be a major determinant of these bryophyte communities, possible correlations with other environmental variables were examined, and it was found that some soil nutrients (B, Ca, Cu, K, Zn) were correlated with bryophyte composition. As sites over thirty years since last fire were slightly more species rich than sites burnt more recently, it is recommended that a selection of buttongrass moorlands over thirty years since last fire are left unburnt by managers to promote optimum bryophyte species diversity.

Introduction

Buttongrass moorland covers 572,000 ha of Tasmania, including vast tracts of the Tasmanian Wilderness World Heritage Area (TVMMP 2005). Buttongrass moorland is highly pyrogenic, burning at higher fuel moisture levels than any other vegetation type in the world (Marsden-Smedley *et al.* 2001). Sites older than twenty years are considered to be a very high fire risk and uncontrollable buttongrass moorland fires spread into other habitats, especially on windy days or when the fuel is particularly dry (Marsden-Smedley & Catchpole 1995a). Some areas of buttongrass moorland have been subjected to fuel reduction burns for many years in an attempt to protect nearby fire-sensitive forests and alpine regions from unplanned fires (Parks & Wildlife Service 1999). Recent catastrophic fires in Victoria (summer 2008-2009) have renewed the political pressure on land managers to engage in large-scale prescribed burning (e.g. Ryan & Norington 2009, but see Cary *et al.* 2003 for a critique on this reaction).

Little published work exists on the biodiversity and ecology of bryophytes in buttongrass moorland (Jarman *et al.* 1988a; Kantvilas & Jarman 1991). In contrast, the vascular vegetation of the buttongrass moorlands (Jarman *et al.* 1988a; Jarman *et al.* 1988b) and its response to fire have been well documented (Marsden-Smedley & Catchpole 1995a; Marsden-Smedley & Catchpole 1995b; Marsden-Smedley *et al.* 1999; Marsden-Smedley & Catchpole 2001; Marsden-Smedley *et al.* 2001). It is known that fire is a controlling factor of bryophyte diversity in many ecosystems. Adult bryophyte plants are exposed to impacts by fire, as they lack adaptations to cope with high intensity fire, unlike vascular plants which can have features such as lignotubers and epicormic buds (Bond & van Wilgen 1996). However, some bryophytes can survive some fires due to underground tubers, spores in the soil and buried lower stems (Bengt Gunnar 1993). Bryophytes are often primary colonisers after fire (Eldridge & Bradstock 1994), increasing physical soil stability, absorbing and immobilising nutrients, and providing reservoirs for mineral elements (Brasell & Mattay 1984; Li & Vitt 1997).

Understanding the response of bryophytes following fire in buttongrass moorland is necessary to fully appreciate vegetation dynamics in such a fire-prone environment, and documenting the diversity of these small plants is important for informed conservation planning. Differences in bryophyte and vascular plant species richness and composition was investigated in buttongrass moorland with time since fire ranging from six months to 67 years. Also studied was the effect of the following variables on bryophyte richness and composition: buttongrass height, buttongrass tussock diameter, space between buttongrass tussocks, percent of vascular plants (other than buttongrass), vascular plant diversity, the percent of open ground and soil nutrients. The results of these studies are presented in this paper.

Method

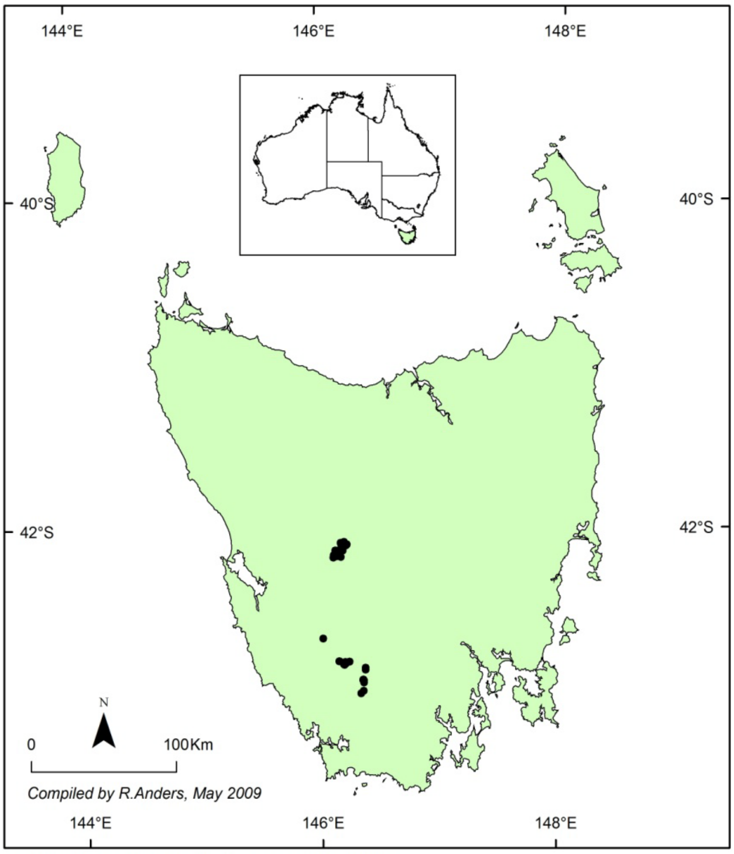
Study area

Buttongrass moorland occurs on poorly drained organic soils in high rainfall areas ranging from valley bottoms to steep slopes and from sea level to subalpine elevations (Pemberton *et al.* 2005). This study focused on buttongrass moorland of differing fire ages (Figures 3.1-3.3) in two different regions of Tasmania (Figures 3.4-3.6).

Figure 3.1. Buttongrass moorland, Lake St. Clair region (one year since fire).

Figure 3.2. Buttongrass moorland, Lake St. Clair region (17 years since fire).

Figure 3.3. Buttongrass moorland, Lake St. Clair region (34 years since fire).



Base data is Copyright Commonwealth of Australia 2006.

Figure 3.4. The study area with the 44 sites shown. The northern cluster of 25 sites surround Lake St. Clair and the southern cluster of 19 sites are in the Lake Pedder region.

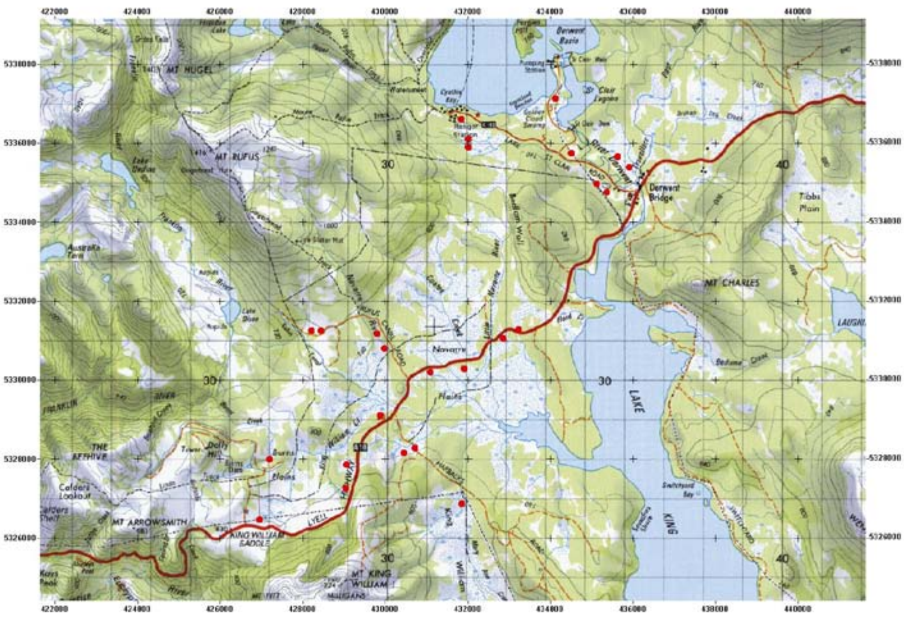


Figure 3.5. Twenty-five sites in the Lake St. Clair region, shown as red dots. Map courtesy of M. Driessen.

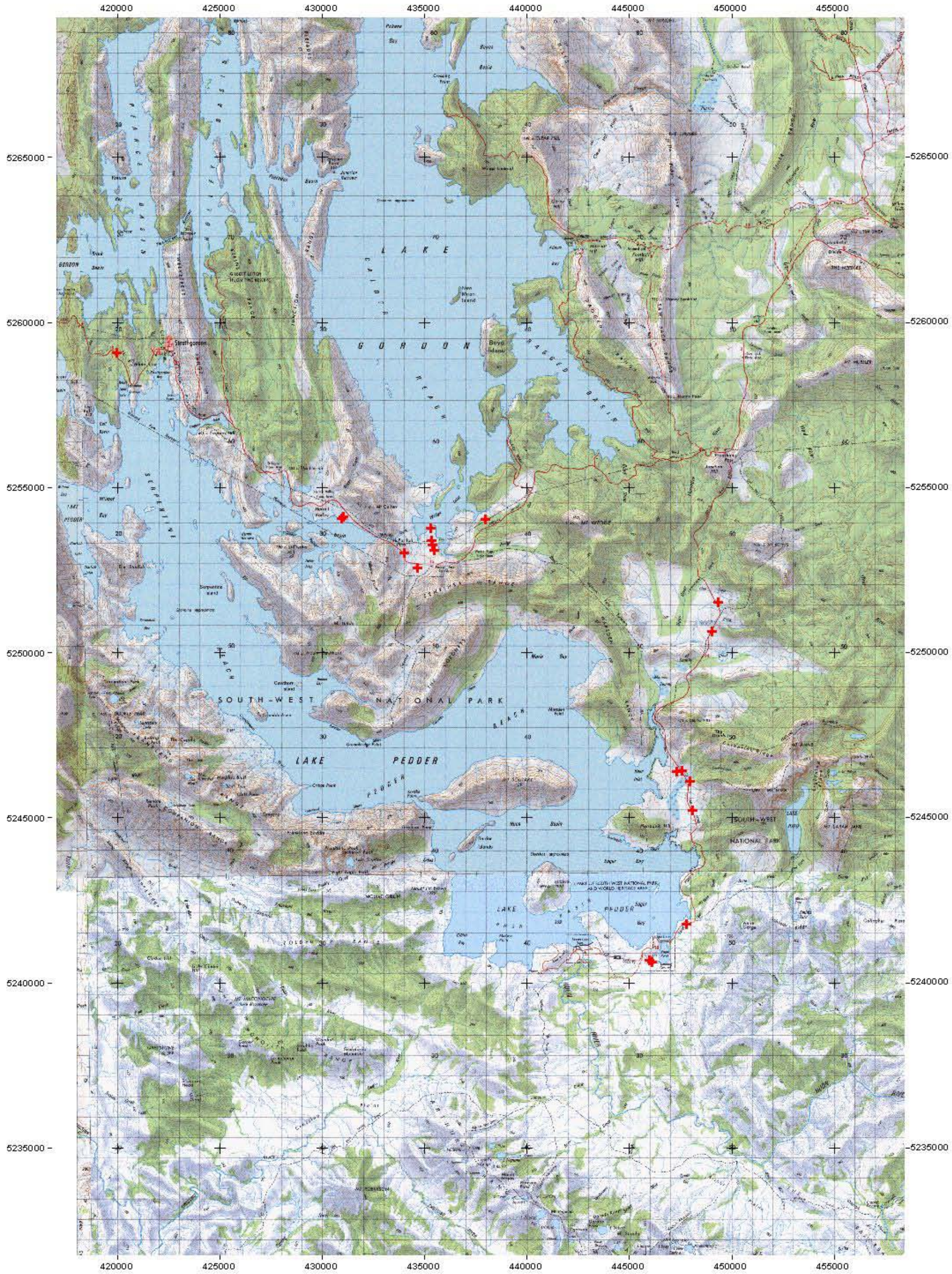


Figure 3.6. Nineteen sites surrounding the Lake Pedder region, shown as red dots. Map courtesy of M. Driessen.

Lake St. Clair is of high altitude (730-800 m asl), relatively fertile occurring on dolerite (Pemberton 1986), and with a mean annual rainfall of 2540 mm (BOM 2008a), whereas Lake Pedder is of lower altitude (305-365 m asl), lower soil fertility on quartz (Pemberton 1989), with a lower mean annual rainfall of 1511 mm (BOM 2008b).

Study design

Nineteen sites were located in the Lake Pedder region, and 25 sites in the Lake St. Clair area. Within each of the two regions, the individual sites were selected based on time since last fire. Sites were chosen by the Biodiversity and Conservation Branch of the Department of Primary Industries, Parks, Water and Environment, Tasmania, and were last burned at times ranging from six months to 67 years. Within the Lake St. Clair region, fires that occurred during the course of the study burnt areas that previously had not been burnt for more than 33 years. Thus no older sites were available in this region for comparison with younger sites. The Lake Pedder region had eleven sites that had not been burnt for more than 33 years.

Vascular plant and environmental data were collected for each site in May 2004 by the Biodiversity Conservation Branch using a 1 m x 1 m grid plot threaded with fine wire to make a grid of 10 x 10 cells, giving a matrix of 100 cells over the 1 m^2 at seven points in each of the 44 buttongrass sites. Vascular plants were identified to species level, and the cover of each species as well as the overall percentage plant cover was recorded to the nearest 1%. If percentage cover was less than 1%, the species was just recorded as 'present'.

The environmental variables investigated were altitude, aspect, soil moisture and soil nutrients. Four soil samples were collected at each site from between clumps of buttongrass vegetation, avoiding pools of water. Soil samples were taken using a 110mm long, 70mm diameter PVC tube that was inserted completely into the peat and then removed. The top 5mm of the sample was sliced off to remove any surface vegetation. The sample was weighed, oven dried for 62 hours at 80°C and then reweighed to determine the percentage moisture content. The four samples from each site were then aggregated and put through a 1 mm sieve to remove any plant roots. The combined soil sample for each site was then analysed by a professional laboratory using the extraction procedures outlined in Table 3.1 to assess the content of the following soil parameters: nitrogen (N), phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn), copper (Cu), boron (B), an estimate of organic content (loss on ignition - LOI), pH and soil conductivity (cond). Altitude, aspect and the soil variables are collectively referred to as 'environmental variables' (Table 3.2).

Table 3.1. Extraction procedures for soil parameters (table courtesy of M. Driessen).

Parameter	Extraction procedure
Total nitrogen (%)	Kjeldahl method
Organic matter (%)	Loss on ignition
pH	1 part soil : 5 parts distilled water, shaken for 60 minutes
Conductivity (us/cm)	1 part soil : 5 parts distilled water, shaken for 60 minutes
Available Phosphorous (ppm)	1 part soil : 20 parts 1N sodium bicarbonate @ pH 8 (Olsen), shaken 30 minutes
Potassium (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Calcium (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Magnesium (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Manganese (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Zinc (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Copper (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes
Boron (ppm)	1 part soil : 5 parts 1N ammonium acetate @pH 4.8, shaken 30 minutes

Table 3.2. Environmental variables at the two sites: Lake St. Clair (n = 25) and Lake Pedder (n = 19).

Environmental Variables	Lake St. Clair		Lake Pedder		Minimum-maximum	
	Mean	Std error	Mean	Std error	St. Clair	Pedder
N (%)	1.25	0.06	0.73	0.07	0.42-1.73	0.33-1.41
Loss on ignition (%)	62.52	3.82	48.26	5.39	21-93	8-25
pH	4.05	0.04	3.73	0.03	3.8-4.7	3.5-4.0
Soil conductivity (us/cm)	323.60	26.29	254.74	13.58	140-810	160-340
P (ppm)	12.36	1.33	8.16	0.68	6-32	4-14
K (ppm)	208.52	27.66	151.84	14.21	74-780	54-270
Ca (ppm)	820.80	101.12	356.84	35.69	300-2640	170-630
Mg (ppm)	443.60	41.33	531.05	65.72	120-930	180-1040
Mn (ppm)	55.45	24.29	6.65	0.17	8.3-520	5-8.1
Zn (ppm)	6.22	0.84	1.05	0.08	1.8-20	0.6-2.0
Cu (ppm)	5.66	0.85	0.35	0.03	1.4-15	0.2-0.6
B (ppm)	2.94	0.19	1.82	0.1	2.1-7	1.4-3.2

All bryophyte data were collected between spring 2005 and autumn 2006. At the same time buttongrass tussock height, tussock diameter, and distance between tussocks were recorded, taking the average of ten measurements at each of the 44 sites. A presence/absence survey for bryophytes was done in five randomly located 2m x 2m plots at each of the 44 sites. Nomenclature followed Buchanan *et al.* (1989) for vascular plants, McCarthy (2003) for liverworts and Streimann & Klazenga (2002) for all mosses except Bryaceae (Spence & Ramsay 2006). At each plot visible open ground (%) and vascular plant cover other than buttongrass (%) were also recorded. Hereafter referred to collectively as 'site variables' are the measurements 'tussock height', 'average tussock diameter', 'average distance between tussocks', 'open ground', and 'vascular plants other than buttongrass'.

Data analysis

The adequacy of bryophyte sampling size was tested in EstimateS 7.5 (Colwell 2005), using abundance-base coverage estimator (ACE) of mean species richness to show the expected species accumulation (Chazdon *et al.* 1998). Variation in species richness (number of bryophyte or vascular species per plot) ascribed to environmental variables was determined using simple regression (Minitab 2000). Best subsets regression was used to determine which combination of site variables accounted for the most variation in bryophyte species richness (Minitab 2000).

Multi-dimensional scaling was performed to produce ordinations of bryophyte and vascular species compositions (PRIMER 5, Bray-Curtis dissimilarity coefficient, 25 restarts; Clarke & Gorley 2001). The first two ordination axes (stress < 0.2) were then imported to Minitab for regression against environmental and site variables. To analyse for similarities between bryophyte and vascular plant composition RELATE in PRIMER, which tests for matched similarity matrices, was used.

Results

Changes in buttongrass vegetation structure

Immediately post-fire, the tussock interspace was wide and the tussocks tended to be shorter and narrower (Table 3.3, Figure 3.7, Appendix 3). Approximately 10 years after fire, the buttongrass tussocks had grown wider, closing the gaps between the tussocks and decreasing the areas of open ground available for bryophyte colonisation. Some variation occurred due to localised differences in buttongrass tussock age with some tussocks not burned during fires.

Table 3.3. Correlation between site variables. % vascular species excludes buttongrass (*Gymnoschoenus sphaerocephalus*).

		Open ground	Time since fire	Tussock diameter	Tussock height	Tussock interspace
Time since fire	R	**-0.425**				
	P	**< 0.001**				
Tussock diameter	R	**-0.372**	**0.505**			
	P	**< 0.001**	**< 0.001**			
Tussock height	R	**-0.438**	**0.512**	**0.743**		
	P	**< 0.001**	**< 0.001**	**< 0.001**		
Tussock interspace	R	**0.224**	**-0.337**	**-0.374**	**-0.251**	
	P	**0.001**	**< 0.001**	**< 0.001**	**< 0.001**	
% vascular sp. (exc. bg)	R	**-0.138**	0.073	-0.119	-0.000	**0.369**
	P	**0.041**	0.279	0.078	0.995	**< 0.001**

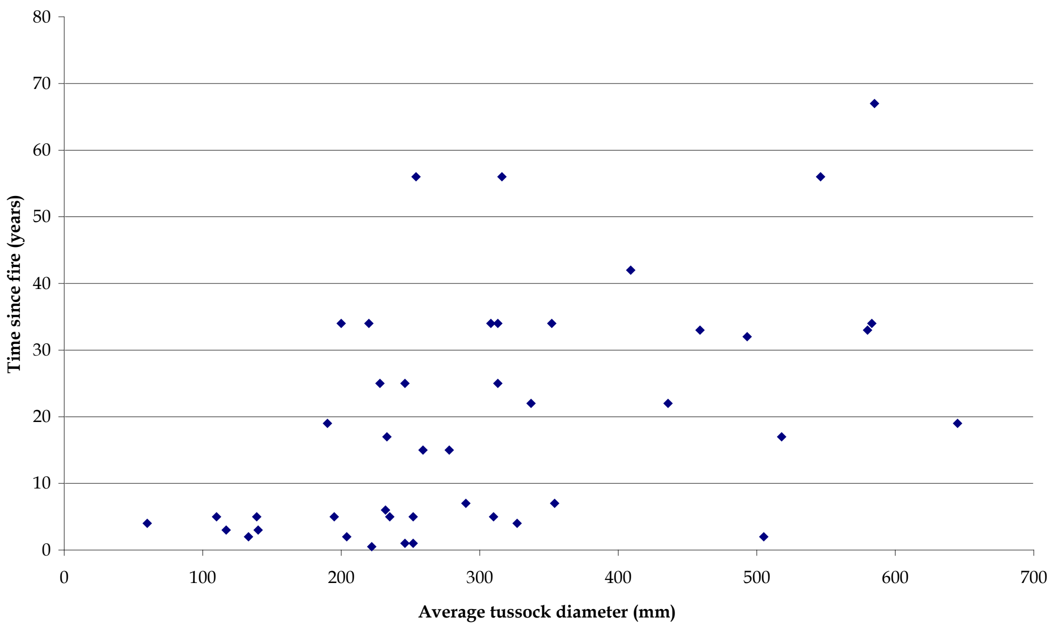


Figure 3.7. Average tussock diameter plotted against time since fire at the 44 sites.

Ten out of 13 environmental variables were significantly different between Lake Pedder and Lake St. Clair; seven correlations were significant at $P < 0.001$ (N, pH, Ca, Zn, Cu, B, altitude) and three at $P < 0.05$ (loss on ignition, soil conductivity, P). Given these differences between Lake Pedder and Lake St Clair, bryophyte richness and composition was analysed for both areas together and then each area separately.

Bryophyte and vascular plant occurrence

A total of 43 bryophyte species (22 moss, 21 liverwort) were found in the 220 plots from the 44 buttongrass sites (Appendix 4). More than double the number of vascular plants, 89 vascular species, were collected in the same 44 sites. However, sampling intensity was lower in the vascular surveying with 7 m^2 searched, while 20 m^2 was surveyed for bryophytes. Seventy-seven percent of the estimated bryophyte species present (ACE mean = 56.24 species) were collected in the 220 plots surveyed.

Most bryophyte species occurred infrequently with thirteen species (30%) being found at only one site and 26 species (60%) being found in less than six sites. This is comparable to the vascular species, with 19 vascular species (21% of total vascular species) found at only one site, and 49 vascular species (55%) occurring in fewer than six sites. Of the thirteen species found at only one site, eight were found in Lake St. Clair region and five in the Lake Pedder region. Five bryophyte species (11%) were in more than half the sites: the moss *Campylopus introflexus* (75% of sites), leafy liverworts *Kurzia hippuroiodes* (66%) and *Goebelobryum unguiculatum* (57%), and thallose liverworts *Riccardia aequicellularis* (61%) and *R. crassa* (59%). Vascular plant species composition was significantly correlated with bryophyte species composition ($R = 0.176$, $P = 0.013$). Of the total 43 bryophyte species found, fifteen species (35% of total bryophyte species found) were classified as uncommon (Table 3.4). For the purposes of this study, uncommon species were classified as those that were seen at two to five sites (therefore found in fewer than 11% of sites). Similar numbers of uncommon mosses and liverworts were seen, with eight uncommon mosses and seven uncommon liverworts recorded (Table 3.4). More uncommon species were found in the Lake St. Clair region, with eleven of the fifteen species classified as uncommon occurring only in this region. Four of the uncommon species occurred at both Lake St. Clair and Lake Pedder, whilst none of the species were found in the Lake Pedder region alone (Table 3.4). The uncommon species were also seen across a range of fire ages, and did not appear to be more prevalent in sites burnt in the last five years, or older sites thirty years since last fire (Table 3.4).

Table 3.4. The distribution of uncommon* bryophyte species between Lake St. Clair and Lake Pedder, and their distribution according to time since fire range. *uncommon classified as occurring in two-five sites.

Species	Region species recorded as present		Time since fire of sites at which species occurred	
	Lake St. Clair	Lake Pedder	Youngest site	Oldest site
Balantiopsis diplophylla	Yes	No	3	32
Campylopus bicolour	Yes	Yes	2	34
Dicranaloma robustum	Yes	Yes	1	56
Fossombronia sp.	Yes	No	1	32
Isotachis sp.	Yes	Yes	15	25
Jackiella curvata	Yes	No	6	7
Jamesoniella colorata	Yes	No	2	19
Kurzia compacta	Yes	No	1	5
Marsupidium surcolosum	Yes	Yes	34	67
Riccardia cochleata	Yes	No	7	33
Rosulabryum billarderi	Yes	No	7	32
Sphagnum australe	Yes	No	19	19
Sphagnum cristatum	Yes	No	4	33
Sphagnum falcatulum	Yes	No	2	17
Tayloria octoblepharum	Yes	No	1	7

Plant richness and time since fire

There was no correlation between time since fire and vascular plant species richness (r^2 = 0.3%, P = 0.740), but time since fire was significantly correlated with bryophyte richness (r^2 = 8.1%, P < 0.001; Figure 3.8), however, this was no longer significant on removal of four of the eleven sites that had not been burnt for more than 33 years. These sites had the highest bryophyte richness (r^2 = 1.4, P < 0.06) and suggests that areas that are unburnt for long periods of time are important for bryophyte species richness (Figure 3.9). When mosses and liverworts were analysed separately there was no significant relationship between moss species richness and time since fire (r^2 = 0.4%, P = 0.360), but liverworts overall were significantly richer in the older sites (r^2 = 9.0%, P < 0.001). On removing six of the older Lake Pedder sites, there was no significant relationship between liverwort richness and time since fire (R^2 = 0.5%, P = 0.177), again suggesting that long periods of time without fire are necessary for bryodiversity, specifically liverworts.

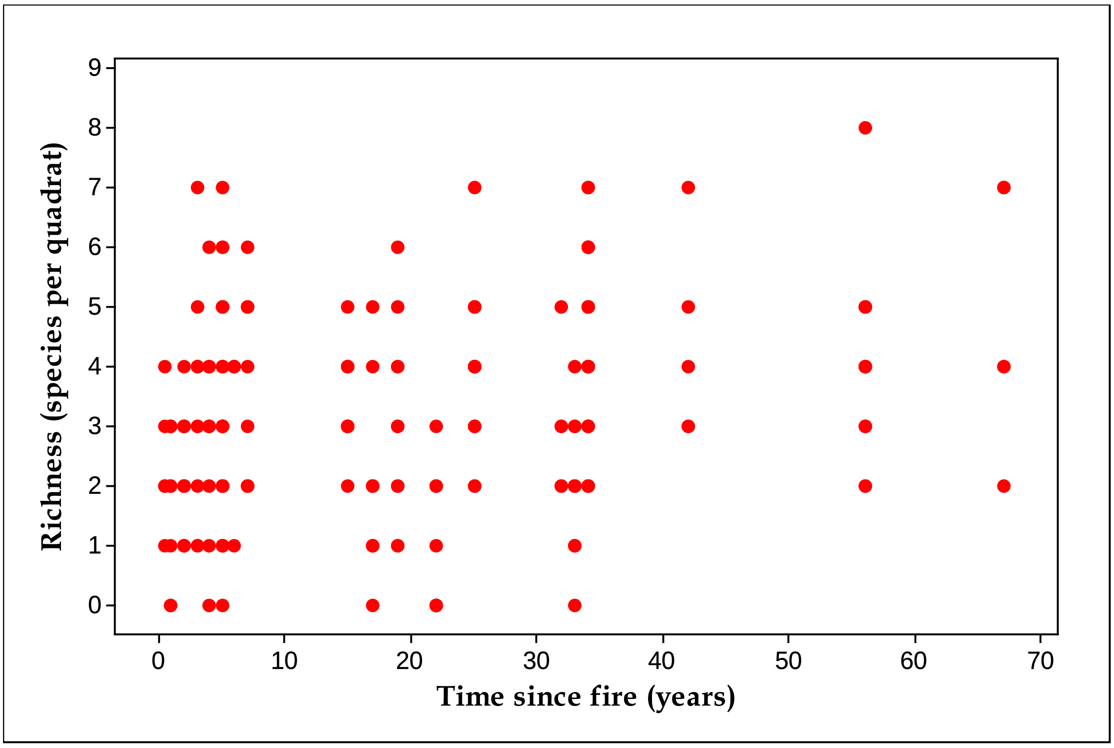


Figure 3.8. Bryophyte species richness per quadrat compared to time since last fire.

No relationship between bryophyte richness and time since fire occurred at Lake St. Clair (r^2 = 2.1%, P = 0.103) but a weak relationship occurred between richness and time since fire at Lake Pedder (r^2 = 5.3%, P = 0.025). Removing one older site to test the strength of the relationship eliminated the significant relationship (r^2 = 2.2%, P = 0.177). This site was last burnt 56 years previously, and it had the highest average species richness (5.2 species) in a 2m x 2m quadrat. No significant relationships were found between mosses and time since fire at either Lake St Clair or Lake Pedder, or between liverworts and time since fire at Lake St Clair (r^2 = 10%, P = 0.002). The liverwort richness of Lake Pedder alone was related to time since last fire (r^2 = 5.3%, P = 0.025). However, once again the removal of four sites older than 33 years since last fire, which had the highest average liverwort species richness, resulted in no significant correlation (r^2 = 3.4%, P = 0.061).

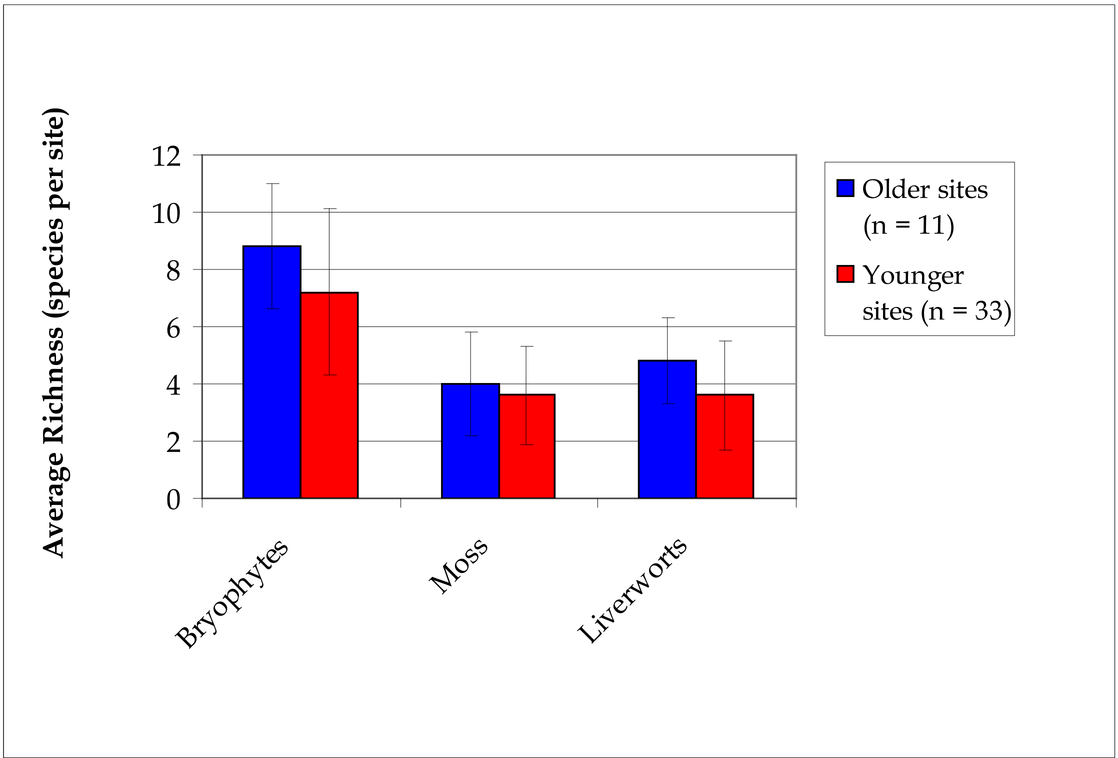


Figure 3.9. A comparison of the average richness of the older (> 33 years) and younger sites.

The structure of the buttongrass was not significantly related to vascular plant richness. Time since last fire was the only individual site variable significantly affecting bryophyte species richness (r^2 = 7.7%, $P < 0.001$). Out of all possible combinations of the six site variables, time since last fire and changes in tussock height together appeared to be affecting bryophyte richness the most (R^2 = 13.3%, $P < 0.001$; Table 3.5). When all six of the site variables (open ground, vascular species other than buttongrass, tussock height, tussock diameter, tussock interspace and time since last fire) combined to best predict changes in bryophyte abundance (R^2 = 18.6%, $P < 0.001$; Table 3.5), there was only an increase of 5.3% on just the effect of time since fire on richness. This reflected the collinearity between time since fire and the rest of the site variables. Of the 15 environmental variables measured, eleven were significantly related to bryophyte richness with $P < 0.05$ (N, loss on ignition, soil conductivity, pH, P, Ca, Zn, Cu, B, altitude, aspect), whilst only two, manganese and altitude, were significantly correlated with vascular richness (Table 3.6).

Table 3.5. Best subset regression of site variables. All p-values were < 0.001.

Number of variables	R^2 (adj)	Tussock height (cm)	Tussock diameter (cm)	Tussock interspace (cm)	Open ground (%)	Vascular sp. (exc. bg) (%)	Time since fire (years)
1	7.7						X
2	13.3	X					X
2	9.6				X		X
3	15.4	X	X				X
3	14.3	X		X			X
4	15.9	X	X			X	X
4	15.9	X	X		X		X
5	17.4	X	X	X		X	X
5	16.7	X	X		X	X	X
6	18.6	X	X	X	X	X	X
6	17.2	X	X	X		X	X

Table 3.6. Relationship between environmental variables and bryophyte and vascular species richness. Significant relationships shown in bold.

	Bryophytes		Vascular plants	
	r^2	**P**	**r^2**	**P**
Nitrogen (%)	**7.7**	**<0.001**	1.3	0.464
Loss on ignition (%)	**5.4**	**0.001**	0.0007	0.984
Soil conductivity (us/cm)	**1.9**	**0.039**	1.2	0.488
pH	**2.3**	**0.026**	5.5	0.127
Phosphorus (ppm)	**3.4**	**0.006**	0.8	0.571
Potassium (ppm)	1.0	0.139	0.4	0.695
Calcium (ppm)	**3.4**	**0.006**	3.3	0.238
Magnesium (ppm)	0.0	0.997	7.4	0.074
Manganese (ppm)	0.0	0.748	**10.2**	**0.035**
Zinc (ppm)	**2.3**	**0.024**	3.1	0.250
Copper (ppm)	**3.0**	**0.010**	0.0	0.943
Boron (ppm)	**8.7**	**<0.001**	0.3	0.729
Soil moisture (%)	0.1	0.678	1.8	0.390
Altitude	**15.7**	**<0.001**	**9.6**	**0.040**
Aspect	**2.6**	**0.016**	4.4	0.173

Plant composition and time since fire

Bryophyte species composition was uniformly low with five very common species (*C. introflexus*, *K. hippuroiodes*, *G. unguiculatum*, *R. aequicellularis*, and *R. crassa*), which resulted in low variation between sites. Average bryophyte species richness was 3.15 ± 0.11 (mean ± standard error) species per plot and 7.59 ± 0.43 species per site, meaning small differences in bryophyte species richness had the potential to make a large difference to composition results.

No site or environmental variables except for time since fire were correlated with bryophyte species composition. In contrast, vascular plant composition was influenced by the majority of environmental variables (Table 3.7), including time since fire (ordination axis 1: $r^2 = 34.5$, $P < 0.001$, ordination axis 2: $r^2 = 0.1$, $P = 0.883$), although no clear pattern can be discerned in vascular species and time since fire (Figure 3.10). However, a distinct difference in vascular plant assemblages at the two areas can be seen (Figure 3.11).

Table 3.7. Vascular species composition analysed by environmental variables.

	Ordination axis 1		**Ordination axis 2**	
	r^2	P	r^2	P
Nitrogen (%)	**46.1**	**<0.001**	6.5	0.095
Loss on ignition (%)	**12.0**	**0.021**	**8.8**	**0.051**
Soil conductivity (us/cm)	**8.8**	**0.05**	**21.0**	**0.002**
pH	**41.2**	**< 0.001**	**10.1**	**0.036**
Phosphorus (ppm)	**12.1**	**0.021**	3.7	0.210
Potassium (ppm)	4.7	0.159	**12.0**	**0.021**
Calcium (ppm)	**26.4**	**< 0.001**	**9.4**	**0.043**
Magnesium (ppm)	2.7	0.288	**11.0**	**0.028**
Manganese (ppm)	7.4	0.074	**13.8**	**0.013**
Zinc (ppm)	**37.7**	**< 0.001**	**19.1**	**0.003**
Copper (ppm)	**40.9**	**< 0.001**	7.0	0.084
Boron (ppm)	**35.7**	**< 0.001**	3.7	0.214
Soil moisture (%)	5.9	0.112	**24.0**	**0.001**
Altitude	**96.7**	**< 0.001**	0.0	0.980
Aspect	7.0	0.082	7.6	0.071

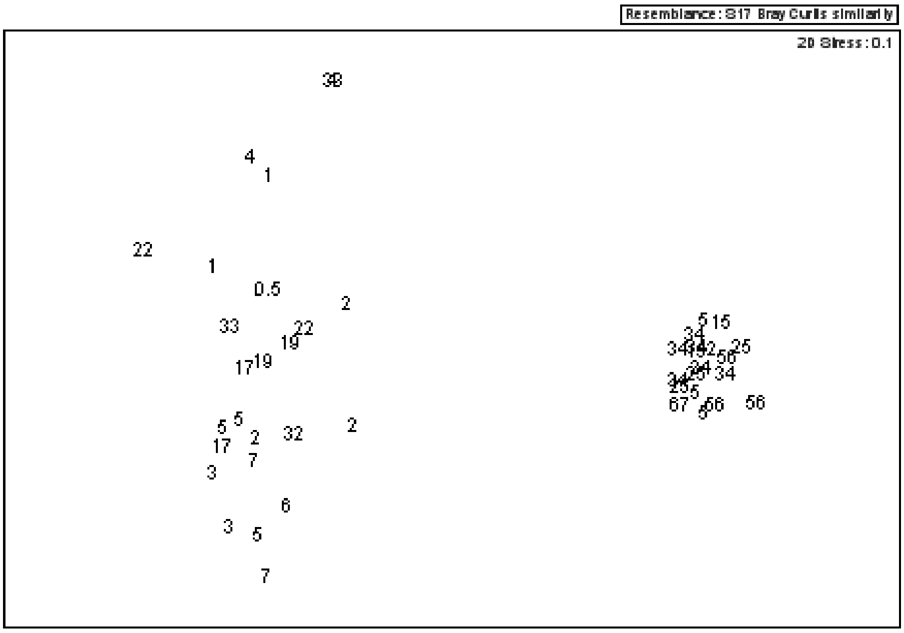


Figure 3.10. Vascular plant composition at the sites plotted by time since fire (years).

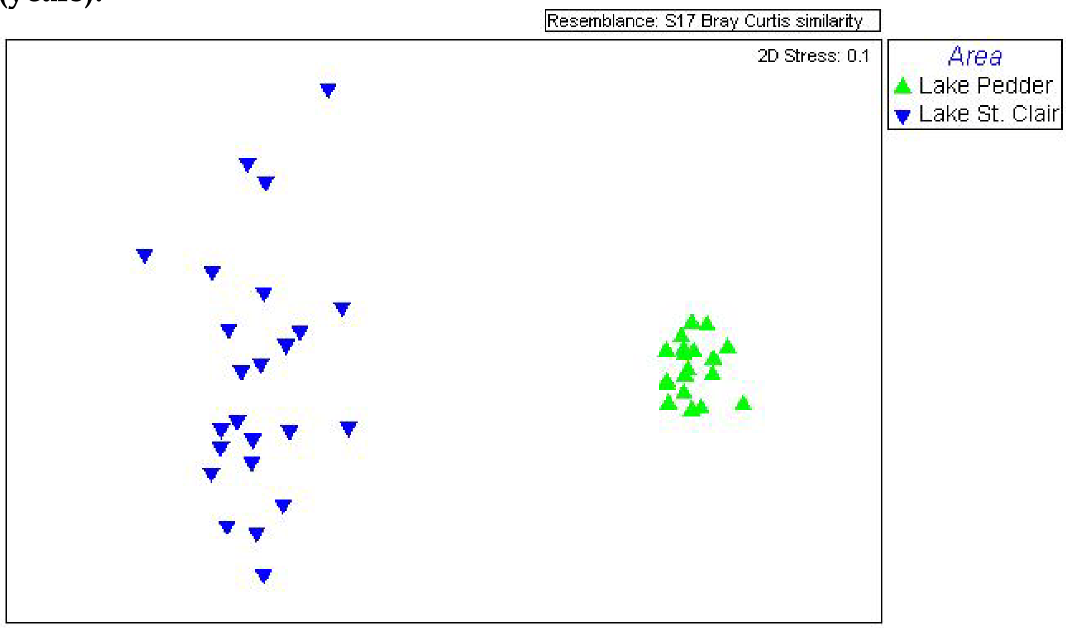


Figure 3.11. Vascular species composition classified by region (Lake Pedder, Lake St. Clair).

The correlation between time since fire and bryophyte species composition was statistically significant (r^2 = 9.2%, P = 0.048), but inspection of a two dimensional ordination revealed no clear trends (Appendix 5). When bryophytes were separated into moss and liverwort species and analysed against time since fire, only liverwort composition was found to be significantly correlated with fire (r^2 = 16.2%, P < 0.001; Table 3.8, Appendix 5). When the overall bryophyte composition of the two areas was tested separately, only the bryophyte composition of Lake Pedder was found to be related to time since fire (r^2 = 19.2%, P < 0.001; Table 3.8, Appendix 5). However, this significance was being driven by two outlying plots in older sites containing a higher liverwort species richness, and once these plots were removed there was no significant relationship between time since fire and bryophyte composition at Lake Pedder (r^2 = 3.8%, P = 0.075). The sites influencing the statistically significant relationship between bryophytes and liverworts and time since fire were all sites at Lake Pedder above 33 years since fire. These sites were not found to have higher average nutrients than the Lake St. Clair sites, although when compared to the younger Lake Pedder sites, some nutrients were slightly higher in these older sites (P, K, Ca, Mg, Cu) (Table 3.9). Mean buttongrass height and width was greater in the older Lake Pedder sites (Table 3.9).

Table 3.8. Bryophyte species composition and time since fire.

Classification	**Ordination axis 1**				**Ordination axis 2**			
	All data		Four older sites removed		All data		Four older sites removed	
	R^2	P	r^2	P	r^2	P	r^2	P
Both sites	0.0	0.774	0.0	0.943	1.8	0.055	**3.0**	**0.017**
Lake St. Clair	1.5	0.202	na	Na	0.2	0.612	na	na
Lake Pedder	**19.2**	**0.001**	**29.4**	**<0.001**	3.6	0.064	2.1	0.220
Liverworts	0.0	0.798	0	0.906	**16.2**	**0.001**	0.3	0.499
Lake St. Clair liverwort	0.9	0.367	na	Na	4.1	0.057	na	na
Lake Pedder liverwort	3.7	0.072	3.8	0.109	**4.4**	**0.052**	2.2	0.227
Moss	0.0	0.907	0.5	0.393	0.1	0.744	0.0	0.955
Lake St. Clair moss	0.1	0.804	na	Na	0.3	0.592	na	na
Lake Pedder moss	1.8	0.235	0.9	0.446	**8.5**	**0.008**	0.1	0.809

Table 3.9. Difference in buttongrass structure and nutrient levels between younger and older sites.

	Lake St. Clair < 34 years since fire		Lake Pedder <34 years since fire		Lake Pedder > 34 years since fire	
	Mean	**St dev**	**Mean**	**St dev**	**Mean**	**St dev**
Tussock height (cm)	65.38	18.27	38.45	7.56	73.18	20.53
Av. Tussock diameter (cm)	306.77	151.60	189.24	73.5	371.45	141.16
Av. Tussock interspace (cm)	47.45	20.94	24.55	7.52	39.18	15.36
N (ppm)	1.21	0.36	0.92	0.36	0.72	0.23
LOI (%)	61	20.26	30.14	23.96	45.12	22.93
pH	4.04	0.21	3.76	0.14	3.72	0.12
Cond (us/cm)	317.3	132.74	186.74	64.51	270	50.79
P (ppm)	12.04	6.74	6.20	3.12	7.82	2.64
K (ppm)	203.69	137.75	108.51	60.1	157.27	65.06
Ca (ppm)	797.69	509.21	422.67	162.67	338.18	154.2
Mg (ppm)	435	207.16	293.96	285.77	473.64	269.79
Mn (ppm)	53.51	119.41	31.97	0.73	6.65	0.56
Zn (ppm)	6	4.28	1.5	0.26	1.13	0.37
B (ppm)	2.89	0.98	1.8	0.11	1.95	0.5
Cu (ppm)	5.45	4.23	1.7	0.13	0.37	0.11

All single occurrence liverworts were removed from the data (*Heteroscyphus coalitus, H. fissitipus, H. varians, Podomitrium phyllantus, Saccogynidium decurvum,* *Temnoma townrowii*) in order to determine the degree to which these singular species were affecting the relationship between fire and bryophytes. Any significant relationship between bryophytes and fire disappeared entirely after the single occurrence liverworts were removed (ordination axis 1: $r^2 = 0.0\%$, $P = 0.830$; ordination axis 2: $r^2 = 0.1\%$, $P = 0.701$). These liverwort species were not tightly clustered in a geographical sense, for example all at the oldest site at Lake St. Clair (Figure 3.12). Liverwort and moss species found just once in the 44 sites were seen at both the Lake St. Clair sites and the Lake Pedder sites.

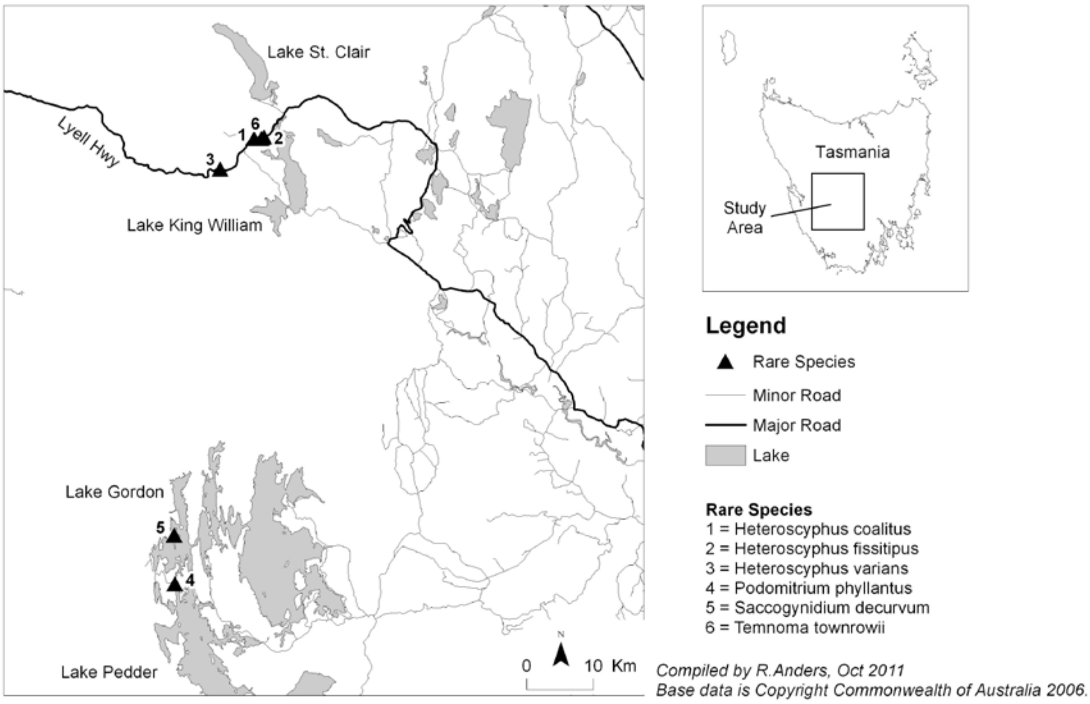


Figure 3.12. Distribution of liverwort species found once in the 44 sites surveyed in the Lake St. Clair and Lake Pedder regions.

Given the change in significance between bryophyte richness and time since fire on removal of the four sites older than 33 years since fire with the greatest bryophyte richness, these four sites were also removed from bryophyte composition and the data was reanalysed with time since fire (Table 3.7).

Discussion

The intensity and frequency of fire greatly affects the form of the vascular vegetation (Harris & Kitchener 2005) and this study found that time since fire was correlated with the amount of open ground and buttongrass tussock height, width and interspace. Previous studies of fire and vascular plants of buttongrass moorlands have found that the frequency of fires was highly correlated with floristic (Brown *et al.* 2002) and structural composition (Brown & Podger 1982). These studies support the patterns in vascular plant and fire relations seen in this study, with fire affecting vascular species composition.

The outcome of this study is supported by the findings of Ferguson *et al.* (2009), the only other study into bryophytes and fire in the buttongrass moorland. They found cool, prescribed burning had no significant effect on bryophyte cover or composition. This study found that bryophyte richness in buttongrass moorland remained relatively stable until sites reached approximately 30 years since fire. Around this time liverwort richness increased slightly and included the species found in younger sites as well as some other species. The significant relationship between liverworts and fire was driven by four richer sites. These four sites older than 33 years since fire were found to have the highest average number of bryophyte species per plot (> 4.6 species per plot), whereas all sites younger than 33 years since fire had fewer than 4.5 species per plot. Morgan (2004) also found that older sites in native grasslands in Victoria had higher bryophyte species richness than sites that were frequently burned, and the frequently burnt sites appeared to support a subset of the bryophyte flora found in the older sites, rather than a different flora containing easily dispersed species that utilise disturbed environments.

While liverwort richness increased slightly in older buttongrass sites, Green (2007) found that the species richness of soil mites increased dramatically once sites were approximately 30 years post-fire. There may be different mechanisms at work for these two very different groups of organisms, but it is possible that both are responding to an increase in soil nutrients as the sites age. When the older Lake Pedder sites are compared to all of the Lake St. Clair sites the nutrients are higher at Lake St Clair, with a few exceptions amongst the younger Lake Pedder sites. Lake St. Clair is known to be more nutrient-rich than the southwest Lake Pedder region due to differences in substrate. Therefore if an increase in liverwort richness was due to an increase in soil nutrients, it would be expected that bryophyte richness would be greatest in the more nutrient-rich Lake St. Clair sites, and not in the older yet comparably nutrient-poorer Lake Pedder sites, which is what was found in this study.

The species increase in these older sites could be due to an increase in light levels as the thick buttongrass tussocks were opened up by vascular shrub species. Kooijman and van der Meulen (1996) observed a decline in bryophyte species composition associated with a decrease in light penetration in grass-dominated vegetation. However, other studies have shown that a decrease in light quantity and a change in light quality associated with growth of grassland species barely affect bryophyte species (van der Hoeven *et al.* 1998; Vanderpoorten *et al.* 2004). If light levels prompted bryophyte species growth in the older buttongrass sites, it could be argued that there would also be more bryophytes in the years immediately after fire, when light levels to the ground surface could be assumed to be at their peak in buttongrass moorland (McCarron & Knapp 2003). A long-term monitoring program could be established in recently burnt buttongrass moorland, looking at changes in bryophytes over the years at the same site, monitoring light levels, amount of vascular plants other than buttongrass and open ground.

If bryophyte species are not being affected by increased light levels due to other vascular species creating gaps in the buttongrass tussocks, then possibly changes in bryophyte composition and richness are associated with a change in the vascular overstorey species, especially given the significant relationship found between vascular and bryophyte composition. In grassland, mixed eucalypt forest and wet sclerophyll forest, vascular plant composition was found to be related to bryophyte composition (Pharo *et al.* 1999; Pharo *et al.* 2000; Pharo *et al.* 2005). Following the classic ecological drift model for

Tasmania (Jackson 1968), as time since last fire increases in moorland, the vegetation progresses to a wet scrub community. It could be that buttongrass moorland communities simply have a low number of bryophyte species, and as the buttongrass moves on successionally into wet scrub an accompanying change in bryophyte species composition and richness occurs. Future studies could compare the bryophytes along a successional gradient from buttongrass moorland, to wet scrub, into wet forest to examine the gradient of species richness and composition as the vegetation type changes, as has been investigated in other environments outside of Australia (Łuczaj & Sadowska 1997; Orczewska & Glista 2005).

The buttongrass plains of Tasmania appear to be relatively poor in bryophyte species, especially when compared to the wealth of bryophytes found in wet forest and rainforest. Liverwort richness was slightly higher in some of the sites older than 33 years, which could be due to differences in light quantity or quality, or a change in overstorey species as the buttongrass moorland moves on successionally into wet scrub. It would be useful to investigate change across vegetation boundaries at the edges of buttongrass moorland to uncover the species that inhabit nearby vegetation but are not found in buttongrass moorland.

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Chapter 4

Change in bryophyte composition and biomass after fire in buttongrass moorland, Tasmania

Abstract

In order to complement a regional space for time study that correlated bryophyte diversity and time since fire over seventy years, in the same region change in a localised study was examined over a seven year period. Bryophyte biomass was measured, and the presence/absence of bryophyte species over two summers (1999/2000, 2006/2007) was recorded. No change was detected in either bryophyte richness or biomass over the six year interval, and there was no significant difference in bryophyte richness or biomass between control and burnt plots. Fire was seen to have a significant effect on the bryophyte composition at two of the three sites studied, although further analyses of the individual quadrats at the sites showed little variation in individual bryophyte species. The common buttongrass moorland bryophytes were present soon after fire, and it could be that some of these small plants are surviving the relatively cool buttongrass fires, although the role of survival versus re-establishment is not clear. Unusually, none of the cosmopolitan pioneering bryophytes were found, despite being the dominant groundcover post-fire in other Tasmanian ecosystems, such as wet sclerophyll forest. It is unclear why cosmopolitan fire moss species should be absent given their considerable dispersal abilities.

Introduction

Some areas of buttongrass moorland have been burnt repeatedly in fuel reduction burns in an attempt to protect nearby forests from unplanned fires as well as reset buttongrass moorland succession (Jarman *et al.* 1988). Although bryophyte response to fire in buttongrass moorland has not been widely documented, we do have a good understanding of the effect of fire on bryophytes in Tasmanian forests. In the years immediately proceeding fire in wet forests, pre-fire bryophytes are replaced with a suite of species colloquially known as the 'fire mosses' (Brasell *et al.* 1986; Cremer & Mount 1965; Duncan & Dalton 1982). These 'fire mosses' typically consist of *Funaria hygrometrica*, *Ceratodon purpureus*, and the liverwort *Marchantia berteroana*, with the moss *Polytrichum juniperium*, which develops more slowly in comparison, joining the other species a year or so post-fire. They colonise freshly burnt ground in great abundance in both the southern (Brasell & Mattay 1984; Brasell *et al.* 1986; Cremer & Mount 1965; Duncan & Dalton 1982) and northern hemisphere (de las Heras *et al.* 1994; Haeussler & Bergeron 2004; Racine *et al.* 2004; Sim-Sim *et al.* 2004).

The functional role of these bryophytes is well understood and includes facilitating the re-growth of vascular plants by reducing raindrop force (Eldridge & Tozer 1996), stabilising soil and reducing erosion (Brasell & Mattay 1984; Delach & Kimmerer 2002; Eldridge & Greene 1994), decreasing the incidence of frost heave (Groeneveld & Rochefort 2005), trapping nutrients and water (Delach & Kimmerer 2002; de las Heras *et al.* 1996; Hörnberg *et al.* 1997; Kinnaird 1974; Sohlberg & Bliss 1984; Sohlberg & Bliss 1987) and thereby changing the microhabitat for the germination and establishment of vascular plants (Cross 1981). As vascular plants re-establish, the cover of fire mosses decreases. By the fifth year post-fire the bryophyte population has shifted away from the early colonising species towards species with longer life-spans (de las Heras-Ibáñez *et al.* 1992; Sim-Sim *et al.* 2004). The species which were present prior to burning re-establish (de las Heras-Ibáñez *et al.* 1992; Sim-Sim *et al.* 2004).

This study was undertaken because fire is a key influence on biota in southwest Tasmania and bryophytes are a conspicuous, and potentially functionally important, component of this iconic vegetation. The aims were to determine 1) how bryophyte species composition changes following fire in buttongrass moorland, and 2) how fire affects the biomass of bryophyte species and the overall bryophyte biomass.

Method

Three sites in southwest Tasmania were chosen by the Biodiversity Conservation Branch, Department of Primary Industries, Parks, Water and Environment, Tasmania (Figure 4.1). Six sites were located at King William Creek, eighteen at Airstrip Road, and twelve at McPartlans Pass. A before-after control-impact (BACI) study was employed, a technique commonly used in observational studies to determine the impacts of disturbances (Green 1979; McDonald *et al*. 2000). Plots were tracked over time after burning, as opposed to the space for time method employed in the previous chapter, which observed the effects of fire on different sites. However, for reasons outlined in the following paragraphs, the BACI technique had to be abandoned for this study as a whole, although it remained in place for the Airstrip Road sites. In 2000, 5m x 5m plots were randomly located at each site and sampled for bryophytes. Sampling intensity depended on the size of the site. A 2.5 m x 20 cm strip plot was harvested from each 5m x 5m plot and all bryophytes were sorted, dried and weighed. The first bryophyte survey and collection was conducted by the Biodiversity Conservation Branch during the summer of 1999/2000 (the '2000' survey). These sites were resurveyed for the current study over the summer of 2006/2007 (the '2007' survey), choosing different locations within each 5m x 5 m plot for the biomass surveying because of the destructive nature of the sampling.

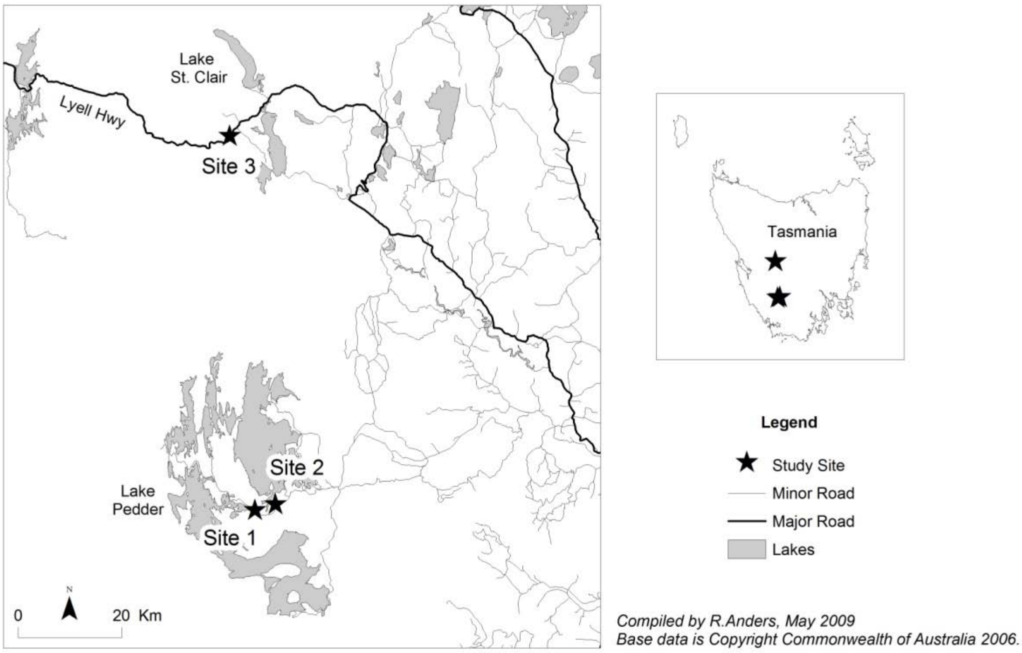

Figure 4.1. Study sites. Site 1 = Airstrip Road, Site 2 = McPartlans Pass, Site 3 = King William Creek.

The fire history of the sites is shown in Table 4.1. The design was complicated by the difficulty of executing planned burns, given weather and resource restrictions. All of the impact sites at McPartlans Pass and Airstrip Road were burned within two months of each other during autumn 2001. The Biodiversity Conservation Branch attempted to establish control plots at each site, which were to remain unburned. At McPartlans Pass, however, all but one of these eight control plots was burned in spring 2001 by an escaped burn, a few months after the impact sites had been burned deliberately. The control plots at the King William Creek site were burnt in 1987. The three 'after' plots were burnt in April 1999, but not surveyed for bryophytes by the Biodiversity Conservation Branch until January 2000.

Table 4.1. Fire history of the study sites.

	n (5 m x 5 m)	Control		Fuel-reduction burns		Escape burns	
		N	Burnt in	n	Burnt in	n	Burnt in
McPartlan Pass	12	1	1972	4*	autumn 2001	7	spring 2001
Airstrip Road	18	9	1972	9	autumn 2001	0	-
King William Creek	6	3	1987	3	autumn 1999	0	-

*Two of the plots burned deliberately in the 2001 burn were burnt again a few months later by an escaped forestry fuel reduction fire.

Upon revisiting the sites in 2006/2007, it became evident that treating all three sites as a BACI study was no longer appropriate. The King William site had no 'before' data collected before they were first burnt in 1999, meaning there was no baseline data to compare the sites to when they were resurveyed in 2006/2007. The McPartlans Pass site only had one control plot left out of the eight control plots first established as an unplanned fire burnt them in 2001. With two of the components of a BACI study missing, the 'before' from King William Creek and the 'control' from McPartlans Pass, it was evident the data could not be analysed as a whole. Instead, the three sites were treated separately, with the Airstrip Road site being the only site to maintain the integrity of the planned BACI design.

As far as possible, all bryophytes were identified to species level. Identifications in the 2000 survey (performed by the Biodiversity and Conservation Branch) were not well resolved for some groups, either because the taxonomic treatment was incomplete (*Campylopus, Dicranaloma*) or because the group itself was particularly difficult (Lepidoziaceae). *Campylopus* species were divided into *C.kirkii/C.bicolor* and 'all other *Campylopus* species'. *Dicranaloma robustum* and *D. billarderi* were lumped together. The same groupings were used for the identification of species in the 2007 survey.

Nomenclature followed Streimann & Klazenga (2002) for mosses and McCarthy (2003) for liverworts.

Data analysis

The King William site was analysed as one data set, because there was no pre-burn data gathered. The McPartlans Pass site was analysed as another data set, as due to unplanned burning events this site was only left with one control plot remaining. The Airstrip Road site was the only site analysed as a BACI study.

The presence/absence data were analysed using analysis of similarity (ANOSIM) to test for differences in species composition between fire ages (Primer version 6; Clarke & Gorley 2001). Taxa that were primarily responsible for an observed difference between groups of samples were used to determine species differences between the burnt and control plots (SIMPER (Similarity Percentage), Clarke 1993). Non-metric multi-dimensional scaling was performed to produce ordinations of bryophyte species composition (PRIMER 5, Bray-Curtis dissimilarity coefficient, 25 restarts; Clarke & Gorley 2001). Change in bryophyte richness according to the occurrence of fire was analysed using one way analysis of variance (ANOVA) in Minitab (2000) (significance taken at $P < 0.05$; F = mean of the within group variance). Difference in bryophyte biomass between fire ages was also tested using analysis of variance (ANOVA) (Minitab 2000). In addition to analysing total bryophyte biomass, change in biomass was analysed for each bryophyte species separately.

Results

Twenty-three taxa were identified, including *Pleurophascum grandiglobum*, which is endemic to the Tasmanian buttongrass moorland. Three taxa found in the survey before fire were not found in the survey after fire (*Ditrichum* sp., *Heteroscyphus billardierei, Lethocolea pansa*), and three new taxa were found in the survey after fire (*Chiloscyphus semiteres, Ptychomnion aciculare, Rosulabryum billarderi*). Bryophyte richness was not significantly different before and after fire at Airstrip Road (F = 2.71, P = 0.077) or McPartlans Pass (F = 2.47, P = 0.109). No significant difference was found between the bryophyte richness of recently burnt plots, plots seven years post fire, and the control plots at King William Creek (F = 0.53, P = 0.608). The variation in average bryophyte richness at the Airstrip Road, McPartlans Pass and King William Creek sites are demonstrated in Figures 4.2, 4.3, and 4.4 respectively.

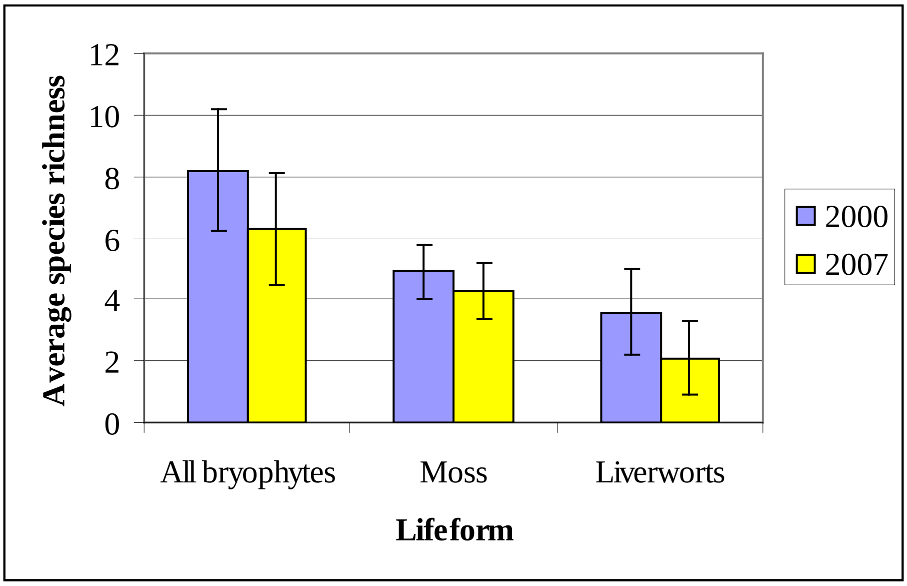

Figure 4.2. Airstrip Road bryophyte richness (taxa per plot) for the impact plots, before (2000) and after fire (2007). Standard deviation shown.

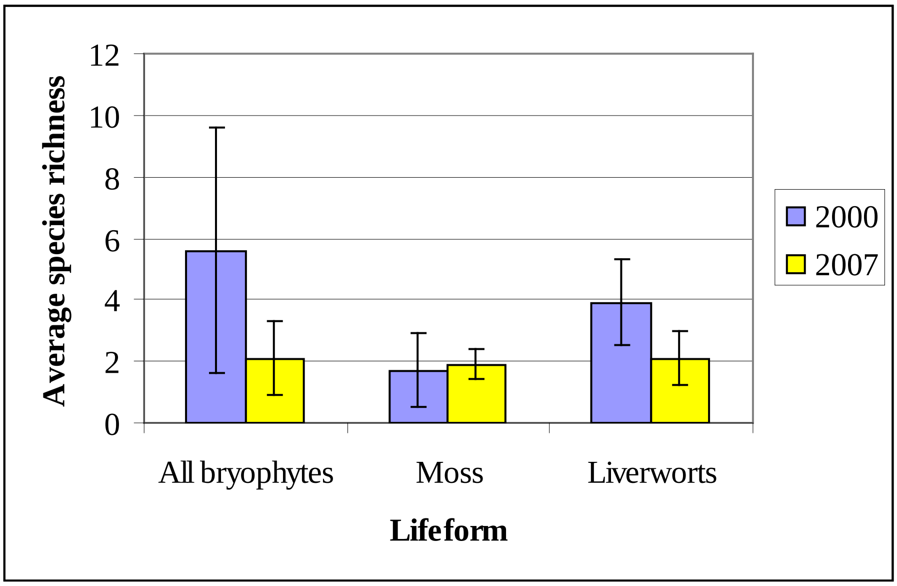

Figure 4.3. McPartlans Pass bryophyte richness (taxa per plot) for the impact plots, before (2000) and after (2007) fire. Standard deviation shown.

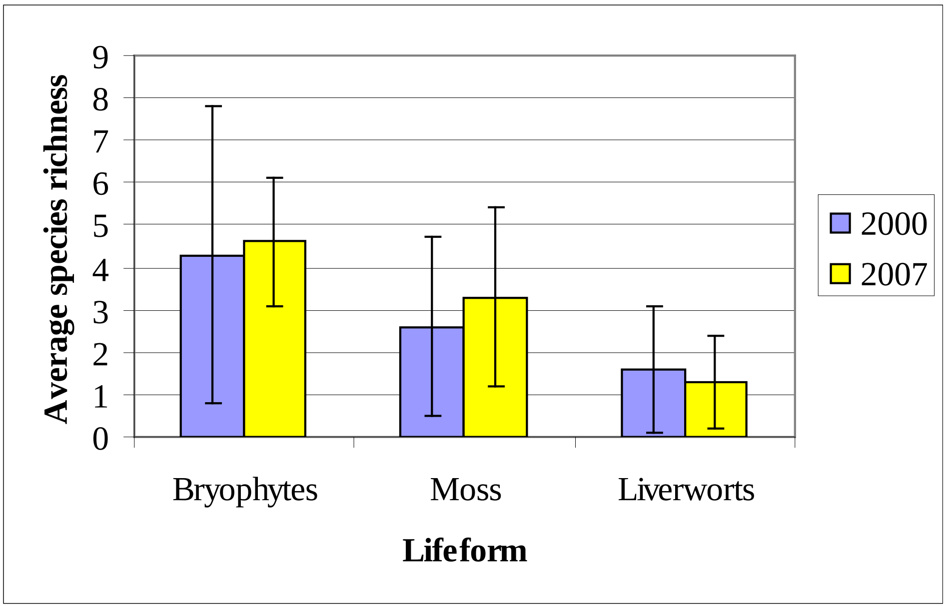

Figure 4.4. King William bryophyte richness (taxa per plot) nine months post-fire (2000) and eight years post-fire (2007). Standard deviation shown.

Fire had a significant impact on bryophyte composition at Airstrip Road (MDS axes 1: F = 3.54, P = 0.04; MDS axes 2: F = 3.56, P = 0.04; Figure 4.5) and McPartlans Pass on one axes (MDS axes 1: F = 4.41, P = 0.025; MDS axes 2: F = 1.34, P = 0.283; Figure 4.6). Upon removal of the one remaining control plot at McPartlans Pass the effect of fire on bryophyte composition remained significant on one axes (MDS axes 1: F = 7.39, P = 0.013; MDS axes 2: F = 2.46, P = 0.132).

Despite bryophyte composition being influenced by fire at McPartlans Pass and Airstrip Road, examination of the bryophyte species showed high similarity between burnt and unburnt plots (Figure 4.5 & Figure 4.6), with no species being unique to a treatment, and most abundance values being similar.

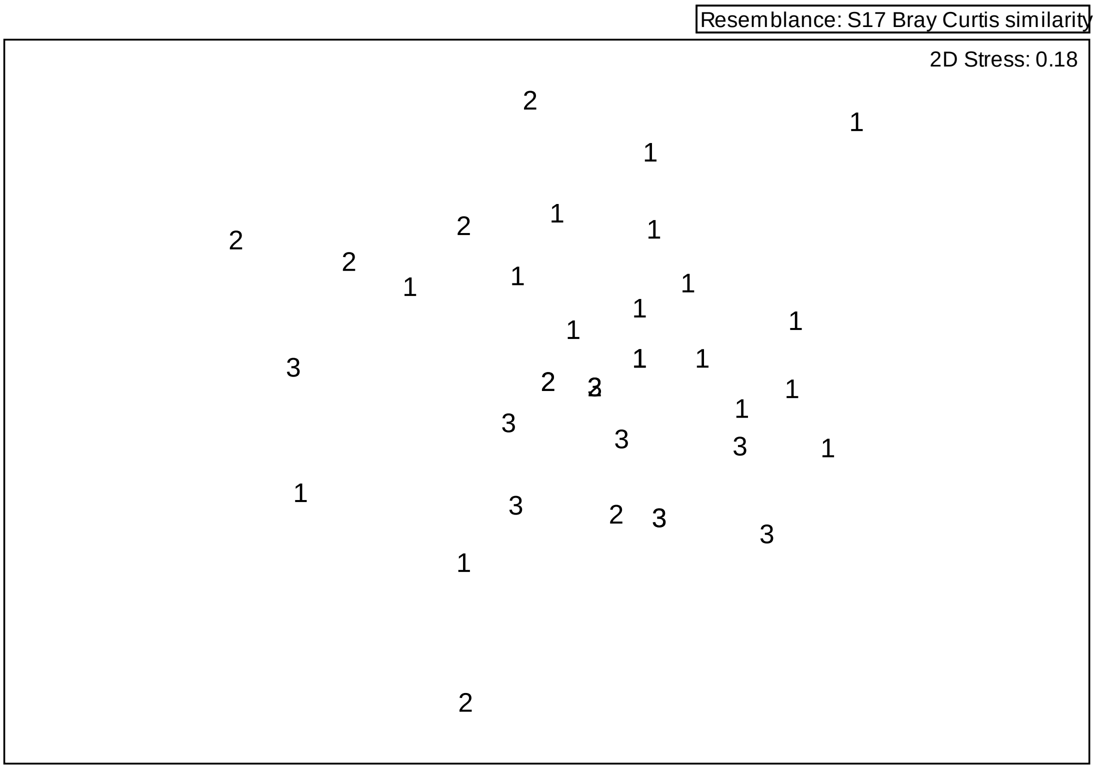

Figure 4.5. Ordination of bryophyte composition at Airstrip Road coded with treatment. 1 = Before fire, 2 = After fire, 3 = Control.
Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

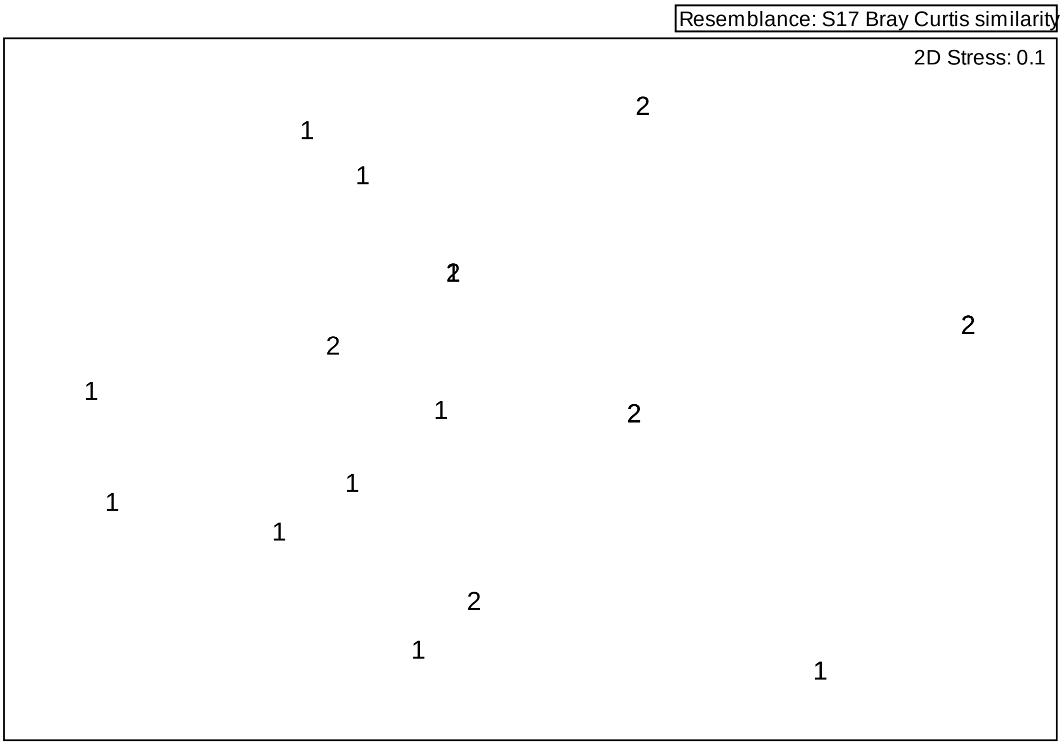

Figure 4.6. Ordination of bryophyte composition at McPartlans Pass coded with before and after fire. 1 = Before fire, 2 = After fire.
Horizontal axis represents MDS 1 and vertical axis represents MDS 2.

Time since fire was not significantly correlated with overall bryophyte biomass or the biomass of any individual bryophyte species at Airstrip Road (Table 4.2) or McPartlans Pass (Table 4.3), with levels remaining relatively consistent before and after fire. There was also no significant change in overall bryophyte biomass and individual bryophyte species biomass at King William from when it was first surveyed nine months post-fire when compared to eight years later (Table 4.4).

Table 4.2. Overall bryophyte biomass (gm/97.2m²) at Airstrip Road and the correlation in biomass change from 2000-2007. Significance taken at P < 0.05.

Species	2000	2007	F	P
All bryophytes	80.92	162.06	0.02	0.884
Acromastigum anistostomum	9.88	18.12	0.91	0.349
Campylopus kirkii/bicolour	21.2	0	2.11	0.158
Campylopus with hairpoints	7.75	77.95	0.06	0.806
Dicranaloma billarderi/robustum	16.01	34.52	0.03	0.860
Dicranaloma eucamptodontoides	8.48	34.54	1.58	0.219
Goebelobryum unguiculatum	6.47	8.52	0.21	0.648
Hypnum sp.	0.08	0	2.60	0.118
Isotachis sp.	0.11	0	0.34	0.565
Lepidoziaceae	0.53	1.244	0.74	0.398
Pleurophascum grandiglobum	7.64	0.278	0.37	0.549
Riccardia aequicellularis	2.55	5.35	2.23	0.146
Riccardia cochleate	0.01	0.12	0.40	0.534
Riccardia crassa	0.21	0	0.89	0.354
Teleranea sp.	0	7.237	0.66	0.423

Table 4.3. Overall bryophyte biomass (gm/64.8m²) at McPartlans Pass and the correlation in biomass change from 2000-2007. Significance taken at P < 0.05.

Species	2000	2007	F	P
All bryophytes	4.73	15.37	0.02	0.884
Campylopus kirkii/bicolour	0.39	5.041	2.11	0.158
Campylopus with hairpoints	1.004	4.323	0.06	0.806
Dicranaloma eucamptodontoides	0.01	0	1.58	0.219
Goebelobryum unguiculatum	0.95	0.50	0.21	0.648
Riccardia aequicellularis	0.11	1.36	2.23	0.146
Riccardia crassa	0.003	0.029	0.89	0.354
Teleranea sp.	0.06	0	0.66	0.423

Table 4.4. Overall bryophyte biomass (gm/32.4m² at King William and the correlation in biomass change from 2000-2007. Significance taken at $P < 0.05$.

Species	2000	2007	F	P
Total bryophytes	1.12	17.32	1.12	0.350
Balantiopsis diplophylla	0.06	0.11	6.72	0.061
Breutelia pendula	0.001	0	1.00	0.374
Campylopus with hairpoints	0	15.72	0.89	0.398
Dicranaloma billarderi/robustum	0	0.14	0.15	0.721
Distichophyllum pulchellum	0	0.9	1.27	0.381
Ditrichum sp.	0.13	0	1.27	0.323
Lepidoziaceae	0	0.17	2.02	0.228
Sphagnum sp.	0.93	0.21	1.30	0.318
Teleranea sp.	0.02	0	1.0	0.374

Discussion

This study was commissioned by the Tasmanian state government based on data that they had collected in 2000. It has been problematic since implementation because an escaped burn destroyed the control plots at one site, and no before data had been gathered at another site. The consultant employed to do the identification in 2000 tended to resolve groups to genus level rather than species level, and upon later examination several voucher specimens were found to be incorrectly identified to species level, necessitating further grouping of species to genus level. However, given the paucity of data and the possibility of strong responses by bryophytes to burning, it was decided to persist with analysing the data. The results found that in fact the response to burning was very muted, with bryophytes having a relatively consistent composition before and after fire in these Tasmanian buttongrass moorland areas. Despite significant differences being found in bryophyte species composition before and after fire at Airstrip Road and McPartlans Pass, plots with different fire age were quite mixed on the ordination diagram and low richness at each plot means that slight differences in composition were translating into statistically significant outcomes. In fact, there was not much difference in individual species between the burnt and unburnt quadrats. At King William, bryophyte species did not change significantly from nine months after burning to the second survey eight years after burning in 2007. The classic successional pattern from well dispersed, cosmopolitan 'fire mosses' through to less disturbance-dependent species was not found. This classic successional scenario has been documented in Tasmanian wet forests (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982) as well as studies in boreal and Mediterranean forests (de las Heras *et al.* 1994; Esposito *et al.* 1999; Morneau & Payette 1989; Puche & Gimeno 2000). However, it may be unreasonable to compare wet forest and northern hemisphere forests with Tasmanian buttongrass moorland. The only published Tasmanian study addressing the recovery of bryophytes after fire in buttongrass moorland was conducted in recently burned sites in the northeast of the state. Reasons for the similar species composition before and after fire could include the small sample size, the unusual environmental conditions of buttongrass moorland favouring a particular set of resilient bryophytes, and competition from the persisting resident bryophyte species excluding pioneering 'fire moss' species. Possible reasons for the lack of fire moss are explored in the following discussion.

'Fire mosses' are known for their ability to colonise recently disturbed environments (de las Heras *et al.* 1994; Esposito *et al.* 1999; Morneau & Payette 1989; Puche & Gimeno 2000), including nearby clearfell burned forests in Tasmania (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982). Their appearance after disturbance in other environments is largely due to their small spore size and survival ability during long dispersal events (Schofield 1985). This study found bryophytes appearing to be highly resilient after disturbance by fire and they also failed to detect fire mosses (Ferguson *et al.* 2009). Elsewhere in this thesis, a distinct lack of fire mosses has been noted in buttongrass moorland of differing fire intervals (Chapter 3). There was also no significant variation in bryophytes found in recently burnt sites and those found in sites 30 years plus since fire (Chapter 3). It is possible that the opportunistic 'fire mosses' were able to reach the buttongrass moorland sites, but prevented from establishing due to the challenging conditions.

The lack of fire mosses in buttongrass moorland post-fire may be due to the dominance of pre-existing bryophyte species immediately following fire. Some moss species (*Dicranaloma* spp., *Campylopus* spp.) survived fire and appeared as blackened patches that still occupied space. Despite the persistence of bryophytes following fire, including the usually fire-sensitive *Sphagnum* in five of the six plots at King William, bryophytes did not totally cover the ground surface and there were usually areas of bare ground. Therefore, competition from surviving communities seems an unlikely explanation (Kimmerer & Driscoll 2000; Zamfir & Goldberg 2000). Even with pre-existing bryophyte species surviving the fires, there still would have been bare ground available for the establishment of opportunistic 'fire mosses'.

The lack of fire mosses in recently burnt buttongrass moorland may also be attributed to the type of fire. Southorn (1977) distinguished two types of fire intensity: hot burns that consume large amounts of fuel and lead to the development of a characteristic community of bryophytes; and cool fires that involve relatively small changes in soil conditions, with bryophyte species persisting from the pre-burn vegetation. The controlled burning method employed in this study created a low-intensity fire with shallow soil heating and a modest post-fire flush of soil nutrients. The controlled burns conducted in this study were done when ground moisture was high enough to prevent uncontrollable fire outbreaks, and to prevent the chance of soil burning. High intensity, uncontrolled summer wildfire could result in different species composition, but given the high similarity of bryophyte species composition around the state (Chapter 2), it appears that any establishment of fire moss after a hot burn must be particularly transient before the usual complement of species re-establishes.

In order to investigate the lack of fire mosses in buttongrass moorland, research could examine bryophyte spores in recently burnt buttongrass moorland, analysing the diaspore bank, to determine whether fire moss spores are present in the soil, and conducting trapping of airborne bryophyte spores (e.g. During & ter Horst 1983; Ross-Davis & Frego 2004). It would be useful to track specific bryophyte patches before and then after fire, seeing which species persist and how long they take to start growing again. Regardless of a documented increase in non-vascular plant cover post-fire in buttongrass moorland (Bridle *et al.* 2003), there appears to be little change in species composition. This raises the question of why fire appears have so little effect on bryophyte species in this vegetation type, with no successional change in bryophyte species following fire in buttongrass moorland when, in other habitat types, there is. The Tasmanian studies into bryophyte recolonisation following fire have all been conducted in either mixed forest (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982) or alpine environments (Askey-Doran 1990). It would be useful to study the effect of fire on bryophytes in ecosystems more challenging than wet forests, such as dry rangelands, to determine if the expected pattern of bryophyte recolonisation following fire is also redundant in other limiting environments.

This study suggests that fire has little effect on bryophytes in buttongrass moorland, a result that has been confirmed independently by a small study of bryophytes and lichens in buttongrass moorland in the north-east of Tasmania (Ferguson *et al.* 2009). It appears that the bryophyte species of buttongrass moorland are relatively stable, despite fire changing the amount of light and nutrients available at the ground level.

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Chapter 5

The effects of canopy removal on bryophytes in buttongrass moorland, Tasmania

Abstract

Fire simultaneously changes the nutrient status, vegetation structure and microclimate of a site. In order to disentangle these influences, sites were compared that had been burnt (exposed to light and nutrient addition) with sites where the canopy was removed by slashing down to the ground level (exposed to light but no nutrient input). Bryophyte cover was recorded annually for three years at the burnt and slashed sites. No significant relationships were seen in overall bryophyte, moss or liverwort cover over the three years at either the burnt or the slashed sites. Mean moss cover increased over the three year period in the slashed plots (from 33.6% to 52.9%), whilst in the burnt plots, bryophyte cover dropped in the year after fire before slightly increasing. A significant relationship was determined between the change in bryophyte cover according to treatment over the first year of surveying. The current buttongrass moorland management regime of prescribed burning is not expected to cause a change in dominant bryophyte species, although bryophyte cover does appear to decrease immediately after fire.

Introduction

The effects of fire on soil nutrients are well documented (Viro 1974). When plant matter is burnt and reduced to mineral ash, nutrients are released for new plant growth (Tolhurst *et al.* 1992) and space is created for the development of new plants (Bond & van Wilgen 1996). Buttongrass moorland, a vegetation type covering vast tracts of Tasmania, is maintained by frequent fire and, despite frequent rainfall, there are relatively few days in the year when buttongrass moorland will not burn (Marsden-Smedley *et al*. 1999).

Fires create a patchwork of buttongrass moorland with differing fire histories in the same region. Despite this variation in burn age, the vascular floristic composition is highly similar in the buttongrass moors of the same region (Brown 1999). However, the vascular plants are not the only floristic component in the buttongrass moorlands of Tasmania, with lichens and bryophytes (mosses and liverworts) present in the ground layer. Following fire in other Tasmanian environments, pre-fire bryophyte species are generally eliminated and replaced with opportunistic bryophyte species that are common colonisers of burnt ground (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982).

Light intensity has been found to influence bryophytes following fire (O'Bryan *et al*. 2009) and mowing (Billeter *et al.* 2007; Caners *et al.* 2009). It is possible then that the removal of the vascular canopy, either through fire or mechanical removal will promote bryophyte cover in buttongrass moorlands, as was seen in Aune *et al.* (1995) and Aude & Ejrnæs (2005). This study sought to determine bryophyte response to fire in buttongrass moorland, which releases the ground surface to light and space (Bond & van Wilgen 1996), as well as providing an increase in nutrients through mineral ash (Tolhurst *et al*. 1992). This study also aimed to determine how the cover of bryophytes changes in a three year period following the burning of the buttongrass canopy, and compared this with the mechanical removal of the buttongrass canopy through slashing, which, like fire, opens the ground surface to space and light, yet lacks the addition of nutrients to the soil that burning facilitates. The study asked whether bryophytes respond differently to the two treatments.

Method

Study area

Six buttongrass moorland plains in the vicinity of Lake St. Clair were selected (Figure 5.1). Lake St. Clair is a high altitude (730-800 m) region (Pemberton 1986) on an underlying dolerite substrate, with a mean annual rainfall of 2540 mm (BOM 2008). Of the six sites, three were burned and three were slashed to remove the canopy. The burned sites were located within existing recently burnt areas in the vicinity of Lake St. Clair.

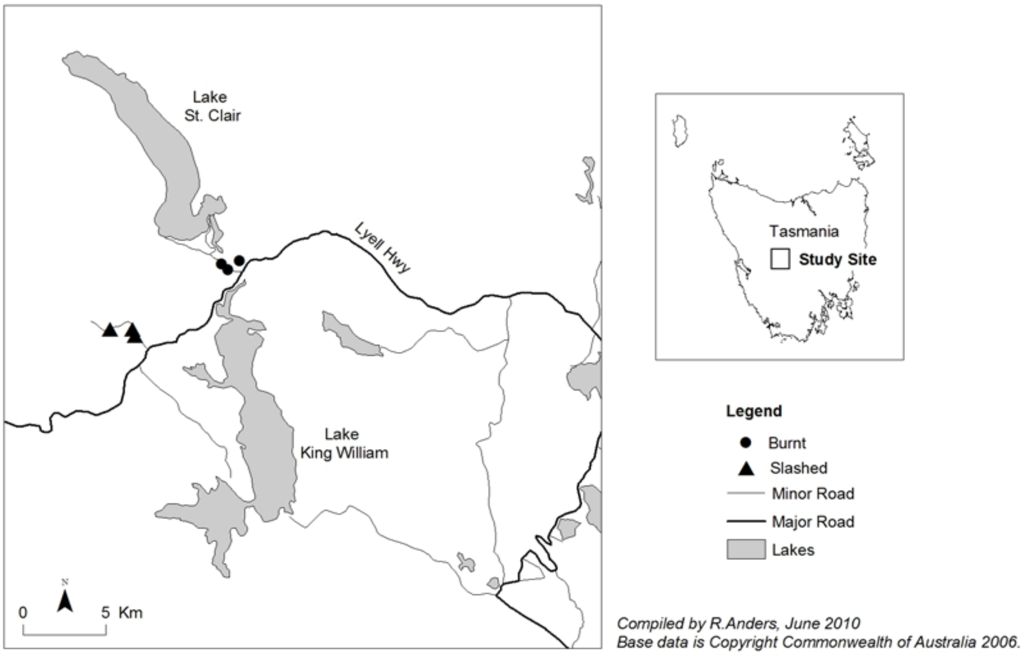

Figure 5.1. Map showing the six study sites in the Lake St. Clair region - three burnt sites and three slashed sites.

Study design

Due to the difficulty, cost and potential for escaped fires when burning small patches of buttongrass moorland, three buttongrass moorland plains were chosen from the same area. Two sites were used that had been burned eight months prior and a third site was selected that had been burnt six months prior by the Parks and Wildlife Service fire management. Five 2 m x 2 m plots were permanently marked in each of the three buttongrass plains (Figure 5.2), and cover of bryophytes in each plot was recorded. Bryophyte cover in the field was estimated visually and bryophyte taxa areas were sketched on grids (10 cm in the field = 1.5 cm on the grid). It proved impossible to map boundaries at the level of individual species because of the subtle differences between species in some of the genera. Therefore, some bryophytes were grouped at the generic level: *Campylopus*, *Dicranaloma*, *Riccardia*, and *Sphagnum*. Taxa not readily visible to the eye, such as some small liverworts, were not included in this survey because it was too difficult to reliably assess their changing cover. Cover was recorded at 4-8 months, 16-20 months, and 28-32 months post-fire.

Three buttongrass moorland plains that were last burned more than ten years ago were selected for the second part of the study, the mechanical removal of the canopy. The slashed plots were in the same area as the burned plots, and appeared similar environmentally with no visible differences in, for example, slope, aspect, degree of waterlogging, or position in the landscape. Five 2 m x 2 m plots were permanently marked at each of the three sites, slashed with a brush-cutter down to ground level, and the resulting slash was removed from the site (Figure 5.3). Bryophyte cover was scored on a grid in the same way as for the burnt plots. However, unlike the burnt plots, the bryophytes in the slashed plots were recorded immediately upon removal of the canopy to gather baseline data.

Figure 5.2. Plot in burned site.

Figure 5.3. Plot in slashed site.

Data analysis

Each 2 m x 2 m plot grid with the map of bryophyte cover was scanned to create a digital array (ITT Visual Information Solutions 2008). Each bryophyte species marked on the digital grid was then manually coded with a colour to represent its taxa. These were the six taxa *Campylopus spp., Dicranaloma spp., Geobelobryum unguiculatum, Pleurophascum grandiglobum, Riccardia spp.,* and *Sphagnum spp.*. These were the taxa present that were clearly and consistently discernable in the plots. The number of pixels in each patch of colour was calculated. The output was a table with each bryophyte genera and the corresponding number of pixels that particular bryophyte genera covered. In real terms, 1 pixel = 1 mm^2 ground covered. The six taxa were further grouped into the three categories of all bryophytes, mosses or liverworts to give greater statistical power during analysis due to the low cover of some taxa.

Two-sample t-tests assuming uneven variance were used to determine if bryophyte cover differed significantly between the burned and slashed treatments over the period 2006-2007 and then 2007-2008. Additional t-tests were used to explore the change in total bryophyte cover, liverwort cover and moss cover from year to year in both the burnt and slashed treatments.

Results

The cover of bryophytes, moss and liverworts varied from 0 mm^2 to 547819 mm^2, 486566 mm^2 and 153143 mm^2 respectively in the burned plots (Table 5.1). The range of bryophyte species cover for the slashed plots was similarly wide, although the lowest cover for bryophytes overall was 859 mm^2 because no plot in the slashed treatments was devoid of bryophytes (Table 5.1). The cover of liverworts was consistently lower than the cover of mosses in both the slashing and the burnt treatment (Table 5.1).

Table 5.1. Range of bryophyte cover: lowest, highest and mean cover for plots incorporating all three years of surveying. Values as mm².

		Lowest cover	Highest cover	Mean cover	Standard deviation
All bryophytes	Slashed	859	501662	128564	120291
	Burnt	0	547819	103338	136118
Moss	Slashed	0	397353	116443	111217
	Burnt	0	486566	88947	119588
Liverworts	Slashed	0	199538	9898	31398
	Burnt	0	153143	6591	24440

In both treatments, bryophyte cover was not correlated with time since fire/slashing (Tables 5.2 & 5.3). In the burnt treatment, mean bryophyte and mean moss cover were highest 4–8 months post-fire and declined over the following year before increasing again by the final survey 28-32 months post-fire (Table 5.2). Whilst liverwort cover followed the same pattern initially, being highest in the first survey, liverwort cover continued to decline after the second survey, although no significant links can be made between time since fire and liverwort cover (Table 5.2). In contrast, in the slashing treatment mean bryophyte cover and mean moss cover increased over the three-year period (Table 5.2), although this was not of significance statistically (Table 5.3). However, mean liverwort cover in the slashed plots increased by 1.8% before decreasing by 6.2% to a cover of just 0.2% (stdev 0.05). Again, this was not of significance statistically (Table 5.3). No significant relationships were detected in bryophyte cover overall, liverwort cover or moss cover (Table 5.3). Visual inspection of overall bryophyte cover showed no patterns across the three years in both the slashed and the burnt treatments, with some slashed plots increasing (e.g. S12) whilst others remain relatively static (e.g. S3, S8, S13) (Figure 5.4). Only one plot in the burnt treatment had an obvious increase in the second year (S6), whilst the majority of the burnt plots decrease in cover then increase again or remain relatively stable (Figure 5.5).

Table 5.2. Total mean percent bryophyte cover and standard deviation (stdev) for each treatment across three years. All values as percentages.

	Treatment	2006 mean	2006 stdev	2007 mean	2007 stdev	2008 mean	2008 stdev
Bryophytes	Slashed	40.7	2.5	50.8	3.5	53.1	3.2
	Burnt	50.9	3.7	30	3.6	35.3	3.0
Moss	Slashed	33.6	2.1	44.4	3.1	52.9	3.1
	Burnt	36.6	2.9	28.2	3.2	35.2	3.0
Liverworts	Slashed	4.6	0.5	6.4	1.3	0.2	0.05
	Burnt	5.5	1	1.8	0.4	0.08	0.02

Table 5.3. Differences in bryophyte cover under burning and slashing over three years.

	Treatment	2006 vs. 2007		2007 vs. 2008	
		t statistic	P two tail	t statistic	P two tail
Bryophytes	Slashed	-0.62	0.54	-0.13	0.90
	Burnt	1.05	0.30	-0.29	0.77
Moss	Slashed	-0.76	0.45	-0.50	0.62
	Burnt	0.50	0.62	-0.41	0.68
Liverworts	Slashed	-0.35	0.73	1.26	0.23
	Burnt	0.91	0.37	1.09	0.29

The difference in cover between the burned plots and the slashed plots was significant for overall bryophyte and moss cover, although the differences in the two treatments, burning and slashing, had little effect on liverwort cover (Table 5.4). After the initial year, the treatments appeared to have no significant effect on bryophyte cover, with the change in bryophytes overall, moss and liverwort cover from 2007 to 2008 not being significantly different according to slashing or burning treatments.

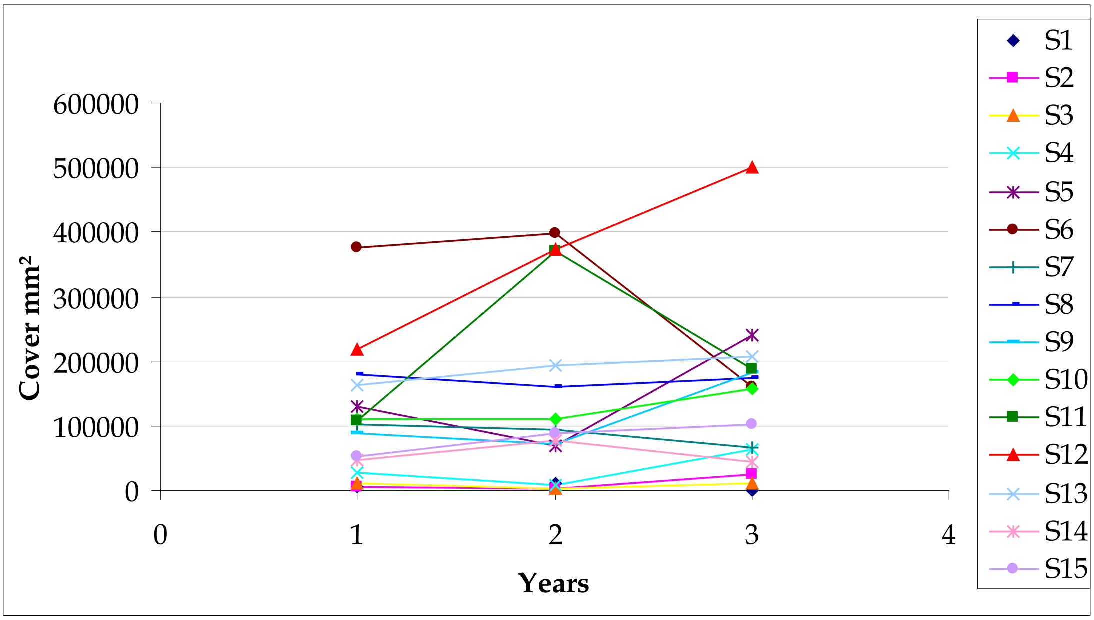

Figure 5.4. Change in bryophyte cover (mm²) in plots at slashed sites. S1-S15 represents the fifteen plots surveyed.

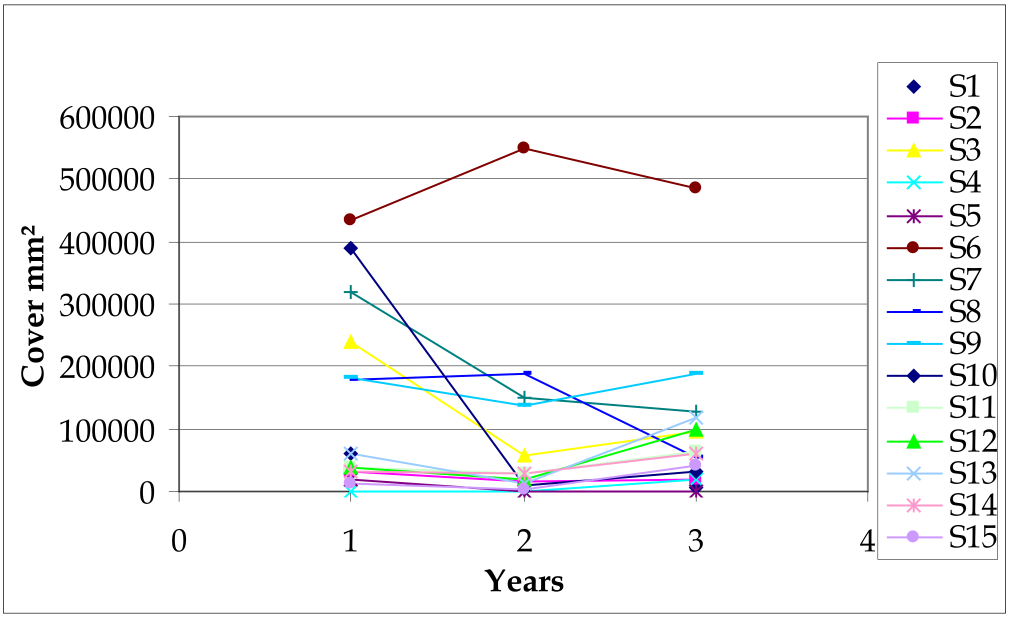

Figure 5.5. Change in bryophyte cover (mm²) in plots at burned sites. S1-S15 represents the fifteen plots surveyed.

Table 5.4. t-test results for the relationship in cover change between the two treatments (2006 to 2007; 2007 to 2008).

	t statistic	P two tail
2006 to 2007		
Bryophytes	-2.29	0.0304
Moss	-2.46	0.0203
Liverworts	-0.14	0.3053
2007 to 2008		
Bryophytes	0.26	0.7981
Moss	-1.04	0.8874
Liverworts	0.86	0.4026

Discussion

With wide variation in bryophyte cover, there was no significant pattern in bryophyte cover change at both the burnt and slashed treatments. This is in accordance with Vanderpoorten *et al*. (2004), who found that the cover of individual bryophyte species in calcareous grassland did not differ significantly despite different mowing regimes. In the current study, there was a general, although not statistically verifiable, trend for mean bryophyte cover to increase after slashing across the years, which is comparable to bryophyte response in Norwegian wooded grasslands, where there was a relatively high cover of bryophytes in slashed compared to unslashed plots (Aune *et al*. 1995). Other overseas studies have also documented an increase in bryophyte biomass after mowing (Huhta *et al.* 2001; Peintinger & Bergamini 2006), with one particular study in Swiss fen meadows finding an increase of nearly 30% in bryophyte biomass after mowing (Billeter *et al*. 2007). While bryophyte species richness has been seen to increase when the vascular biomass was removed by defoliation in experiment microcosms (Aude & Ejrnæs 2005), the species richness in the plots surveyed remained uniformly low.

The increase in mean moss cover and the reduction in mean liverwort cover after the removal of the vascular overstorey through slashing may be attributed to the type of environmental conditions the common bryophyte species of buttongrass moorland prefer to inhabit. The two liverworts commonly found in buttongrass moorlands, *Riccardia spp.* and *Goebelobryum unguiculatum*, are typically found on damp soil (Meagher & Fuhrer 2003). The brighter and more open conditions the removal of the buttongrass moorland canopy created at ground level appear to have created conditions less suited to these liverworts. The most abundant buttongrass moorland mosses, *Campylopus spp.*, are tolerant of a range of conditions, although some species (e.g. *Campylopus kirkii*) prefer damp habitats (Scott & Stone 1976).

Bryophytes lack the sclerenchyma found in vascular plants (Schofield 2001), which therefore imposes a limit to the erect height bryophytes can reach (Scott 1994). This makes bryophytes vulnerable to competitive exclusion by the usually taller vascular plants. Whilst many bryophytes are adapted to low light levels (when compared to vascular plants), the total obscuring of the ground by leaf litter makes it almost impossible for bryophyte survival (Glime 2007). The vascular canopy also commonly prevents light penetrating to the ground surface. Studies have shown that the richness and cover of bryophytes was significantly associated with light levels and the removal of litter (Bergamini *et al*. 2001; Peintinger & Bergamini 2006; O'Bryan *et al*. 2009). In accordance with Aune *et al.* (1995) and Aude & Ejrnæs (2005), the mechanical removal of the canopy saw a general increase in mean moss cover over the three year period in my study, although this was not statistically correlated. However, in the burnt plots mean moss cover was seen to drop in the year after fire before slightly increasing.

Mean bryophyte cover was seen to decrease in the burnt plots over the second year following fire. This decrease could be attributed to the fact that, whilst in the slashing plots the data was first recorded immediately upon slashed, in the burnt plots the first survey for data occurred approximately 6-8 months post-fire. It is possible that in the first survey, the bryophytes recorded were those that initially survived the fire and over the interceding year they died off due to increased exposure and harsh environmental conditions. Immediately after fire in other buttongrass moorlands, it has been observed that some mosses, notably *Campylopus spp.* and occasionally *Dicranaloma* spp., survived. It could be that, in the initial months following fire, bryophytes are responding to the post-fire nutrient flush, and those bryophytes that have survived the fire then thrive. A temperate grassland in Western Australia had a dramatic increase in cryptogam richness under a frequent (two year) burning regime (O'Bryan *et al*. 2009). The decrease in mean bryophyte cover experienced in the second year since fire could be attributed to the loss of the post-fire nutrient flush, or the harsh conditions post-fire of exposure, water pooling or run-off (Hylander *et al.* 2005; Prober *et al.* 2008). The plots in the slashing treatment were still offered some protection from the elements due to the surrounding buttongrass, whereas the plots exposed after fire were more open.

There was a significant relationship between changes in bryophyte cover from 2006-2007 when the two treatments were compared. This could possibly be attributed to the differences in timing in the initial surveys at each different treatment, e.g. that bryophytes were first surveyed a few months after fire in the burning treatments yet surveyed immediately after slashing. The mean bryophyte cover declined at the burnt sites over this first year yet increased at the slashed sites.

Fire alters the entire environment, changing everything from overall vegetation structure to soil nutrient status (Bond & van Wilgen 1996; Tolhurst *et al.* 1992), whilst the removal of the canopy through slashing allows for an increase in light to the ground surface in those particular plots (Phillips & Shure 1993; Reader & Bricker 1992). It follows therefore that immediately after fire the dramatic changes to the environment will have a greater effect on bryophytes than the mechanical removal of the canopy. No significant difference was found in the changing bryophyte cover from 2007-2008 regardless of whether burned or slashed.

This study determined that bryophyte cover was not affected by the addition of nutrients through fire and an increase in light caused by the removal of the canopy through both fire and slashing, although a significant relationship was discerned in the different effect of the two treatments on bryophyte cover over the first year of the study. The effect of fire and canopy removal on the bryophytes of buttongrass moorland appears to be negligible, according to the results of this study. The current buttongrass moorland management regime of fuel reduction burning will assumedly have little effects on bryophytes.

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Chapter 6

Do vertebrates graze moss after fire in buttongrass moorland?

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Introduction

The consumption of bryophytes (mosses, liverworts and hornworts) by vertebrate herbivores is widely documented for the Northern Hemisphere, mainly in boreal and arctic environments where nutrient sources are limited for at least part of the year (Prins 1982; Staaland & White 1991; van der Wal *et al*. 2001; Virtanen *et al*. 1997). Prins (1982) suggested that mosses provide little energy for herbivores but supply polyunsaturated fatty acids such as arachidonic acid that most likely increase the cold resistance of these herbivores and their young. Generally, moss-eating animals live permanently in cold environments, or migrate to these environments annually (Prins 1982). In Australia, the degree to which bryophytes are eaten by vertebrate herbivores is virtually undocumented.

Research into the effects of grazing on bryophytes in Australia has been carried out on the effects of trampling (Eldridge *et al.* 2000) and the nitrogen content of moss beds after the exclusion of grazing (Carr *et al*. 1980), rather than vertebrate consumption of moss. Given that bryophytes are mainly used as a food source by vertebrate herbivores when other nutrient sources are limited, such as in extreme cold conditions, we wondered whether bryophytes may be utilised by vertebrates as a food source in challenging habitats in Australia, such as in the buttongrass moorlands of Tasmania.

The buttongrass moorlands of Tasmania are often burnt and are an extremely low nutrient environment. The foliage of the dominant plant (*Gymnoschoenus sphaerocephalus*) has high silica levels and the lowest recorded phosphorus levels in its foliage of any plant species (Bowman *et al.* 1986). The buttongrass moorlands are periodically inundated with water, yet the soil surface may be dry, cracked and hard in summer (Driessen 2007). Possibly due to the harsh and changeable conditions, only a few mammals are known to spend their entire lifecycle in the buttongrass moorlands: Swamp Antechinus (*Antechinus minimus*), Broad-toothed Mouse (*Mastacomys fuscus*) and the Swamp Rat (*Rattus lutreolus*) (Driessen 2007). Several other mammals use buttongrass moorland for feeding but usually shelter in other habitats: Common Wombat (*Vombatus ursinus*), Bennetts Wallaby (*Macropus rufogriseus*), Eastern Quoll (*Dasyurus viverrinus*) and the Short-beaked Echidna (*Tachyglossus aculeatus*) (Driessen 2007).

The lack of mammals that spend their entire lifecycles living in the buttongrass moorlands could also be a response to the regularity of fire. Buttongrass moorlands are frequently burnt by natural and human induced fires. Following fire, patches of moss are often visible between the remaining short charred buttongrass tussocks. Given the loss of vegetation and potential food sources for the vertebrate herbivores that feed in the buttongrass moorlands, we investigated whether vertebrate herbivores were grazing moss in recently burnt buttongrass moorland.

Method

A buttongrass moorland near Lake St. Clair burnt in spring 2005 was selected as the study site (Figure 6.1).

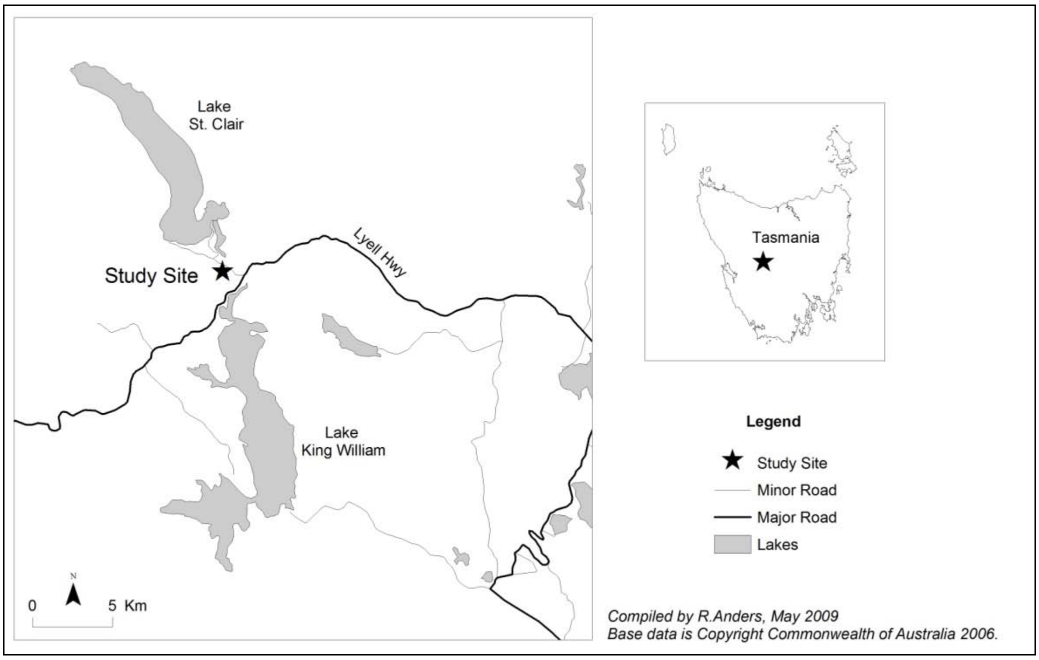

Figure 6.1. The study area.

Twenty wire cages (30 cm x 30 cm x 20 cm) were used as grazing exclosures, with a wire mesh of 1 cm that allowed invertebrate but not vertebrate access (Figure 6.2). In spring 2005, twenty patches of moss (either *Campylopus* spp. or *Dicranoloma* spp.) with a minimum diameter of ten centimetres were selected in the recently burnt buttongrass moorland. One cage was placed over half of each moss patch, so that one side of the moss patch was exposed to possible grazers, and one half was protected beneath the cage. Cages were dug down 3 cm below the ground surface and secured with four pegs. The difference in height of the moss patches on either side of the cage barrier was recorded yearly, concluding in spring 2008. Data was analysed using two-way ANOVA (Minitab 2000) to determine if grazers were significantly impacting on the growth of moss patches.

Figure 6.2. Grazing exclosures in the buttongrass moorland.

Results

There was no significant difference in moss growth beneath the grazing exclosures compared to the moss exposed to grazers across the three years (Year: $P = 0.345$; $r^2 = 2.15\%$; df = 2; Grazing: $P = 0.986$; $r^2 = 2.15\%$; df = 1). After years one and two, no differences were recorded in moss growth on either side of the grazing barriers at any of the twenty grazing exclosures. During the third and final survey of the grazing exclosures, three of the twenty cages had disappeared entirely. However, no difference was recorded between the height of the moss patches enclosed by the cage and the part of the moss patches exposed to potential gazers bryophyte height between the enclosed and exposed bryophyte patches at the seventeen remaining grazing trials (Table 6.1). A potential moss grazer, the wombat, was sited at dusk, and wombat scats were found throughout the study site (Figure 6.3).

Figure 6.3. Wombat scats provide evidence of the presence of this mammal in the study area.

Table 6.1. Change in moss height from 2005–2008.

Cage number	**Base height 2005 (cm)**		**Height 2006 (cm)**		**Height 2007 (cm)**		**Height 2008 (cm)**	
	inside cage	**outside cage**	**inside cage**	**outside cage**	**inside cage**	**outside cage**	**inside cage**	**outside cage**
1	18	18	18	18	19	19	19	19
2	15	15	15	15	17	17	17	16
3	12	12	14	14	14	14	14.5	14.5
4	21	21	21.5	21.5	21	20	0	0
5	25	25	25	25	25	25	27	27
6	13	13	13	14	14	14	14	14
7	17	17	15	14	15	15	17	17
8	24	24	24	25	28	28	28	28
9	16.5	16.5	17	17	19	19	19	19
10	11	11	11	11	14	14	15	15
11	19	19	21	21	21	21	21	21
12	25	25	24	24	24	24	0	0
13	20	20	22	22	22	22	23	23
14	15.5	15.5	16.5	16.5	17	17	17.5	17.5
15	18	18	17	17	18	18	18	18
16	14	14	13	13	15	15	0	0
17	26	26	25	25	26.5	26.5	27	27
18	22	22	22	22	22	22	23	23
19	24	24	26	26	26	26	28	28
20	17	17	19	19	20	20	22	22

The patches of moss used in this study were never observed to fruit, and any herbivory of sporophytes went unrecorded. In another buttongrass moorland plain we observed capsules of the moss *Tayloria tasmanica* that appeared to have been grazed (Figure 6.4). The moss *Pleurophascum grandiglobum*, endemic to the Tasmanian buttongrass moorlands, is known for its pale green ball-like capsules. Whilst not seen in the study site, in other buttongrass moorlands the capsules of this moss sometimes appeared ragged, as if they had been grazed.

Figure 6.4. *Tayloria tasmanica* with grazed capsules.

Discussion

Patches of moss persisting from pre-burn vegetation are often one of the only remaining groundcovers besides charred and much-reduced buttongrass tussocks in burnt buttongrass moorlands. However, native grazers were not eating the moss patches we monitored. It is possible that the cages were somehow deterring the grazers from approaching the moss patches, but we did not observe any other evidence of moss being grazed at the site despite the presence of wombat scats and extensive moss cover.

The presence of a potential grazer, the wombat, was confirmed at the study site. The main food source of wombats are native grasses, with shrubs, roots, sedges, bark and herbs also eaten, with moss supposedly being a particular delicacy (Parks & Wildlife Service 2008). It has been observed that some moss species are favoured by wombats when they are green and moist, but usually ignored when dry (Triggs 1996). Triggs (1996) suggested that mosses are primarily eaten for their water content because mosses have little nutritional value. Wombats and other vertebrates found in buttongrass moorland may access adequate food by roaming into neighbouring scrub and forests to feed, where food sources can be found that have a greater nutrient content than moss. Wombats are known to roam many kilometres at night and would have no difficulty moving into adjacent habitats (Parks & Wildlife Service 2008). If snow lie and the cold-adapted vegetation are important limiting factors for grazers in Northern Hemisphere winters, vertebrate herbivores would be not be able to roam into more favourable feeding environments. It may be the difference between the scale of the buttongrass plains and the scale of the arctic tundra or boreal forests that has necessitated the Northern Hemisphere vertebrate herbivores to adapt to consuming any available food source, such as mosses and lichens.

Mosses are difficult to digest, with high holocellulose and crude fibre (Walton 1985), and a low caloric value (3.7-4.8 Kcal/g; Forman 1968, 1969; Rastorfer 1976a, b in Glime 2007) when compared to vascular plants (Glime 2007). Due to a high concentration of a polyphenolic lignin-like compound, the cellular contents of mosses are less accessible to the digestive enzymes of herbivores (Prins 1982). Polyphenols in some mosses can also have an antibiotic action which is likely to impede the digestion of ruminants or hindgut fermenters (Prins 1982). Given that wombats are hindgut fermenters (Hume 1999) it is possible that this is why wombats avoid consuming the mosses in buttongrass moorland.

No quantitative studies investigating the direct consumption of bryophytes by vertebrate herbivores have been performed that we are aware of, and any references to mammals grazing on bryophytes are purely observational. The dispersal of bryophytes by the spectacled flying fox (*Pteropus conspicillatus*) in the wet tropics of Queensland was established by Parsons *et al*. (2007), although they suggested that bryophytes were consumed indirectly with grooming, rather than directly grazed as a food source. It is possible that herbivores may consume only the fruiting capsules of moss. This was not addressed in this study, although the moss *Pleurophascum grandiglobum*, seen fruiting in other buttongrass moorlands, frequently appeared to have ragged sporophytes that could be attributed to grazing. However, it is possible that this is due to the manner in which the capsule releases its spores – it simply breaks open at the side.

While our study did not include any trials to determine which, if any, invertebrates consumed bryophytes in buttongrass moorlands, internationally few invertebrate species have been found to eat moss plants readily (Davidson *et al.* 1990), although many invertebrates use bryophytes for shelter (Gerson 1982). Insects are the most commonly found arthropod sheltering in bryophyte communities, with some insects feeding on bryophytes by sucking the juices from leaf cells (Schofield 2001).

It appears that bryophytes are probably not eaten by many vertebrate animals in Australia. Studies are needed to confirm whether wombats do eat moss and under what conditions, and whether there are other animals, vertebrate or invertebrate, that also consume moss on occasion. In terms of buttongrass moorland, the close proximity of more benign feeding environments may mean that animals have not needed to use the unpalatable food source that moss presents. More comprehensive studies are needed that look at landscape scale grazing dynamics and the possibility of moss being consumed in other environments, if only to establish that bryophytes are a last resort for hungry vertebrates in Australia.

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Chapter 7

Discussion

The preceding chapters catalogued the bryophytes found in the Tasmanian buttongrass moorlands, and examined their correlation with location, altitude and fire, and looked at their response to light and grazing. This chapter considers the impacts of the unique buttongrass moorland environment on bryophytes and the implications for management. The buttongrass moorland bryophytes are explored in the context of other environments, and in bryophyte ecology more generally.

Buttongrass moorland: a unique environment

Buttongrass moorland is where the boundary between wetland and terrestrial ecosystems blurs (Harris & Kitchener 2005). In Australia, *Sphagnum* peatlands are an unusual and infrequent component of the environment (Whinam *et al.* 2001). However, they do occur in the Tasmanian central highlands on relatively infertile substrates, occurring beneath buttongrass in poorly drained, cold sites (Whinam *et al.* 2001). This study found four *Sphagnum* species occurred in buttongrass moorland: *S. australe, S. cristatum, S. falcatulum* and *S. novozelandicum*. The most widespread species was *S. cristatum*, and this only occurred in eight of the 100 sites surveyed. However, Australian *Sphagnum*-dominated peatlands are generally small in area and restricted in distribution (Whinam *et al.* 2003).

Based on the results of this study, the Tasmanian buttongrass moorlands appear to have low bryophyte diversity. Sixty-two bryophyte species were recorded overall. This included species found growing on rocks, on a log and in sandy pans. In comparison, the documented vascular plant flora of the buttongrass moors is quite diverse, having more than 272 species (Jarman *et al.*

1988). This is in direct contrast to the wet sclerophyll forests and cool temperate rainforests of Tasmania, where bryophyte species commonly outnumber vascular species (Jarman & Kantvilas 1994; Pharo & Blanks 2000).

Buttongrass moorland may experience snows, frosts and storms, yet dry soils occur during summer in the buttongrass moorlands areas of Tasmania that are normally considered very wet (Jarman *et al.* 1988). Given the highly pyrogenic nature of *Gymnoschoenus sphaerocephalus*, it will burn over a very wide range of conditions (Marsden-Smedley *et al*. 1999). The periodic dryness of the buttongrass moorland may prevent a considerable number of bryophyte species that require moist habitats from establishing. Bryophytes are known to thrive in moist environments (Lee & La Roi 1979; Söderström 1981), with site moisture found to be influencing bryophyte richness in Tasmanian old-growth mixed eucalypt forest (Turner *et al.* 2006).

In Tasmania, grassy woodland generally occurs on good quality soils in low rainfall areas, where the fire frequency is invariably high, whilst buttongrass moorland, sedgeland and scrub communities occur on soils of low nutrition, that are sometimes sandy and poorly drained, where fires are a common occurrence (Jackson 1999). Whilst the bryophyte diversity of buttongrass moorlands is low in comparison to the old-growth eucalypt forests of Tasmania (Turner *et al.* 2006), it is more comparable to numbers found in a small valley in central Tasmania in grassy woodland and sedgeland by Pharo (2002), where just 18 bryophyte species were found, and a small study by Ferguson *et al.* (2009) in a grassland plain where just three bryophyte species were recorded.

Buttongrass moorland was very 'substrate-poor', having few different substrates besides the ground. Epiphytic substrates such as living and dead wood, rocks or even large, moist leaves provide unique microhabitats and often support diverse bryophyte assemblages (Jarman & Kantvilas 1995; Kantvilas & Jarman 2004; Roberts *et al.* 2005; Turner & Pharo 2005). The lack of trees removes two potential habitats, those of living and decaying wood, plus the absence of ferns also reduces the potential for bryophyte diversity, as some Tasmanian bryophytes are epiphytes which prefer growing on tree-ferns (Meagher & Fuhrer 2003). A distinct lack of rocks in the buttongrass moorland also removes another potential substrate for bryophyte colonisation, with some bryophyte species being specific colonisers of rock, e.g. *Grimmia spp.* (Meagher & Fuhrer 2003). The common rock colonists, the mosses *Grimmia* spp. and *Racomitrium* spp. are known to be present in sub-alpine sedgeland and grassy Eucalypt woodland approximately twenty kilometres away from buttongrass moorland sites surveyed around Lake St. Clair, therefore they are not absent from the buttongrass moorlands due to geography (Pharo 2002). The lack of rocks, ferns and woody substrates in buttongrass moorlands automatically reduces the potential for bryophyte diversity. The importance of substrates for the presence of bryophytes was shown by Turner *et al.* (2006), where bryophyte and moss species richness and composition were significantly positively correlated with the percentage cover of above-ground substrates in an old-growth mixed eucalypt forest.

The effects of disturbance on buttongrass moorland bryophytes

Fire is one of the most important agents of disturbance in many ecosystems (Ryömä & Laaka-Lindberg 2005). Due to the flammability of the buttongrass moorlands (Brown 1993), it was expected that fire would dominate the bryophyte composition of this ecosystem. However, it was instead found that fire did not significantly affect bryophyte composition and richness in the buttongrass moorlands, both in immediate post-fire impacts and in the longer term. Ferguson *et al.* (2009) found a weakly significant difference in bryophyte species composition between burned and unburned quadrats in buttongrass moorland, with further inspection of the data showing no separation of species groups and all had similar composition.

High intensity, uncontrolled summer wildfire could result in different species composition, but given the high similarity of bryophyte species composition around the state in buttongrass moorland, it appears that any establishment of fire moss after a hot burn would have to be particularly transient, e.g. have established and died within six months of burning, given that six months was the earliest sites were surveyed in this study after fire and none of these sites had fire mosses. Whilst the common initial colonisers following fire, known from mixed and wet forest in Tasmania, the mosses, *Funaria hygrometrica, Ceratodon purpureus,* and the liverwort *Marchantia berteroana* do show a faster growth rate than those species which appear later in succession (Duncan & Dalton 1982), they are normally still present up to five years after fire (Brasell & Mattay 1984; Cremer & Mount 1965; Duncan & Dalton 1982) so this theory of very rapid colonisation and senescence seems unlikely. Future studies may like to monitor bryophyte recolonisation in buttongrass moorland over a period of years following a high-intensity, summer wildfire and compare bryophyte recolonisation patterns after a low-intensity controlled burn.

The presence of the same suite of post-fire bryophytes in recently burnt sites has been reported from different vegetation types and under different climatic conditions across the world (Duncan & Dalton 1982; Esposito *et al.* 1999; Thomas *et al.* 1994). These include peatlands - in a New Zealand peat-bog, the common post-fire coloniser *Marchantia berteroana* was present after fire (Johnson 2001). However, the pre-fire bryophyte species are generally replaced with pioneering post-fire bryophytes (Brasell & Mattay 1984; Ryömä & Laaka-Lindberg 2005) which are easily dispersed with a fugitive or colonist life-strategy (During 1979). This Tasmanian study found no significant difference in bryophyte diversity or biomass between burnt and control plots, with the common buttongrass moorland bryophytes being present immediately post-fire. Generally, bryophyte communities arise from a combination of air-borne propagules and the stored propagule bank and vegetative fragments in the soil (Ross-Davis & Frego 2004). The same common buttongrass moorland bryophytes are present after fire. The common post-fire bryophytes are not known to be limited by dispersal abilities, and further research needs to analyse the soil bank for bryophyte diaspores to see if the post-fire bryophytes are present in the buttongrass moorland soil and failing to establish, or if they are absent altogether.

The importance of canopy removal through grazing or mowing for bryophytes is well-established (Ari-Pekka *et al.* 2001; Aune *et al.* 1995; Aude & Ejrnæs 2005; Bergamini *et al.* 2001; Billeter *et al.* 2007; Richards 1928; Vanderpoorten *et al.* 2004). Bryophyte species richness has been found to both increase (Aude & Ejrnæs 2005) and decrease (Vanderpoorten *et al.* 2004) with the mechanical removal of the canopy. The removal of the buttongrass canopy through slashing (mechanical removal) was not seen to significantly affect bryophyte cover. Given that the much more extreme disturbance of fire was not found to significantly affect bryophytes in buttongrass moorland, this tallies with previous results that bryophytes in buttongrass moorlands are not significantly influenced by disturbance.

There was no evidence that bryophytes are being used as a food source by native vertebrate grazers in recently burnt buttongrass moorlands, although as no fruiting material was observed, conclusions cannot be drawn as to whether grazers consume bryophyte capsules. Bryophytes were also not found to be grazed in either burnt or unburnt plots in buttongrass moorland by Ferguson *et al.* (2009). This could be due to two factors: 1) Given that the vertebrates present in buttongrass moorland are relatively mobile they are able to travel into neighbouring habitats for more palatable food sources than bryophytes (Driessen 2007); and 2) Bryophytes are just so unpleasant to eat that vertebrates only turn to them as a last-resort food source (White & Trudell 1980). Further research could employ infra-red video monitoring in buttongrass moorlands to establish the feeding patterns of vertebrates, and should include observations of fruiting bryophyte patches.

Management implications for buttongrass moorland bryophytes

It is common for buttongrass moorland fires to have moderate to high rates of spread and intensity even under what are considered for most vegetation types to be low to moderate levels of fire danger, and to expand more rapidly than fire suppression can be applied (Marsden-Smedley & Catchpole 1995). Fire management therefore is a major problem due to the ability for buttongrass to carry fires into other more fire-sensitive areas like alpine environments and the need for fire to maintain buttongrass as a community in itself to prevent its progression into heathland (Jackson 1968; Marsden-Smedley *et al.* 2001). For these reasons, prescribed burning is performed across large tracts of buttongrass moorland for asset protection and conservation management (Marsden-Smedley *et al.* 2001).

Given that chapter three looked at the influence of time since fire (which included prescribed burns) on bryophyte richness and diversity, and found no correlations between bryophytes and time since fire once a few older sites were removed, the current management regime appears to be having no ill-effects on bryophytes in buttongrass moorland, providing that some plains are left unburnt for over thirty years to promote maximum liverwort species diversity.

Study limitations

This study was restricted by problems in experimental design associated with furthering studies established by other people. In the space for time study in chapter three and the before-after control-impact study in chapter four, sites were used which had already been established by the Biodiversity Conservation Branch of the Department of Primary Industries, Parks, Water and Environment. Using these sites ensured that necessary funding was secured for the study. With the space for time study, environmental data were also available for comparison with bryophyte species distribution. The main limitation of the space for time chapter was that due to a number of fires occurring since the sites were first established, the mix of site ages in the Lake

St. Clair region was considerably diminished. No sites were above 33 years since last fire. It was necessary to then rule out if any differences in bryophyte composition or richness thought due to time since fire were not in fact due to regional differences between Lake St. Clair and Lake Pedder.

Serious design limitations were seen with the before-after control-impact study. The first and perhaps most obvious flaw was that no 'before' data was collected for the bryophytes at the King William site. The second problem was the fact that at McPartlans Pass an escaped fire burnt seven of the eight control sites. These two problems meant that the study was not in fact a before-after control-impact study, missing two of the crucial characters needed to be such a study, the before data and the control sites. The third problem was bryophyte classification. The first bryophyte survey was carried out by a research assistant employed by the Biodiversity Conservation Branch, and some species were lumped to family or, upon inspection of voucher specimens, shown to be incorrectly identified at species level, necessitating the loss of a level of data as the species that were incorrectly identified were then grouped to families out of necessity.

Ideally, the BACI and space for time study design would have been balanced. However, the nature of the ecosystem means that frequent fires occur. The furthering of these studies secured funding crucial to the operation of this post-doctorial study. The advances of building on existing environmental and vascular plant datasets, as well has having access to expertise and funds, outweighed the disadvantages, especially given that very little was known about bryophytes in this ecosystem.

The limitation of funding and practical difficulty was evident in chapter 5. Ideally, slashing and burnt quadrats would have been located side by side in the same buttongrass moorland plain. Unfortunately, due to the expense and difficulty associated with gaining approval to burn multiple 2 m² quadrats in the highly flammable buttongrass moorland environment and then executing these burns, quadrats had to be established in recently burnt buttongrass plains meaning no data was gathered as to the bryophyte cover before burning for comparison with after burning, as there was in the slashed sites.

Conclusions

In summary, a relatively limited suite of bryophytes may be able to deal with the multiple challenges associated with living in buttongrass moorland: frequent fire, summer drought, flooding, periodic snow and frost, and shading. There is no evidence that fire impacts on bryophytes in buttongrass moorlands, and bryophytes appear not to be utilised as a food source for vertebrate herbivores. Altitude appears to be the only environmental factor to have any impact on the bryophyte composition of the buttongrass moorlands, with time since last fire and location not showing any correlation with species distribution. Current management regimes of periodic prescribed burning in some areas appear adequate to maintain species diversity, providing some buttongrass moorlands are allowed to reach upwards of thirty years since last fire.

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Chapter 8 – Appendices

Appendix 1. Richness, time since fire and tussock variables for sites with differing fire histories.

Site Name	Vascular richness	Bryophyte richness	Moss richness	Liverwort richness	Region P=Pedder C=St.Clair	Time since fire	Tussock height	Average tussock diameter	Average tussock interspace
Airstrip East	21	8	4	4	P	34	50	220	57.5
Airstrip Old	15	5	0	5	P	56	80	316	72
Beehive Canal North	17	9	4	5	C	32	80	493	45.5
Beehive Canal South	31	15	7	8	C	7	65	354	55.5
Burns Dam	15	6	2	4	C	7	50	290	31
Bedlam	10	0	0	0	C	22	90	436	61
Coates Creek	14	7	3	4	C	17	90	518	25
Condominium Creek North	17	10	5	5	P	34	70	308	33.5
Condominium Creek Northwest	22	9	3	6	P	25	70	246	26
Condominium Creek Southeast	26	7	6	1	P	25	50	228	41
Edgar	24	10	5	5	P	56	50	254	34.5
Flood Creek	19	6	2	4	C	17	60	233	26.5
Gelignite Creek	19	7	2	5	P	34	50	200	25.5
Harbacks Road North	27	8	5	3	C	3	40	117	52.5
Harbacks Road South	22	13	6	7	C	3	40	140	51
King William East	16	5	1	4	C	5	70	195	47
King William Plains	17	5	1	4	C	2	40	133	104
King William West	22	5	1	4	C	5	80	252	40
McPartlans Pass Canal	21	6	4	2	P	5	45	139	47
McPartlans Pass East	19	9	4	5	P	5	55	110	45
McPartlans Pass West	20	11	5	6	P	5	60	235	47.6
Mt Anne	20	12	6	6	P	42	60	409	31
Navarre East	11	4	2	2	C	19	55	190	68.5
Navarre River	20	11	5	6	C	5	55	310	35

Site Name	Vascular richness	Bryophyte richness	Moss richness	Liverwort richness	Region P=Pedder C=St.Clair	Time since fire	Tussock height	Average tussock diameter	Average tussock interspace
Navarre West	26	8	4	4	C	6	55	232	38.7
Pumphouse Point	5	4	3	1	C	33	70	459	18.5
Rufus Canal East	13	12	6	6	C	19	75	645	30.5
Rufus Canal North	19	8	4	4	C	2	45	204	44.2
Rufus Canal West	10	5	3	2	C	33	120	580	21
Research A	21	7	3	4	P	15	60	278	38
Research B	18	8	5	3	P	15	65	259	53
Sandfly Creek	18	5	2	3	P	25	65	313	30
Sentinels	19	8	6	2	P	34	75	313	37
Settling Ponds	17	5	4	1	C	22	75	337	32
St Clair Rd North	5	6	4	2	C	4	45	60	42
St Clair Rd South	20	6	4	2	C	2	60	505	58.9
St Clair Rd West	14	7	4	3	C	0.5	60	222	90.5
Stillwater North	18	7	4	3	P	56	100	546	23.5
Stillwater South	16	10	5	5	P	34	90	352	34
Travellers Rest East	8	5	4	1	C	1	70	252	72.8
Travellers Rest West	15	7	2	5	C	1	70	246	65.8
Wedge Inlet	20	8	3	5	P	34	70	583	28
Weather Station	10	9	6	3	C	4	70	327	50.5
White Spur	23	12	4	8	P	67	110	585	54.5

Appendix 2. Incidence-based coverage estimator (ICE) of bryophyte species richness for the statewide buttongrass moorland bryophyte survey.

Samples	Individuals (computed)	ICE Mean (sp.)	ICE SD (runs)
1	7.41	38.01	38.37
2	14.83	69.57	86.25
3	22.24	49.54	53.17
4	29.66	34.37	13.99
5	37.07	35.64	13.42
6	44.48	39.46	13.74
7	51.9	40.49	12.51
8	59.31	42.29	12.34
9	66.73	45.55	12.57
10	74.14	47.13	12.18
11	81.56	48.16	11.2
12	88.97	49.46	10.24
13	96.38	50.9	10.54
14	103.8	52.47	10.41
15	111.21	53.87	11.1
16	118.63	55.95	9.85
17	126.04	57.07	9.82
18	133.45	58.48	10.08
19	140.87	59.6	10.57
20	148.28	60.59	10.72
21	155.7	61.78	10.95
22	163.11	62.06	10.94
23	170.53	62.56	10.56
24	177.94	62.77	9.1
25	185.35	62.54	8.64
26	192.77	62.15	8.77
27	200.18	62.4	8.5
28	207.6	62.07	8.41
29	215.01	62.5	8.32
30	222.42	62.92	9.75
31	229.84	63.26	9.63
32	237.25	62.44	8.94
33	244.67	63.52	9.16
34	252.08	63.03	8.42
35	259.49	63	8.24
36	266.91	62.13	6.36
37	274.32	62.2	6.52
38	281.74	62.3	6.56
39	289.15	62.15	6.21
40	296.57	61.83	5.51
41	303.98	61.96	5.26
42	311.39	61.86	3.86
43	318.81	61.7	3.93
44	326.22	61.61	4.15
45	333.64	61.33	4.15

Samples	Individuals (computed)	ICE Mean (sp.)	ICE SD (runs)
46	341.05	61.3	4.44
47	348.46	61.75	4.35
48	355.88	61.86	4.39
49	363.29	62.16	4.34
50	370.71	62.26	4.43
51	378.12	62.34	4.67
52	385.54	62.33	4.77
53	392.95	62.34	4.48
54	400.36	62.69	4.1
55	407.78	62.54	3.72
56	415.19	62.62	3.58
57	422.61	62.68	3.66
58	430.02	62.72	3.73
59	437.43	62.73	3.79
60	444.85	62.5	3.77
61	452.26	62.51	3.8
62	459.68	63.04	3.8
63	467.09	63.21	3.61
64	474.51	63.34	3.5
65	481.92	63.34	3.67
66	489.33	63.64	3.72
67	496.75	63.74	3.65
68	504.16	63.8	3.55
69	511.58	63.9	3.61
70	518.99	64	3.4
71	526.4	64.16	3.55
72	533.82	64.55	3.58
73	541.23	64.6	3.55
74	548.65	64.59	3.37
75	556.06	64.7	3.35
76	563.47	64.82	3.36
77	570.89	65.02	3.23
78	578.3	65.28	3.21
79	585.72	65.2	3.08
80	593.13	65.26	2.96
81	600.55	65.21	2.79
82	607.96	65.16	2.69
83	615.37	65.4	2.63
84	622.79	65.45	2.41
85	630.2	65.55	2.47
86	637.62	65.62	2.52
87	645.03	65.61	2.41
88	652.44	65.67	2.21
89	659.86	65.68	2.26
90	667.27	65.57	2.1
91	674.69	65.58	1.69
92	682.1	65.52	1.66
93	689.52	65.61	1.5

Samples	Individuals (computed)	ICE Mean (sp.)	ICE SD (runs)
94	696.93	65.65	1.2
95	704.34	65.59	1.1
96	711.76	65.6	0.87
97	719.17	65.53	0.63
98	726.59	65.47	0.63
99	734	65.55	0

Appendix 3. Buttongrass sites across Tasmania: geology, date of last fire* and metres above sea-level. ***For sites with available fire histories.**

Site name	Date of last fire*	Basic Geology	Contour (m a.s.l.)
Above Mt Franklin	6/04/2000	Pelite	390
Airstrip East		Mudstone	310
Airstrip Old		Undifferentiated	300
Ansons Bay Rd 1		Granite	140
Ansons Bay Rd 2		Granite	120
Ansons Bay Rd 3	13/10/2004	Granite	120
Ansons Bay Rd 4		Granite	60
Arthur Pieman 1		Quartzite	60
Arthur Pieman 2	24/02/1995	Pyritic siltsone	60
Arthur Pieman 3	27/09/2001	Pyritic siltsone	190
Arthur Pieman 4		Pyritic siltsone	240
Arthur State Forest	1/01/1984	Pyritic siltsone	150
Badger Ck		Alluvial	140
Bedlam		Glacial	750
Beehive Canal North		Glacial	770
Beehive Canal South	1/04/1999	Glacial	800
Bills Ck		Schist	400
Burns Dam	9/03/1984	Schist	810
Cardigan Ck		Schist	420
Coates Creek		Glacial	730
Coles Bay Rd 1	3/01/2006	Alluvial	20
Coles Bay Rd 2	9/04/1997	Granite	50
Coles Bay subdivision	6/05/1997	Alluvial	20
Coles Bay Tip	6/05/1997	Alluvial	30
Condominium Creek North		Quaternary sediments	340
Condominium Creek North West	1/01/1977	Quaternary sediments	330
Condominium Creek South East		Quaternary sediments	340
Edgar		Quaternary sediments	310
Flood Creek	1/01/1996	Glacial	740
Gelignite Creek	1/11/1971	Glacial	370
Harbacks Road North	14/10/2003	Glacial	750
Harbacks Road South	14/10/2003	Glacial	760
Henty River	1/01/1985	Nonmarine	30
King William East	4/05/2001	Glacial	750
King William Plains		Glacial	770
King William West		Glacial	780
Lake Burbury overall	1/01/1982	Glacial	240
MacPartlan Pass Canal		Glacial	780
MacPartlan Pass East	11/10/2001	Quaternary sediments	340
MacPartlan Pass West	1/01/1991	Quaternary sediments	330

Site name	Date of last fire*	Basic Geology	Contour (m a.s.l.)
Mathinna Plains 1		Quartzwacke	790
Mathinna Plains 2		Quartzwacke	790
Mathinna Plains 3		Quartzwacke	790
Mathinna Plains 4		Glacial	820
Milkshake Reserve		Pyritic siltsone	190
Mt Amos		Granite	320
Mt Anne		Quaternary sediments	340
Mt Balfour	15/11/2003	Pyritic siltsone	230
Mt Dundas Lookout	1/01/1989	Glacial	130
Mt Gell	1/01/1994	Glacial	410
Mt Sprent 1		Quartzite	500
Mt Sprent 2		Quartzite	620
Navarre East	12/11/1988	Glacial	730
Navarre River	4/05/2001	Glacial	760
Navarre West	5/02/2001	Glacial	730
Near Cool Ck		Schist	380
Pandora hillbase	26/09/2000	Quaternary sediments	20
Pandora hillmiddle	26/09/2000	Quaternary sediments	30
Pandora hilltop	26/09/2000	Quaternary sediments	40
Pandora transect	26/09/2000	quaternary sediments	10
Pandora Valley Foreground 1	26/09/2000	Quaternary sediments	10
Pandora Valley Foreground 2		Quaternary sediments	10
Port Davey Track 1		Quaternary sediments	10
Port Davey Track 2		Quaternary sediments	10
Port Davey Track 3		Quaternary sediments	10
Port Davey Track 4		Quaternary sediments	10
Port Davey Track 5		Quaternary sediments	10
Pumphouse Point		Glacial	740
Refinery	7/05/2003	Glacial	220
Research A	1/01/1991	Quaternary sediments	320
Research B	11/10/2001	Quaternary sediments	320
Rufus Canal East		Glacial	770
Rufus Canal North		Glacial	800
Rufus Canal West		Glacial	800
Sandfly Creek	1/11/1971	Quaternary sediments	330
Savage River	8/02/1982	Quaternary	240

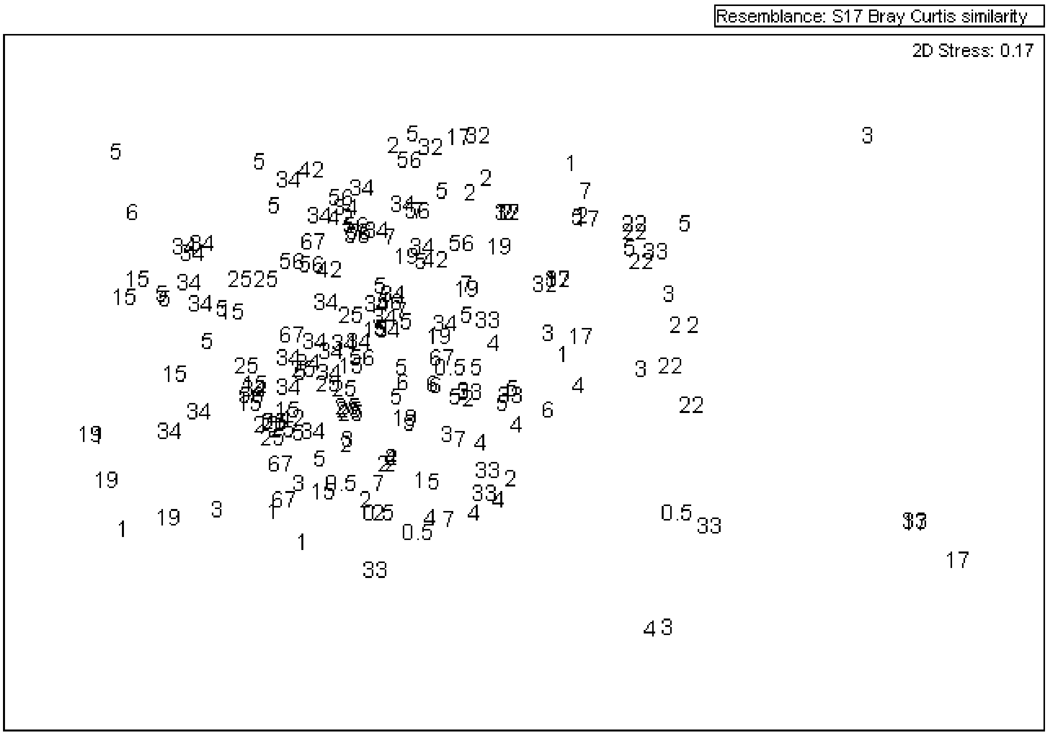
		sediments	
Site name	**Date of last fire***	**Basic Geology**	**Contour (m a.s.l.)**
Scottsdale roadside		Quaternary sediments	130
Sentinels		Quaternary sediments	340
Settling Ponds		Glacial	750
Snug Tiers		Alluvial	600
South Arthur 1		Pyritic siltsone	150
South Arthur 2		Pyritic siltsone	130
South Arthur 3		Pyritic siltsone	180
South Arthur 4		Pyritic siltsone	190
St Clair Rd North	30/04/2002	Glacial	740
St Clair Road South		Glacial	730
St Clair Road West		Glacial	730
Stillwater North		Quaternary sediments	320
Stillwater South		Quaternary sediments	320
Strahan	1/01/1982	Nonmarine	60
Tahune Airwalk 1		Alluvial	60
Tahune Airwalk 2		Alluvial	60
Tim Shea		Glacial	640
Travellers Rest East		Glacial	730
Travellers Rest West		Glacial	730
Wallaby Creek		Quartzite	20
Weather Station	30/04/2002	Glacial	740
Wedge Inlet		Quaternary sediments	310
White Spur		Pelite	360

Appendix 4. Bryophyte species found in the space-for-time sites.

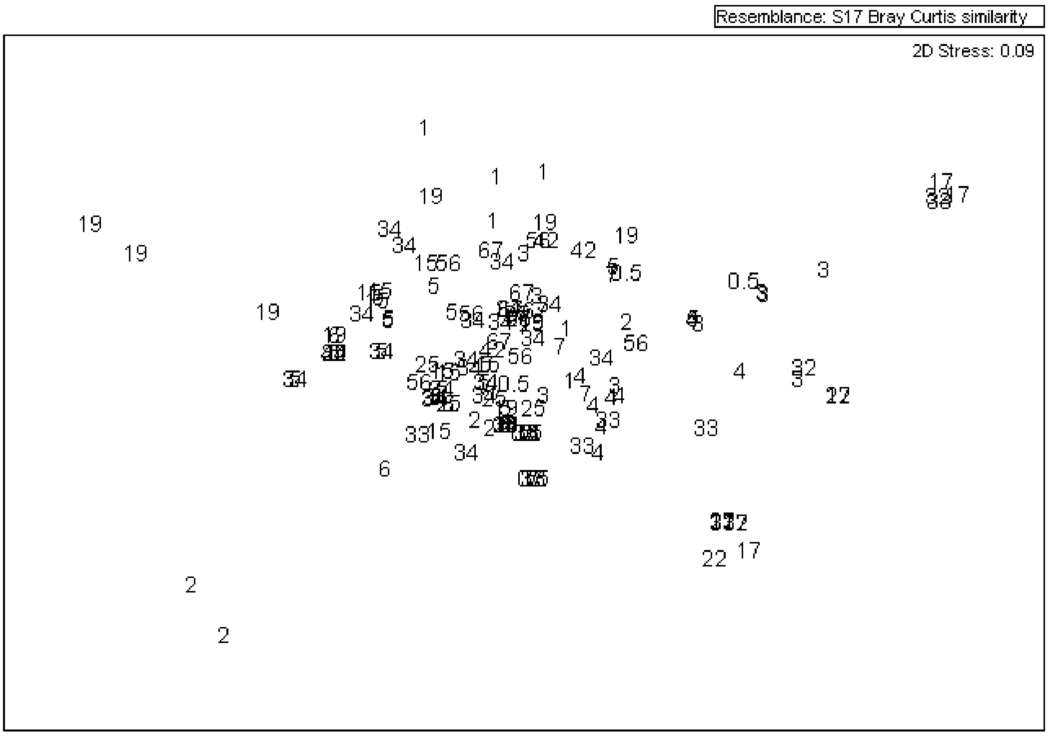
Acromastigum anistostomum
Acromastigum mooreanum
Balantiopsis diplophylla
Breutelia affinis
Campylopus acuminatus var. *kirkii*
Campylopus bicolor var. *bicolor*
Campylopus introflexus
Campylopus pyriformis
Ceratodon purpureus subsp. *convolutus*
Dicranaloma billarderi
Dicranaloma eucamptodontoides
Dicranaloma robustum
Distichophyllum crispulum
Fossombronia sp.
Gemmabryum australe
Goebelobryum unguiculatum
Heteroscyphus billardierei
Heteroscyphus coalitus
Heteroscyphus fissitipus
Heteroscyphus varians
Hyalolepidozia longiscypha
Hypnum cupressiforme var. *tectorum*
Isotachis sp.
Jackiella curvata
Jamesoniella colorata
Kurzia hippurioides
Kurzia compacta
Marsupidium surculosum
Pleurovascum grandiglobum subsp. grandiglobum
Podomitrium phyllanthus
Pohlia nutans
Polytrichum juniperinum
Riccardia aequicellularis
Riccardia cochleata
Riccardia crassa
Rosulabryum billarderi
Rosulabryum microrhodon
Saccogynidium decurvum
Sphagnum australe

Sphagnum cristatum
Sphagnum falcatulum
Sphagnum novozelandicum
Tayloria octoblepharum
Temnoma townrowii
Wijkia extenuate

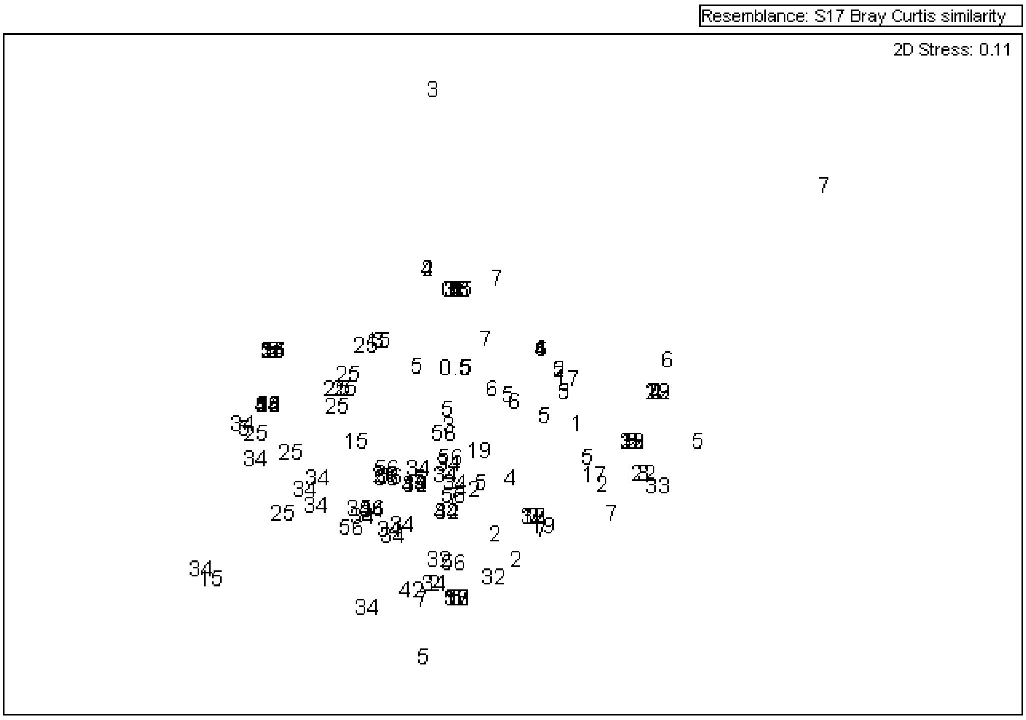
Appendix 5. Ordination graphs for bryophyte, moss and liverwort composition and time since fire.



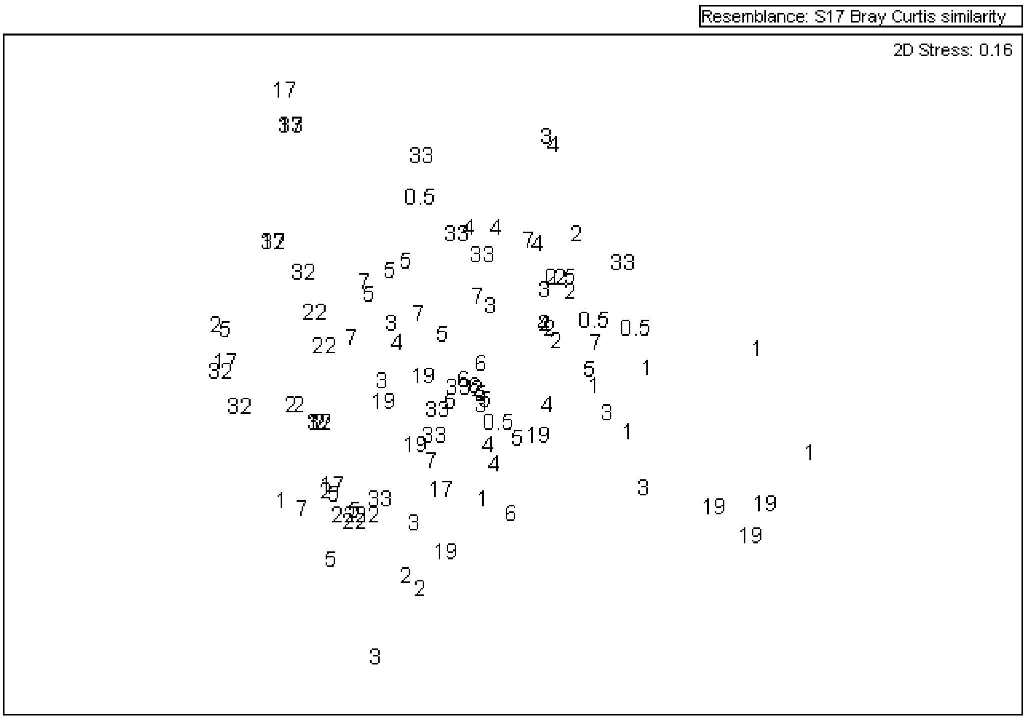
Ordination of bryophyte composition by time since fire.



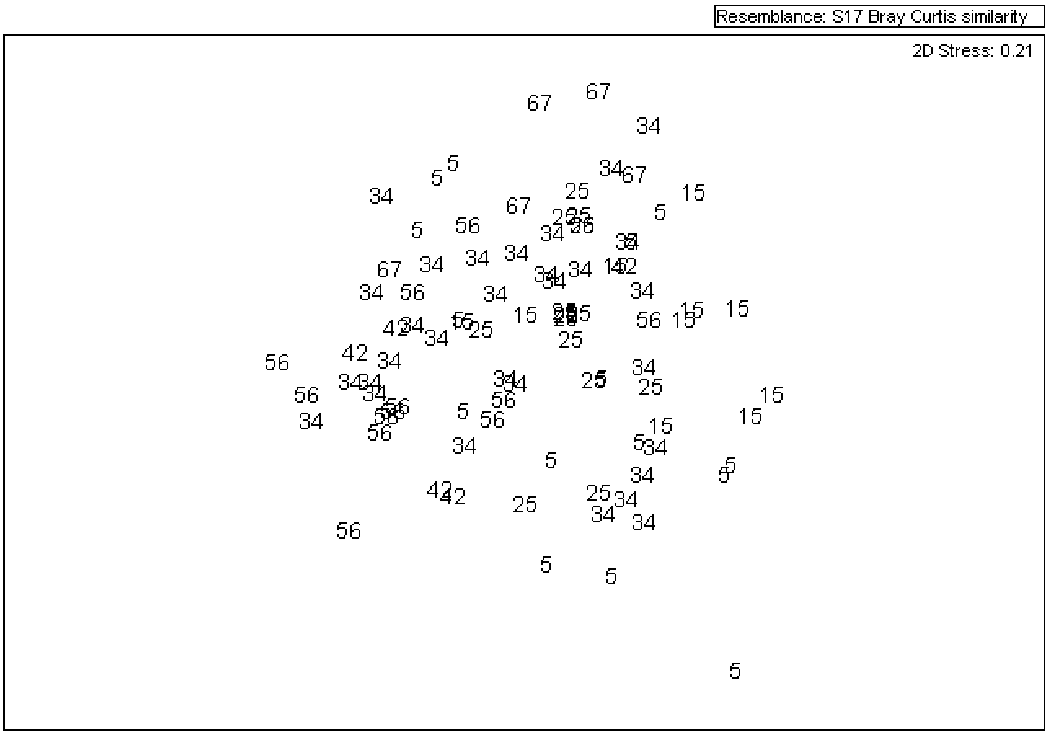
Ordination of moss composition by time since fire.



Ordination of liverwort composition by time since fire.



Ordination of the bryophyte composition of Lake St. Clair by time since fire.



Ordination of the bryophyte composition of Lake Pedder by time since fire.