The influence of fire on vegetation dynamics of a New Zealand restiad bog

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Abstract

New Zealand restiad bogs have a history of natural fire, yet little is known about their fire ecology compared to other frequently burnt ecosystems. Previous research has identified general vegetation recovery trends, but it remains unclear how certain species increase their dominance following fire and what the main environmental changes associated with burning are. To address these research gaps, this study focussed on three areas of varying last burn date (2017, 2005, and 1974) within Kopuatai Bog.

Measures of vegetation dynamics, light availability, and nutrient concentrations (in peat and foliage) were compared between burnt and adjacent unburnt sites. At the 2017 burn site, post-fire flowering of the sedge species, *Machaerina teretifolia* and *Schoenus brevifolius*, was assessed. At the same site, near-surface temperature fluctuations were monitored for almost one year, and samples collected two weeks post-fire were used to test for immediate nutrient enrichment. The role of the peat seed bank was tested experimentally, by exposing peat to heat and/or smoke and assessing germination.

Species capable of vegetative recovery dominated within the first two years post-fire. By 14 years, vegetation had largely recovered to pre-fire composition, although percent cover of *Leptospermum scoparium, Machaerina teretifolia, Schoenus brevifolius,* and *Epacris pauciflora* were higher on the burnt area. *Leptospermum*'s response can be explained by its well-documented serotinous capability. The increase in sedge species is attributed to their strong fire-stimulated flowering response, particularly in *Machaerina*, which averaged 30.4 flowering heads m^{-2} at the 2017 burn site. *Epacris* recovered from a rich peat seed bank, as demonstrated by the response in the germination experiment of 3143 seedlings m^{-2}, on average. The effect of heat on germination was unclear. Further research, including improved heat treatments, is required to determine the effect of heat on seeds of restiad species, *Empodisma robustum* and *Sporadanthus ferrugineus*, which were relatively common in the control and smoke treatments.

Fire resulted in immediate increases in peat total P, S, Ca, Mg, K, Na, Fe, Mn, Cu concentrations. These effects had declined by two years post-fire, although foliar nutrients

suggest that plant-available nutrients may have still been elevated at this time. Peat total N was unaffected. Near-surface maximum and average air temperatures were found to be consistently higher on the burn, while minimum temperatures were seasonally variable. Fire caused an increase in light availability from 0.1-0.2% diffuse light availability under an intact *Empodisma*-dominated canopy to 19.5% 16 months post-fire – an effect which had subsided completely by 14 years post-fire.

While nutrient enhancement, particularly in P, may temporarily enhance plant productivity, the most important driver of vegetation dynamics appears to be light. Fire opens up the canopy, providing an opportunity for seedlings to become established – an opportunity which *Leptospermum*, *Epacris*, and the sedge species take advantage of.

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Chapter One

Introduction to fire ecology and restiad bogs in New Zealand

1.1 Introduction

Restiad bogs of New Zealand have a history of natural fire (Newnham *et al.*, 1995; McGlone, 2009; Perry *et al.*, 2014), yet there are still many uncertainties regarding the ecology of fire in these ecosystems. Previous research has identified general trends of vegetation recovery and related some of these patterns to species' life history traits (Timmins, 1992; Clarkson, 1997; Johnson, 2005). For instance, serotiny (the fire-triggered release of seeds from plants) and survival of underground organs have been recognised as enabling species with these traits to recolonise a site quickly and temporarily increase their dominance (Clarkson, 1997; Johnson, 2005; Battersby *et al.*, 2017a). However, other plant responses to fire that can lead to changes in vegetation dynamics are largely unknown. For instance, it is unknown whether fire stimulates germination from a peat seed bank or causes increased flower production in certain species – responses that are common in plants of fire-prone ecosystems worldwide (Bond & van Wilgen, 1996). While fire-induced changes in light and nutrient availability have frequently been suggested by researchers to drive species compositional change in restiad bogs (de Lange, 1989; Clarkson, 1997; Norton & de Lange, 2003), these variables have not been well-studied.

1.2 Fire ecology

Fire ecology, the scientific discipline concerned with the ecological effects of fire, is a reasonably new field of science. Historically, wildfires were viewed as harmful to nature, a view based on the belief that disturbances disrupt a natural state of equilibrium (Clements, 1916, 1936). The Clementsian concept of a self-sustaining climax community, however, is of limited use when describing systems which experience regular fire events. In fire-adapted systems, many plants possess adaptations enabling them to quickly recolonise a site, such as resprouting from surviving rhizomes or fire-stimulated germination of seeds in a seedbank. The term climax, therefore, has little meaning, as "climax" species from the pre-burn community may reappear rapidly after fire. Beginning in the 1970s, there has been a paradigm shift away from this view of stability, to a non-equilibrium paradigm in which patch dynamics and regular disturbance events are recognised as important drivers of ecosystem characteristics and plant species evolution (Pickett & White, 1985; Wu & Loucks, 1995). Under this view, the local fire regime (comprised of fire intensity, severity, frequency, season, and type) is an important regulator of floristic composition (Christensen, 1985; Keeley *et al.*, 2011) and can direct pathways of vegetation change, rather than simply restarting them (Noble & Slatyer, 1980).

To survive in an environment subject to burning, a plant species not only has to survive a single fire, but also has to persist under a fire regime defined by the frequency, intensity and seasonality of burning (Gill, 1975; Bond & van Wilgen, 1996). Adaptations which increase the chances of long-term persistence in fire-prone ecosystems may relate to survival through fire and/or timing reproduction to fire. Survival may be achieved via thick protective bark or resprouting from underground organs, insulated from fire by a layer of soil (Gill, 1981). Subterranean positions are valuable refuges for living matter during fires because most of fire's heat rises and only a small proportion penetrates the soil (Gill, 1981). Common mechanisms by which plants reproduce and enhance seedling recruitment after fire are (a) serotiny whereby plants retain seeds during inter-fire periods and release them in the incidence of fire, (b) synchronous germination from a below-ground seed bank, or (c) fire-stimulated flowering which leads to high seed set when competition is low (Whelan, 1995; Bond & van Wilgen, 1996). The effect of a single fire event on vegetation composition depends, at least partly, on the presence of these adaptations in a community.

Fire also leads to numerous environmental changes, often causing temporary increases in light, temperature, and nutrients, thereby offering fitness benefits to plants that time reproduction to fire events. The primary effect of fire on an ecosystem is to remove biomass, yet there are several other resultant modifications to the biotic and abiotic environment which also affect ecosystem function. Defoliation by fire often alters the physical environment at the soil surface by increasing insolation and changing temperature regimes – generally causing greater daily temperature fluctuations (DeBano *et al.*, 1998; Geiger *et al.*, 2009). The chemical environment is affected by volatilisation of certain nutrients and depositions of others in ash, with these relative losses and gains dependent on fire severity and the threshold temperatures of nutrients (Pyne *et al.*, 1996; Neary *et al.*, 1999). It is common for fire to result in temporary nutrient enhancement, although the magnitude of this change and which nutrients are affected is contingent on properties of the pre-fire vegetation, soil, and the fire itself – e.g. its temperature and whether it burns underground or not (Neary *et al.*, 1999; Smith *et al.*, 2001). If fire causes shifts in surface microclimate and/or fertility which considerably increase the chances of seedling success, then fire may select for species which exploit these opportunities.

1.3 Fire history of restiad bogs

Despite New Zealand having an overall low rate of natural fire prior to human settlement (Ogden *et al.*, 1998), charcoal bands in peat cores indicate that restiad bogs of New Zealand, particularly those in the northern North Island, experienced natural fires relatively frequently (Newnham *et al.*, 1995; Perry *et al.*, 2014). That a type of wetland burns easily can largely be explained by the type of vegetation cover. Restiad bogs are so-named due to the dominance of species from the rush-like Restionaceae family. At Kopuatai Bog, the site of this research, *Empodisma robustum* and *Sporadanthus ferrugineus* are the restiad species present, although *Empodisma minus* and *Sporadanthus traversii* grow in other parts of New Zealand. *Empodisma robustum* (henceforth *Empodisma*) develops negatively geotropic roots and root hairs (cluster roots) which form large masses on the peat surface. These roots are visually and functionally similar to *Sphagnum* mosses which dominate Northern Hemisphere peatlands, capable of absorbing and storing large amounts of water, which contributes to peat formation (Agnew *et al.*, 1993). Unlike *Sphagnum* however, *Empodisma* forms a dense canopy up to approximately 0.7 m tall of intertwined dead and living stems.

Several characteristics of the *Empodisma* canopy make it highly flammable. As Kopuatai is an ombrotrophic ecosystem, relying on rainfall for nutrient input, nutrient levels in plant tissues are inherently low (Clarkson *et al.*, 2005). Low litter quality and slow decomposition rates lead to the accumulation of dead plant parts, which are necessary for fire to be sustained (Bond & van Wilgen, 1996). The high retention of dead plant material is thought to be the main reason that, globally, oligotrophic ecosystems burn more readily than eutrophic ecosystems (Christensen, 1987; Lugo, 1995). Flammability is also influenced by the type and arrangement of plant parts. Plants with high surface area to volume ratios ignite more readily due to the way that moisture is driven out of them (Whelan, 1995). An arrangement which enables airflow is also necessary (Whelan, 1995). The *Empodisma* canopy, composed of fine dead and living stems in a well-aerated arrangement, therefore provides a highly flammable fuel bed. Furthermore, restiad bogs tend to lack natural firebreaks due to their low and relatively uniform vegetation cover, leading to widespread fires. North Island bogs, such as Kopuatai, have been shown to have experienced higher rates of fire than South Island bogs historically, and Perry *et al.* (2014) suggested that this is because of more uniform rainfall patterns in the south compared to the seasonal patterns of wet winters and dry summers in the north.

Human modification of the local fire regime in restiad bogs may have long-term consequences for vegetation dynamics. For instance, an increase in burning in Waikato bogs associated with land clearing and conversion to agricultural land is widely regarded as the cause of decline in *Sporadanthus ferrugineus* (henceforth *Sporadanthus*) at Kopuatai (de Lange *et al.*, 1999; Reeves & Shannon, 2009). Prior to the mid-1970s, unintentional fires were a frequent occurrence in Waikato peatlands, with a 1974 report recounting major fires of anthropogenic origin at Kopuatai every 3-5 years (Harris, 1974). Since then, however, the decline in use of fire for land clearing, combined with stricter fire management policies, has reduced the frequency of fire, potentially to below its natural rate. The current management approach of extinguishing fires, even those naturally ignited, may be protecting sensitive species such as *Sporadanthus* but having negative consequences for other species for which recruitment is limited during fire-free periods. Plants which have reproduction keyed to fire require successive fires within the period represented by their life span, plus the length of time their seeds remain viable, to remain in the community (Noble & Slatyer, 1980). Based on the current literature, a long-term lack of fire in restiad bogs could contribute to a decline in species such as *Leptospermum scoparium* (mānuka), which regenerates via serotiny, and *Corybas carsei* (swamp helmet orchid) which flowers after fire (Norton & de Lange, 2003; Battersby *et al.*, 2017a). However, there is a lack of knowledge regarding fire-stimulated flowering in other species and the role of fire in stimulating germination from a peat seed bank.

1.4 Fire ecology of restiad bogs

While several studies have tracked vegetation recovery following fire in restiad bogs (e.g. Timmins, 1992; Clarkson, 1997; Johnson, 2001), there are still several unknowns regarding the links between fire and vegetation in these ecosystems. A study of two Waikato restiad bogs found that the vegetation at Moanatuatua took 11.5 years to reach pre-burn cover, twice as long as at Whangamarino (Clarkson, 1997). At Eweburn Bog, in the South Island of New Zealand, total vegetation cover and species diversity had almost fully recovered 4.5 years after fire, although species dominance and, to some extent, species composition still differed (Timmins, 1992). Following fire in Awarua Bog, South Island, 100% canopy cover was reached by 4.5 years, and vegetation composition by 10 years was assumed to be similar to pre-fire composition (Johnson, 2001). These studies describe general trends of dominance from "resprouters" which survive fire to "seeders" which take longer to recover. There has not been much focus, though, on specific vegetation changes which persist for several years, and how these changes come about. Fire recovery research has not been carried out at Kopuatai, New Zealand's largest bog, which is possibly home to the most fire-adapted plant communities (Battersby *et al.*, 2017a). A comparison of three sites of known burn date and their neighbouring unburnt areas (as proxies for pre-burn vegetation) within Kopuatai would reveal clearly which changes in species assemblages are long-lasting. The fire-related processes which drive these differences can then be examined.

Less work has been done to assess the effect of fire on physical and chemical environments in restiad bogs. Researchers have hypothesised that fire-related nutrient increases in restiad bogs are responsible for flushes in plant productivity and the temporary colonisation by exotic adventives and normally rare species (de Lange, 1989; Clarkson, 1997; Norton & de Lange, 2003). Except for an increase in pH detected after fire in a restiad bog (Norton & de Lange, 2003), which is suggestive of an increase in basic cations deposited in ash, these hypotheses have not yet been verified with evidence. A little more is known about how fire affects light availability and temperature regimes near the surface. Norton and de Lange (2003) found that photosynthetically available radiation (PAR) and daily maximum soil temperatures (10 cm depth) were higher on a burnt area for at least 4.5 years after fire. However, their measurements were based on only two replicates each in a burnt and unburnt area and their ability to detect seasonal differences in temperature regimes was limited by their sampling design. Quantification of the changes in physical and chemical environments at Kopuatai Bog would enable us to form a better understanding of how fire affects the environment which plants are exposed to, and why it is advantageous to recolonise a site quickly or reproduce after fire.

1.5 Kopuatai Bog

At approximately 100 km^2, Kopuatai is the largest remaining example of a restiad bog in New Zealand – an ecosystem type which is considered nationally endangered (Holdaway *et al.*, 2012). Due to widescale draining and conversion to farmland, wetlands in New Zealand have been reduced to 10% of their original extent, and bogs to 26% (Ausseil *et al.*, 2008). Kopuatai, however, remains largely intact and unmodified, despite being located in the Hauraki Plains of the Waikato region, which has been extensively drained (Figure 1.1). It is the only restiad bog to retain its natural vegetation and contains the largest communities of *Sporadanthus ferrugineus,* which has been eliminated from 95% of its known range (de Lange, 2020; de Lange et al., 1999). However, frequent fires accidentally caused by humans are believed to be responsible for the reduction in cover of *Sporadanthus* at Kopuatai (de Lange *et al.*, 1999; Reeves & Shannon, 2009). Drainage has also caused some changes in marginal vegetation (Irving *et al.*, 1984; Newnham *et al.*, 1995). Since the mid-1970s, Kopuatai has not experienced large-scale fires, primarily due to the conclusion of land development, but also because of regulated fire management. Kopuatai Bog's size, its intactness, and the occurrence of recent small burns (2017 and 2005) and older fires (the last fire of significance being in approximately 1974) make it an ideal location for furthering fire ecology research in restiad peatlands.

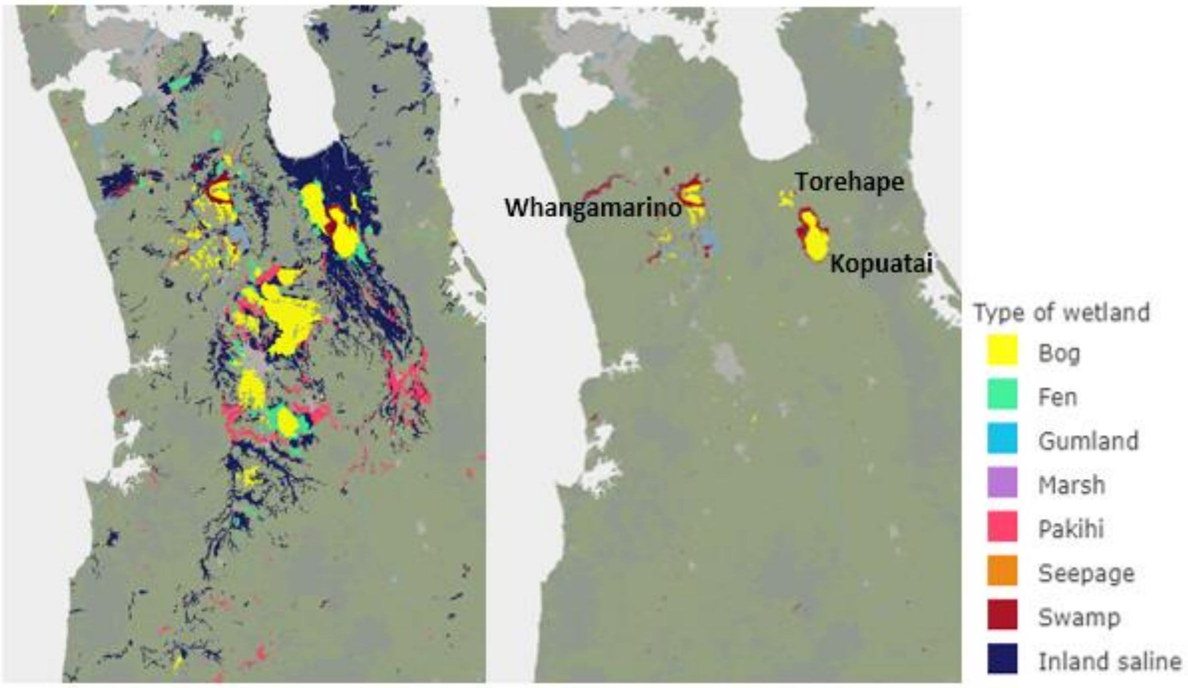


Figure 1.1. Wetland coverage in the Waikato region of New Zealand prior to human settlement (left) and in 2008 (right) (Adapted from Landcare Research, 2017)

Kopuatai's status as New Zealand's largest and best-preserved peat bog confers both national and global significance. Globally, peatlands are gaining increasing recognition for their potential as efficient and long-term carbon storers. The Intergovernmental Panel on Climate Change (IPCC) recently recommended the conservation of these high-carbon ecosystems, emphasising their role in carbon sequestration and thus climate change mitigation (IPCC, 2019). Based on eddy covariance gas exchange studies from 2012 to 2015, Kopuatai is a substantial contemporary carbon sink, storing 134.7 – 216.9 g C m^{-2} yr^{-1} (Goodrich *et al.*, 2017). Relative to similar wetlands in the Northern Hemisphere, this is high, primarily due to the year-round growing conditions in New Zealand (Goodrich *et al.*, 2017). Kopuatai is internationally recognised as a Ramsar wetland of importance (one of six in New Zealand) for its biodiversity and climate change values (Myers *et al.*, 2013). It is home to several threatened plants species, such as, among others, the clubmoss *Lycopodiella serpentina* (Threatened - Nationally endangered), the swamp shield-fern *Cyclosorus interruptus* (At risk – declining), the bladderwort *Utricularia deliculata* (At Risk – Relict), the liverwort *Goebelobryum unguiculatum* (Threatened – Nationally endangered) and *Sporadanthus ferrugineus* (At Risk – relict) (Reeves & Shannon, 2009). The site includes the best example in New Zealand of *Sporadanthus ferrugineus* rushland and one of the largest and least modified examples of kahikatea (*Dacrycarpus dacrydioides*) forest (Reeves & Shannon, 2009). The endemic moth, *Houdinia flexilissima* (At risk – relict), whose larvae live exclusively within the stems of *Sporadanthus ferrugineus*, is also restricted to raised bogs of the Waikato region (Watts *et al.*, 2013). Kopuatai also has significant cultural value to the indigenous people Ngāti Hako, who are kaitiaki (guardians) of this area, which they consider a taonga (treasure). Increasing the knowledge of the ecosystem at Kopuatai could contribute to conserving its multiple values.

1.6 Thesis aims and objectives

The aim of this research is to better understand the influence of fire on vegetation dynamics at Kopuatai Bog, including its effect on environmental variables and reproductive responses of plant species. In order to achieve this aim, the research objectives are to:

- Assess and attempt to explain plant community recovery trends by measuring species composition and structure at three sites of known burn date (2017, 2005, and 1974), using their adjacent unburnt areas as proxies for pre-burn vegetation.
- Quantify the fire-stimulated flowering response in the sedge species, *Machaerina teretifolia* and *Schoenus brevifolius.*
- Experimentally assess the role of the peat seed bank in vegetation recovery, including whether germination is stimulated directly by fire-related cues (heat and smoke).
- Determine whether ash deposition and other fire-related changes lead to immediate increases in nutrients, and how long these persist for, based on peat and foliage analysis.
- Characterise the effect of fire on light availability at the peat surface and determine the time taken to return to a pre-fire light environment
- Assess the effect of fire on the near-surface air temperature regime at daily and seasonal timescales.

1.7 Thesis outline

Chapters 2-4 describe the main results of the research. As they were written with the intention of publication, there is some repetition among these chapters, particularly with respect to introduction material.

Chapter 2 seeks to identify and explain fire-related changes in restiad bog vegetation dynamics at various timescales. I report on the findings from vegetation surveys at sites of various time since last fire and their adjacent unburnt areas. Information from published literature, measurements of a fire-stimulated flowering response in certain species, and a peat seed bank germination experiment (Chapter 4) are then used to explain the most significant differences.

Chapter 3 focuses on the environmental effects of fire in restiad bogs. By assessing nutrient concentrations in peat and foliage from sites which last burnt at various times, I aim to determine whether fire leads to an immediate increase in fertility – and if so, in what specific nutrients, and how long for. I also describe the effects of fire on light availability and air temperature near the peat surface.

Chapter 4 seeks to elucidate the possible role of the peat seed bank in post-fire vegetation recovery. Here, I aim to ascertain which plant species store substantial quantities of viable seed in peat and whether germination is triggered directly by fire-related cues (heat or smoke) or more general environmental changes which occur after fire (e.g. increases in light or temperature).

Finally, Chapter 6 summarises the main findings of this research, providing conclusions on the fire ecology at Kopuatai Bog and identifying areas for further research.

Chapter Two

Post-fire vegetation dynamics

2.1 Introduction

Fire can lead to short- and long-term changes in vegetation structure and species composition. In fire-prone ecosystems, the fire regime, which incorporates the frequency, intensity, and seasonality of burning, is an important regulator of vegetation composition, ultimately selecting for plants that are capable of persisting through recurrent burning (Bond & van Wilgen, 1996; Keeley *et al.*, 2011). Fire-adaptive traits assist this persistence by enhancing survival, such as the ability to resprout from surviving underground organs, or reproduction, such as the serotinous release of seeds from a canopy, the synchronous germination of seeds from a soil seed bank, or fire-stimulated flowering (Gill, 1981; Whelan, 1995). These adaptations enable early colonisation when resource availability is high and competition is low, and potentially lead to an increase in dominance at the expense of less fire-adapted species (Noble & Slatyer, 1980).

Although fires were generally uncommon in prehuman New Zealand (Ogden *et al.*, 1998), restiad bogs of New Zealand, particularly those in the Waikato region, have a history of natural fire (Newnham *et al.*, 1995; Haenfling *et al.*, 2017). While the New Zealand bog flora is naturally species-poor, the influence of the fire regime is demonstrated by the presence of fire-adaptive traits in several species. For instance, *Leptospermum scoparium* (mānuka) growing in restiad bogs is highly serotinous, releasing few seeds in fire-free years (Battersby *et al.*, 2017a); *Gleichenia dicarpa* (tangle fern) and the sedges, *Machaerina teretifolia* and *Schoenus brevifolius*, survive fire by resprouting from fire-protected rhizomes (Clarkson, 1997); and fire-stimulated flowering has been experimentally detected in the swamp helmet orchid, *Corybas carsei* (Norton & de Lange, 2003). *Machaerina* and *Schoenus* have also been observed to flower following fire (Clarkson, 1997).

Previous research has documented the regeneration of restiad bog vegetation following fire at Eweburn (Timmins, 1992) and Awarua (Johnson, 2001) in the South Island and at Moanatuatua and Whangamarino in the Waikato region of the North Island (Clarkson 1997). Overall, vegetation was found to have returned to approximately pre-fire condition by 16 years at Awarua and Eweburn (Johnson, 2005) and 6-12 years in the Waikato (Clarkson, 1997) and the patterns of regeneration can largely be explained by individual species responses to fire. For instance, while the “resprouter” species described above were quick to re-establish on burnt sites, “seeder” species such as *Empodisma robustum* (wire rush) were slower to recover due to their reliance on seed dispersal (Clarkson, 1997). This study expands on the current knowledge by carrying out thorough vegetation surveys at three sites of known burn date within a restiad bog, using the surrounding unburnt vegetation as a reference for the pre-fire communities. These sites essentially act as replicates at different stages of recovery, providing a detailed timeline of recovery.

Alongside measuring vegetation recovery, this study also evaluates the recovery of *Empodisma* cluster roots and standing litter layer, both of which are important for peat formation, yet have not been assessed in previous studies. It is *Empodisma*'s upward growing roots and root hairs (cluster roots) with high water-holding capacity and base exchange properties that make up the bulk of peat (Agnew *et al.*, 1993). As fire kills *Empodisma* (Clarkson, 1997), it can also be expected to interrupt peat formation. Also implicated in peat formation is the dense layer of standing litter which *Empodisma* forms. It accounts for 51% of the total canopy biomass at Kopuatai and helps maintain peat-forming conditions by providing a mulching effect which insulates the moist peat from the drying atmosphere (Keyte-Beattie, 2014). When intact, it effectively doubles the density of the canopy, highly restricting light penetration near the peat surface and creating conditions which are hostile to the growth of seedlings. While the literature reports that *Empodisma* becomes dominant after 4 years (Clarkson, 1997), it is unknown whether cluster roots or standing litter recover within the same timeframe.

This study expands on the existing literature by comparing sites in a single ecosystem burnt at various dates within the last 50 years (2017, 2005, and 1974) at New Zealand’s largest extant bog, Kopuatai. These sites are treated as a chronosequence, enabling inferences to be made about how fire affects vegetation dynamics over a longer time period than previous studies. This study has two aims: (1) to assess in detail what compositional and structural changes are caused by fire and how long these changes persist for and; (2) to explain any changes using published and gathered knowledge of individual species fire-related responses.

2.2 Methods

2.2.1 Study area

Kopuatai Bog is an area of 105.4 km^2 (Ausseil *et al.*, 2008) located on the Hauraki Plain southeast of Auckland (Figure 2.1). Toward the central part of the bog, peat has been forming since 11,700 years BP and reaches depths of up to 14 m (Newnham *et al.*, 1995). Although the Hauraki Plains have undergone extensive draining for agriculture, Kopuatai is essentially unmodified except by fire, with only the margins affected by drainage (Irving *et al.*, 1984; Newnham *et al.*, 1995). Sampling was done in the ombrotrophic bog area which, due to its elevation, is more nutrient-depleted and species-poor than groundwater-fed marginal areas (Clarkson *et al.*, 2004a).

The primary peat-forming species are members of the Restionaceae, *Empodisma robustum* (henceforth *Empodisma*) and, in places, *Sporadanthus ferrugineus* (henceforth *Sporadanthus*). Pervasive across the bog, the *Empodisma* canopy is composed of a network of intertwined dead and living stems up to around 0.7 m high in open sites but scrambling to about 2 m when supported by taller shrubs and *Sporadanthus* plants (Clarkson & Clarkson, 2006). It is *Empodisma*'s upward growing roots and root hairs (cluster roots) that form the bulk of the peat. *Sporadanthus* is also an important peat former, although its cluster roots are less developed than those of *Empodisma* and do not emerge above the peat surface (Clarkson & Clarkson, 2006). *Sporadanthus* is a late successional species, establishing after *Empodisma*, and eventually becoming the physiognomic dominant (Clarkson *et al.*, 2004a). At Kopuatai, it occurs in distinct patches and grows tall stems up to about 2.5 m high; the support provided by this species enables other bog plants to reach greater heights than they do when free-standing. The tangle fern, *Gleichenia dicarpa* (henceforth *Gleichenia*) and two sedge species, *Machaerina teretifolia* (henceforth *Machaerina*) and *Schoenus brevifolius* (henceforth *Schoenus*), also have a significant presence in the bog. Woody species, mānuka, *Leptospermum scoparium,* and tamingi, *Epacris pauciflora* (henceforth *Epacris*), occur patchily as shrubs up to about 2.5 m tall.

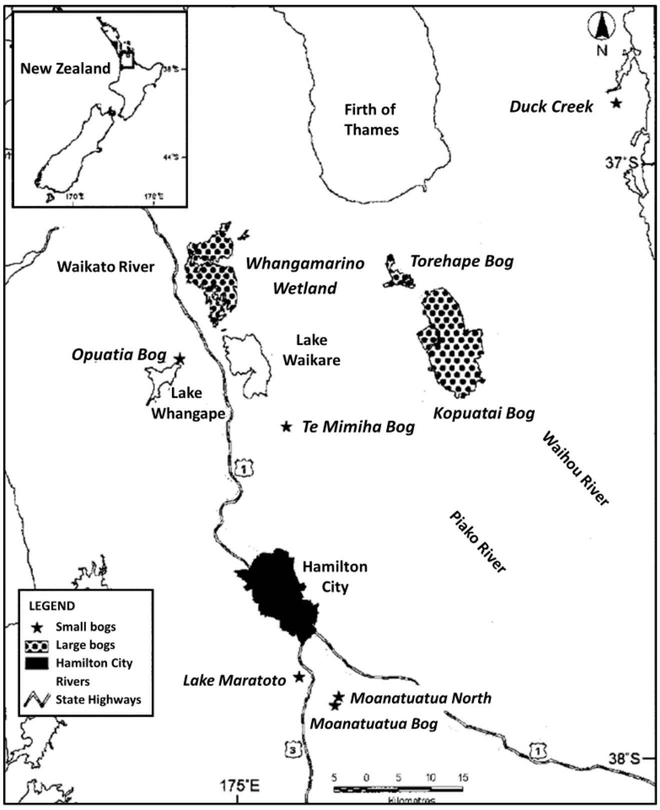


Figure 2.1. Location of Kopuatai and other bogs in the Waikato region, North Island, New Zealand. From Clarkson *et al.* (2004).

Figure 2.2. Location of sampling sites within Kopuatai. Source: Google Earth.

Records of Kopuatai's recent fire history identified three sites burnt within the last five decades. At the time of surveying in 2019, these were burnt approximately 16 months, 14 years, and 45 years previously. The most recent fire was ignited by lightning on 14 November 2017, near the north-west margin of Kopuatai (Figure 2.2). It was extinguished with water by helicopters using monsoon buckets at the behest of the Department of Conservation, resulting in a burn scar of approximately 5000 m^2 (Figure 2.3). On 14 September 2005, a fire of similar nature was started by a lightning strike also on the western side of Kopuatai (Figure 2.2). The fire was mostly put out by rain, but helicopters and monsoon buckets were also used. It is not recorded whether a wetting agent was used. The resulting burnt area was approximately 7500 m^2 (Figure 2.4). Both fires removed surface vegetation except for small patches within the burnt area which were unaffected (Figure 2.3; Figure 2.4). In 2010 satellite imagery, the 2005 burn is distinguishable from surrounding vegetation, being brighter green and less textured than the surrounding *Empodisma*-dominated vegetation (see Figure 2.6).

The 2017 and 2005 fires both occurred in areas with vegetation classified as "wire rush rushland" which is the most common vegetation community type at Kopuatai, occupying 52.3 km^2 (Beadel *et al.*, 2016). This vegetation consists of a canopy dominated by *Empodisma,* with *Machaerina, Schoenus* and *Gleichenia* also present, and mānuka and *Epacris* as occasional emergents. The 2005 fire was also near to an area of *Sporadanthus ferrugineus* rushland vegetation type, described below (Reeves *et al.*, 2009).

A much more widespread fire occurred in about 1974 (Irving *et al.*, 1984; de Lange *et al.*, 1999). While the exact extent of this fire has not been recorded, aerial imagery suggests that it burned a major portion of Kopuatai. An aerial photograph from January 26 1975 (Figure 2.5) displays streaky patterning on Kopuatai's surface, consistent with recent large-scale burning. The 1974 fire is the last widespread fire that occurred during a period of frequent burning at Kopuatai when surrounding land was burnt for development (Irving *et al.*, 1984). A 1974 document advising the Hauraki Catchment Board on fire management describes how, at the time, Kopuatai averaged a major fire at 3-5 yearly intervals (Harris, 1974). The following quote is an excerpt from the same document:

> *"Experience has shown that the fire risk comes almost wholly from the fringe area, closest to road access, land development, etc. From these areas the fires spread into the main 20,000 acres where the fires literally rage out of control, sometimes from one end to the other, as the winds take them, destroying vegetation on the dome and probably the peat surface, aside from the serious damage they cause in the fringe areas"* (Harris, 1974).

We chose to sample at a site within the 1974 burn that had been surveyed in 1995, approximately 20 years after the fire (de Lange *et al.*, 1999). Therefore, while this site does not have an adjacent "unburnt" comparison site, it can at least be compared to the vegetation described in 1995. The site is in the northeast of Kopuatai (Figure 2.2) and has a vegetation type classified in 2008 as "*Sporadanthus ferrugineus* rushland" (Reeves *et al.*, 2009). This plant community type covers 10.3 km^2 of the entire bog area at Kopuatai and is dominated by *Sporadanthus,* with common *Empodisma* and *Schoenus,* and occasional mānuka and *Epacris* shrubs (Reeves *et al.*, 2009). Within Kopuatai, *Sporadanthus* cover used to be more extensive but has declined in recent centuries due to the increase in fire frequency relating to land clearing (de Lange, 1989; Newnham *et al.*, 1995; de Lange *et al.*, 1999).

Figure 2.3. The 5000 m^2 area burned by the 2017 fire. Source: Nick Hamon (The Department of Conservation).

Figure 2.4. The 7500 m^2 area burnt by the 2005 fire. Source: The Department of Conservation.

Figure 2.5. 1975 aerial image of the south end of Kopuatai showing patterning assumed to be caused by a recent fire. Photo was taken on January 26, 1975. Source: retrolens.nz

2.2.2 Sampling methods

A point intercept method (PIM) was used to sample vegetation composition and structure. It involved sampling at discrete points along a series of transects within a defined area. The sampling area was chosen based on the size of the burnt area (except for at the 1974 burn site) so that the burnt and unburnt areas could be sampled in approximately equal proportions. Transects of equal length were established perpendicular to a baseline and measurements were taken at random distances along each transect (Figure 2.6). Vegetation surveys were carried out at the 2017 site between February and April 2019 (15-17 months post-fire); at the 2005 site in October 2019 (14 years and 1 month post-fire); and at the 1974 site in November – December 2019 (45 years post-fire).

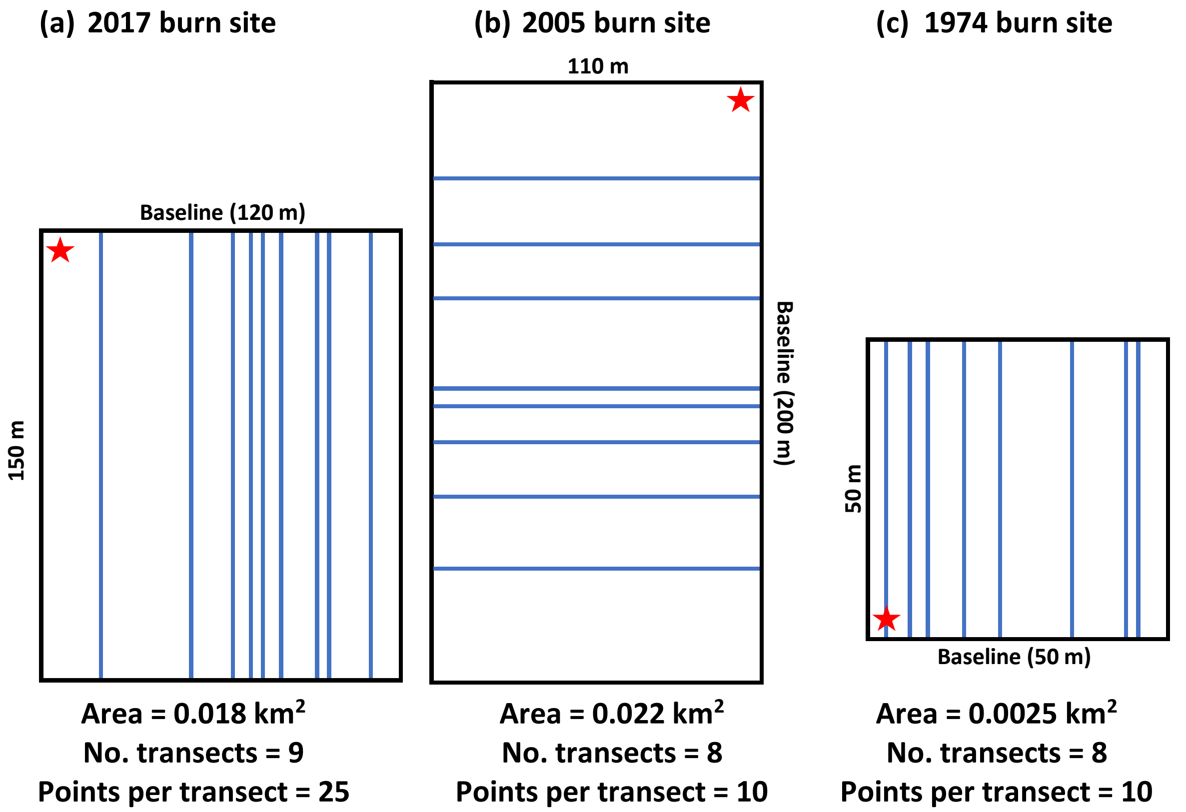


Figure 2.6. Vegetation survey sampling plans for (a) the 2017 burn site, (b) the 2005 burn site, and (c) the 1974 burn site. Blue lines represent randomly spaced transects which ran perpendicular to the baseline. Red stars represent the start of the baseline which was at (a) -37.37640, 175.52330, (b) -37.447914, 175.53508, and (c) -37.371175, 175.553673. All diagrams are aligned north.

The PIM method involved recording the vertical distribution of plant contact with a 2.5 m metal rod at random intervals along each transect. At each randomly chosen point along a transect, a 4 mm diameter steel rod was driven vertically into the peat. Sampling points were displaced 50 cm from the transect to avoid taking measurements from trampled vegetation. Records were made of the species touching the rod and the height of contact. Only vascular species were recorded. Percent cover for a species was calculated by dividing the number of points it was recorded as present at by the total number of points sampled. A PIM was chosen because it provides a more objective estimate of cover than the qualitative methods used in visual estimates of cover. PIMs have the drawback of tending to miss rare species, especially if they are small (Caratti, 2006). We therefore complemented our PIM measurements with species lists of all vascular plants observed within a hoop of 0.38 m radius (area = 0.45 m^2) centred on the rod. Note that this was not done for the first two transects at the 2017 burn site. The presence of *Empodisma* cluster roots at the peat surface and the height of the standing *Empodisma* litter layer were also recorded at each point.

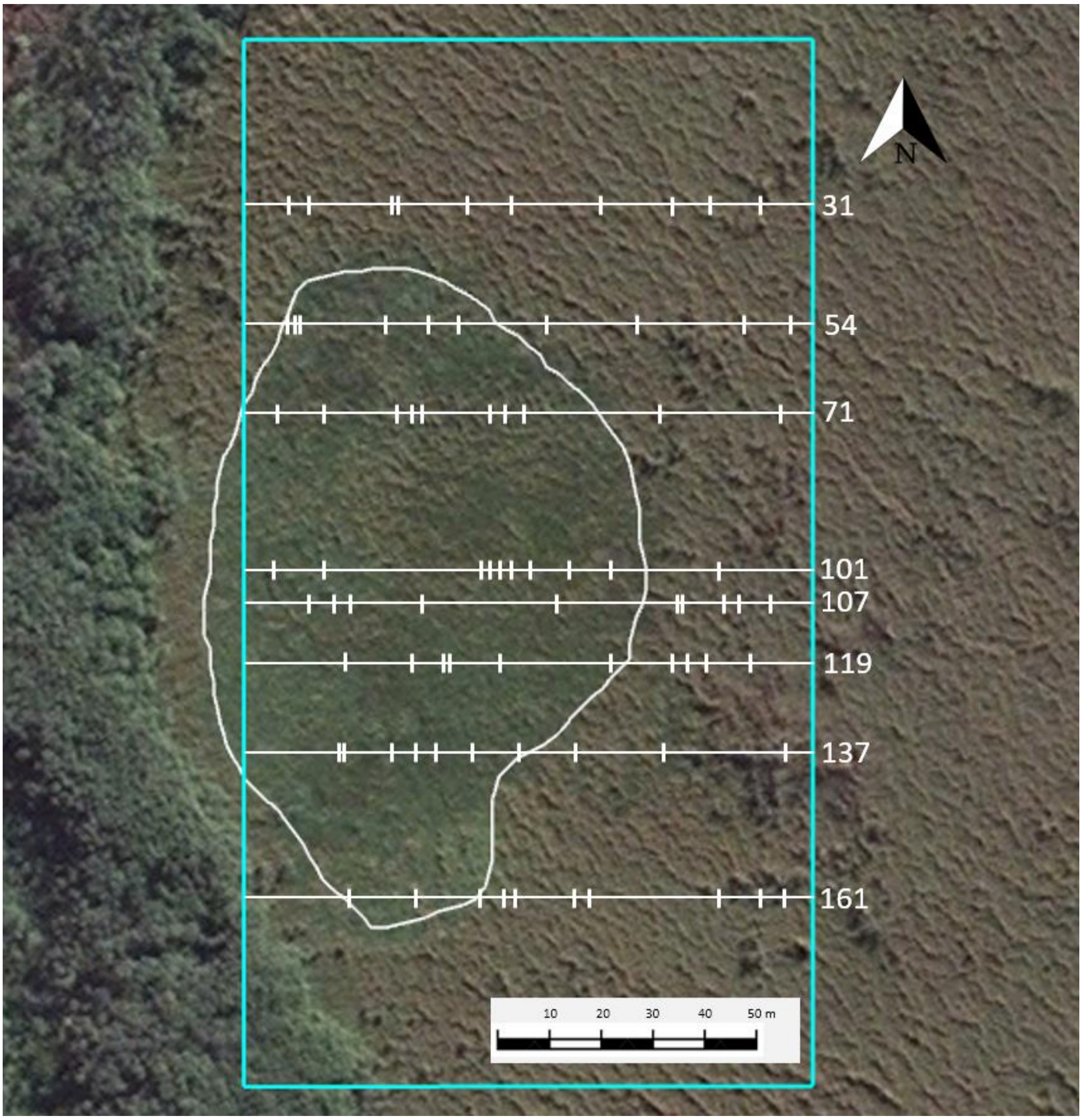


Figure 2.7. The sampling plan for the 2005 burn site. This satellite image from 2010 shows the burnt area (outlined) as brighter green and less textured than the unburnt vegetation. The blue box represents the 110 x 200 m sampling area. White east-west lines represent transects beginning at random distances (numbered) along a north-south baseline, and white vertical marks represent sampling points. Marginal vegetation (left) was avoided. Adapted from Google Earth.

The sedges appeared to be flowering more profusely on the area burnt in 2017 compared to the surrounding unburnt areas. A survey was therefore carried out to quantify this effect, during a visit to the site in January 2020 (26 months post-fire). It was achieved by sampling at five transects in the area previously surveyed. At ten random distances along each transect, point intercept data were gathered for the two sedge species only, their presence within the 0.45 m^2 hoop recorded, and the number of flowering stems in the hoop counted.

Differences were observed between plant communities where *Sporadanthus* was present and where it was absent at the 1974 burn sampling site, prompting assessment of chemical and physical properties of the differing areas. Within the sampling area, three peat cores and three samples of *Gleichenia dicarpa* foliage were collected from each vegetation type (where *Sporadanthus* was present and where it was absent) for nutrient analysis. Collection points were determined by randomly selecting a subgroup of vegetation sampling points. Samples of *Gleichenia* were taken from the nearest plants, with effort made to collect young looking foliage. Two peat samples were taken at each point using a standard peat corer (5 cm depth, 6 cm diameter). At each peat collection point, water table measurements were taken by creating a hole and measuring the distance from the peat surface to the surface of pooled water. This was done in December 2019. Foliage and peat samples were dried and analysed for carbon (C), nitrogen, (N), nitrogen-15 ($\delta^{15}N$; in foliage only), phosphorus (P), and potassium (K). C and N concentrations were analysed by an Elementar Isoprime 100 analyser and $\delta^{15}N$ concentrations were determined by a fully automated Europa Scientific 20/20 isotope analyser, both at the University of Waikato Stable Isotope Unit. P and K were assessed by ICP-MS at the University of Waikato. Detailed methods of sample preparation can be found in the methods section of Chapter 3.

2.2.3 Statistical analysis

Differences in plant composition among sites (2017 burnt, 2017 unburnt, 2005 burnt, 2005 unburnt, 1974 burnt) was tested by permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis similarity index. To achieve this, the height data was categorised into five height classes (0-50, 51-100, 101-150, 151-200, 201-250 cm) and percent frequency for each species within each height category was then averaged across transects so that each transect was treated as one replicate sample. Non-metric multidimensional scaling (NMDS) was used to display these compositional relationships visually. Both of these procedures were carried out using the vegan package of R (Oksanen *et al.*, 2010). An analysis of variance (ANOVA) and post-hoc Tukey’s HSD tests were carried out to test for differences in the height of the standing litter layer among sites. To assess nutritional differences between areas at the 1974 burn site where *Sporadanthus* was present and where it was absent, a series of t tests was carried out on peat and foliage nutrient levels. A t test was also performed on the water table data from this site.

2.3 Results

2.3.1 Immediate effects of fire

The 2017 fire was essentially an above-ground or "cool" fire which burnt off surface vegetation but did not penetrate into the peat (Figure 2.8 a). All herbaceous vegetation was destroyed, but some woody stems of mānuka and *Epacris* were left standing. *Machaerina* culms were displaying fresh growth two weeks post-fire (Figure 2.8 b).

Figure 2.8. Images taken two weeks after the 2017 fire showing (a) the edge of the burnt site and (b) fire-cropped *Machaerina teretifolia* showing fresh growth. Source: Dave Campbell.

2.3.2 Species composition

Data was collected from 90 points in the area burnt by the 2017 fire (Table 2.1). At the time of sampling, 16 months post-fire, the vegetation was dominated by *Gleichenia*, followed by

Machaerina, both of which had higher percentage cover on the burn than the unburnt area (1.4 and 1.2-fold greater, respectively) (Table 2.1). *Schoenus* displayed higher cover on the burn (Table 2.1), although its overall presence was low, so this result may be due to chance. Mānuka, *Epacris*, and *Empodisma* seedlings were common but small and so were often undetected by the PIM, contributing to high discrepancies between the hoop and PIM results (Table 2.1). For instance, mānuka was detected by PIM as 4.4% cover, 6.3-fold greater than on the unburnt area, although it was present in 43.2% of hoop species lists (Table 2.1). PIM data for *Epacris* indicates a 2.7-fold lower abundance on the burn (1.1% cover), although it was encountered in 13.5% of hoop species lists. *Empodisma* showed the largest difference in cover between burnt (1.1% cover) and unburnt (88.1% cover) areas, although the hoop data indicates a high presence of seedlings at the burnt site (Table 2.1). Exotic plants *Holcus lanatus* (Yorkshire fog) and *Epilobium ciliatum* (willow herb) occurred respectively in 1.4% and 2.7% of hoop species lists from the burn (Table 2.1).

Data was collected from 135 points in the unburnt area surrounding the 2017 burnt site (Table 2.1). The most abundant species was *Empodisma*, followed by *Gleichenia* and then *Machaerina* (Table 2.1). *Schoenus* was uncommon at this site and was not detected in the unburnt vegetation, although a later survey into fire-stimulated flowering picked up one individual *Schoenus* plant. Mānuka and *Epacris* were occasional emergents (Table 2.1). The forked sundew, *Drosera binata*, was encountered once but only within a hoop species count (Table 2.1).

Data was collected from 43 points on the area burnt in 2005 (Table 2.1). *Empodisma* and *Gleichenia* had similar cover estimates as on the unburnt area (Table 2.1). *Machaerina*, *Schoenus*, *Epacris*, and mānuka all had much higher cover on the burn than on the unburnt area (Table 2.1). *Sporadanthus* was not encountered by either method on the burnt area, nor observed there (Table 2.1).

Data was collected from 37 points on the unburnt vegetation adjacent to the 2005 burn area (Table 2.1). *Empodisma* was the most dominant species followed by *Gleichenia* (Table 2.1). *Sporadanthus* was the third most abundant (Table 2.1). The sedges, *Machaerina* and *Schoenus*, had a minor presence, as did *Epacris* (Table 2.1). Mānuka was not encountered in the unburnt vegetation by either method (Table 2.1).

Data was collected from 80 points at the 1974 burn site (Table 2.1). *Empodisma* had the highest percent cover, followed in order of dominance by *Sporadanthus*, Mānuka, *Gleichenia*, *Schoenus*, *Epacris*, and *Machaerina* (Table 2.1).

Table 2.1. Percent vegetation cover of plant species at five surveyed sites at Kopuatai. Percentage frequency in a 38 cm radius from the point intercept pole are in parentheses.

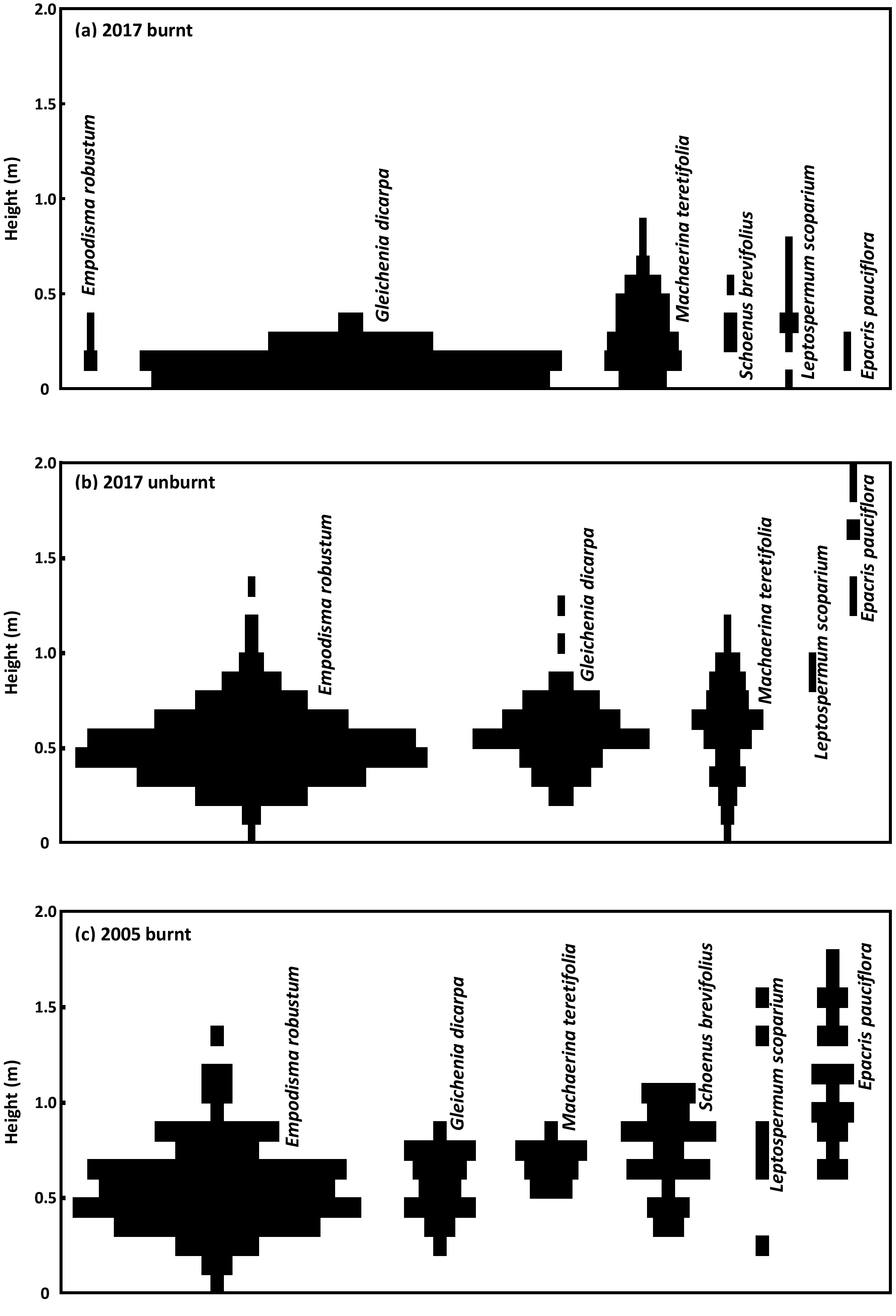
Species	**2017 burnt (n=90)**	**2017 unburnt (n=135)**	**2005 burnt (n=43)**	**2005 unburnt (n=37)**	**1974 burnt (n=80)**
Empodisma	3.3 (29.7)	88.1 (92.1)	93.0 (100.0)	97.3 (100.0)	96.3 (100)
Gleichenia	94.4 (100.0)	69.6 (100.0)	37.2 (100.0)	37.8 (100.0)	28.8 (96.3)
Machaerina	42.2 (100.0)	35.6 (99.0)	25.6 (60.5)	2.7 (2.7)	5.0 (15.0)
Schoenus	3.3 (8.1)	- (-)	37.2 (62.8)	5.4 (29.7)	15.0 (32.5)
Mānuka	4.4 (43.2)	0.7 (1.0)	9.3 (23.3)	- (-)	31.3 (33.8)
Epacris	1.1 (13.5)	3.0 (5.9)	23.3 (59.1)	5.4 (8.1)	11.3 (11.3)
Sporadanthus	- (-)	- (-)	- (-)	8.1 (8.1)	48.8 (71.3)
Drosera binata	- (-)	- (1.0)	- (-)	- (-)	- (-)
*Epilobium ciliatum**	- (2.7)	- (-)	- (-)	- (-)	- (-)
*Holcus lanatus**	- (1.4)	- (-)	- (-)	- (-)	- (-)

* Non-native species

2.3.3 Height structure and composition

Compared to the unburnt area, *Gleichenia* was more abundant, but present at lower heights, by 16 months post-fire (Figure 2.9 a, b). By 14 years, it had returned to a state similar to at unburnt sites (Figure 2.9 b-d). The cover of *Machaerina* by 16 months was similar to that on the unburnt area, but its height distribution was slightly lower (Figure 2.9 a, b). By 14 years post-fire, both sedge species, *Machaerina* and *Schoenus,* had substantially greater cover on the burnt area compared to the unburnt area (Figure 2.9 c, d). Compared *to Gleichenia* and *Machaerina, Empodisma* was less abundant and of shorter stature after 16 months (Figure 2.9 a), although by 14 years post-fire, its distribution was broadly similar to that at the unburnt sites (Figure 2.9 b-e). This differed slightly at the 1974 burn site, where *Empodisma*'s maximum height and most common height were elevated by about 0.3 m (Figure 2.9 e).

Mānuka and *Epacris* both showed increasing heights with time since fire, with the tallest plants recorded at the site burnt 45 years prior (Figure 2.9). These species were also intercepted at a wider range of heights at the 1974 burn site than any other sampling area (Figure 2.9). *Sporadanthus* was only present at the 2005 unburnt area occasionally and at the 1974 burnt area where it was abundant between 0 and 2.4 m (Figure 2.9 d, e).


(a) 2017 burnt
Height (m)
2.0
1.5
1.0
0.5
0
Empodisma robustum
Gleichenia dicarpa
Machaerina teretifolia
Schoenus brevifolius
Leptospermum scoparium
Epacris pauciflora
(b) 2017 unburnt
Height (m)
2.0
1.5
1.0
0.5
0
Empodisma robustum
Gleichenia dicarpa
Machaerina teretifolia
Leptospermum scoparium
Epacris pauciflora
(c) 2005 burnt
Height (m)
2.0
1.5
1.0
0.5
0
Empodisma robustum
Gleichenia dicarpa
Machaerina teretifolia
Schoenus brevifolius
Leptospermum scoparium
Epacris pauciflora

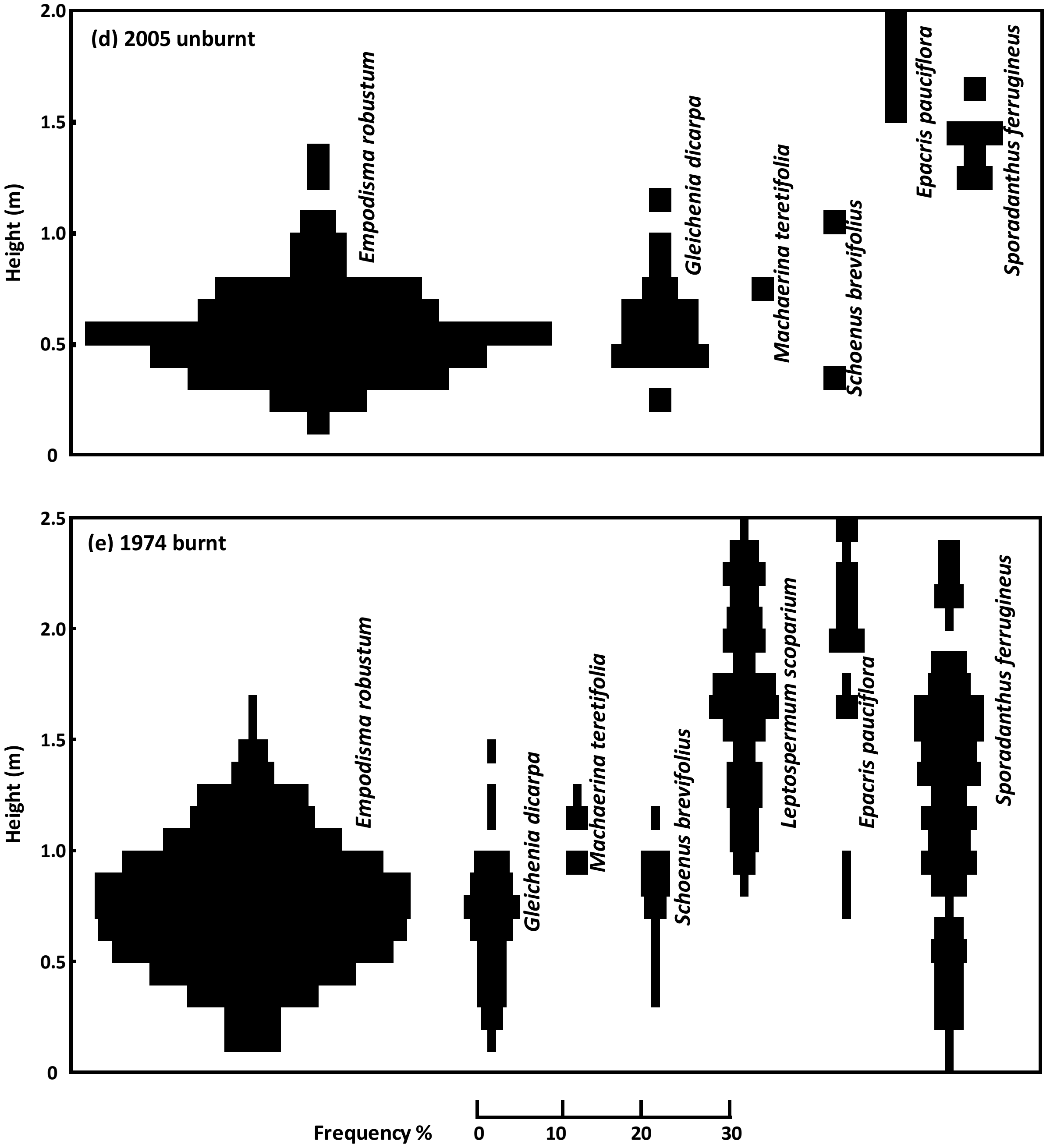


Figure 2.9. Height frequency diagrams showing structure and composition at (a) the 2017 burn site and (b) adjacent unburnt area, (c) the 2005 burn site and (d) adjacent unburnt area and (e) the 1974 burn site based on vegetation surveying carried out in 2019.

Dividing the 1974 vegetation data into two categories based on whether *Sporadanthus* was present (n = 66) or not (n = 14) revealed that several species were taller growing on the *Sporadanthus*-dominated areas (Figure 2.10). These species include *Empodisma, Gleichenia,* mānuka and *Epacris*. *Machaerina*, mānuka, and *Epacris* also had higher percentage cover where *Sporadanthus* was present (Figure 2.10).

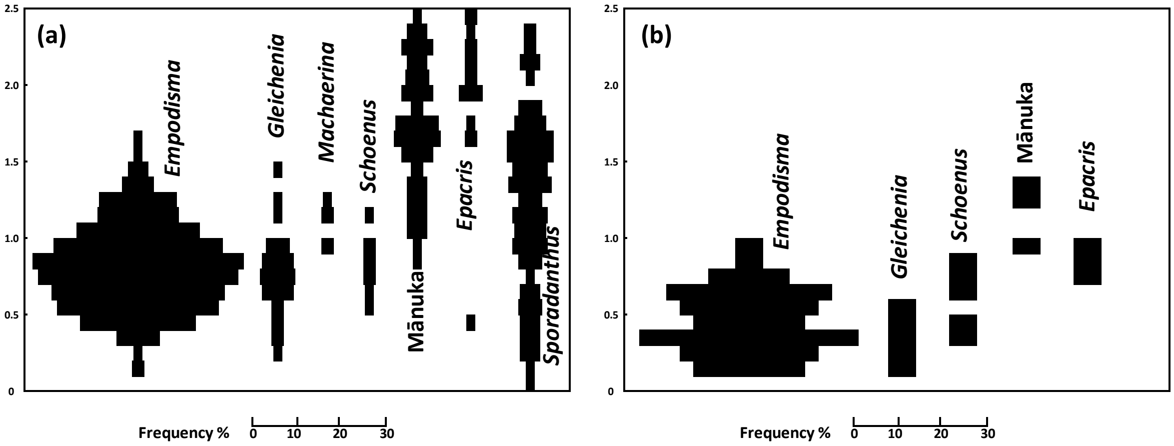


Figure 2.10. Height frequency diagrams showing structure and composition at the 1974 burn site where (a) *Sporadanthus* is present and (b) it is absent.

PERMANOVA found that community composition and structure varied significantly among the five sampling areas (Table 2.2). Pairwise comparisons found that composition and structure differed between all combinations of sites, except between the 2005 burnt and nearby unburnt areas (Table 2.2), despite the notable differences in structure and composition between these areas discussed above. These findings are illustrated in the NMDS plot (Figure 2.11) which shows that the 2017 burnt site had the most distinctive plant community of the five sites, whereas there is some overlap between the other four sites, especially among the 2005 burnt and unburnt areas and the 2017 unburnt area.

Table 2.2. PERMANOVA results showing differences in composition and structure based on Bray-Curtis similarities between all pairs of sites. Values in bold are significant ($p < 0.05$).

Site 1	Site 2	F	R^2	*p*
All	All	12.03	0.579	**0.001**
2017 burnt	2017 unburnt	23.50	0.610	**0.001**
2017 burnt	2005 burnt	12.18	0.484	**0.001**
2017 burnt	2005 unburnt	17.31	0.553	**0.001**
2017 burnt	1974 burnt	18.16	0.565	**0.001**
2017 unburnt	2005 burnt	2.56	0.155	**0.001**
2017 unburnt	2005 unburnt	5.66	0.274	**0.003**
2017 unburnt	1974 burnt	14.18	0.486	**0.001**
2005 burnt	2005 unburnt	2.18	0.143	0.050
2005 burnt	1974 burnt	9.98	0.434	**0.001**
2005 unburnt	1974 burnt	7.31	0.343	**0.001**

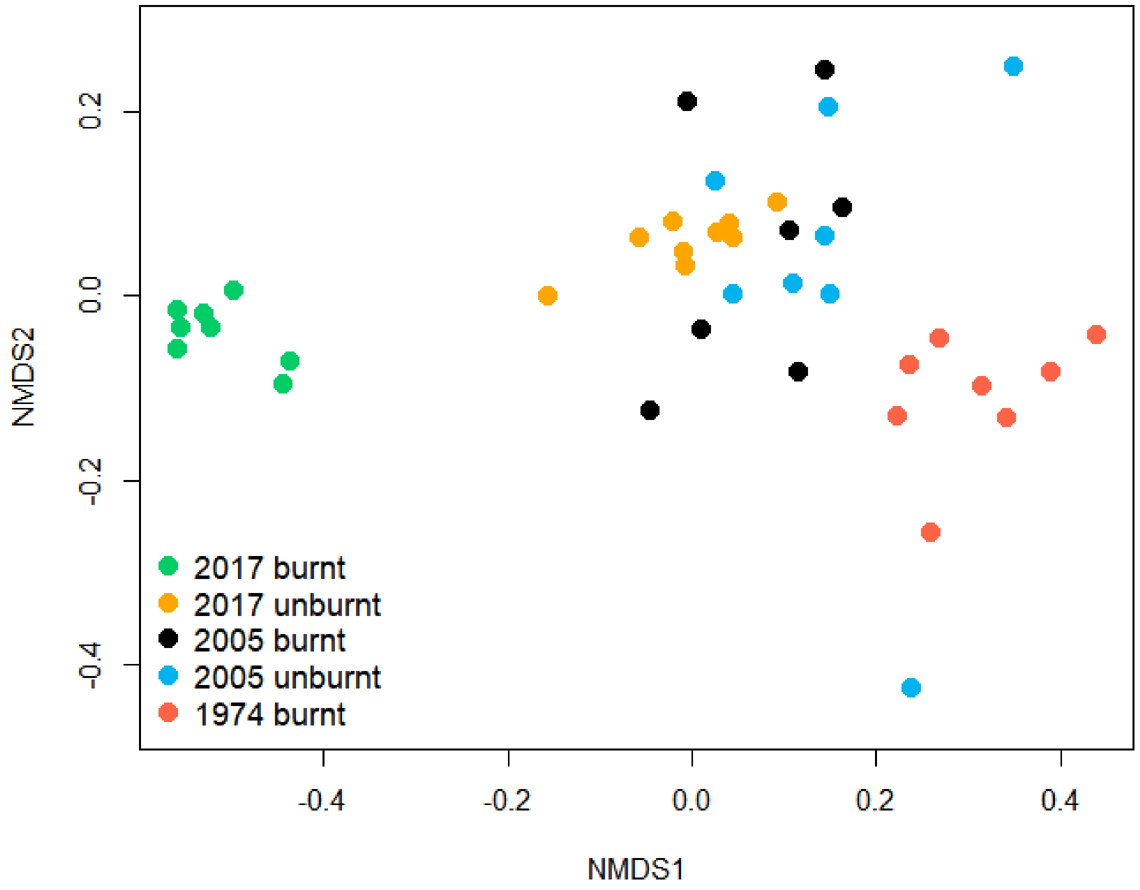


Figure 2.11. Non-metric multidimensional scaling (NMDS) plot illustrating compositional and structural relationships between sites sampled.

2.3.4 Fire-stimulated flowering

Machaerina was found to be flowering at a substantially greater rate on the 2017 burnt area than the unburnt area. *Machaerina* was present in the hoop at 100% of points measured inside the burn (n=22) and at least one culm was flowering in 77.3%. The highest number of flowering culms in one hoop was 96 and the average was 13.7 flowering culms per hoop which equates to 30.4 m^2. On the adjacent burnt area, while *Machaerina* was also encountered at 100% of sampling point (n=28), no flowers were encountered although they were observed in the area very occasionally. *Schoenus* was present in the hoop three times in the burnt area (13.6%) and once in the unburnt area (3.6%). *Schoenus* flowers were recorded twice on plants in the burnt area but not on plants growing in the unburnt area. While this survey focussed only on the sedges, mānuka seedlings were also observed to be flowering and producing seed capsules on the burnt area sixteen months post-fire.

Figure 2.12. *Machaerina teretifolia* in flower at the 2017 burn site. Photo taken January 2020, 26 months post-fire.

2.3.5 Recovery of *Empodisma* cluster roots and standing litter layer

Empodisma's peat-forming cluster roots were not present at any points on the 2017 burn site. However, they were apparent at every point at the other sites, indicating that a burnt site recovers peat-forming function by at least 14 years.

ANOVA found that the height of the standing litter layer differed significantly between sites (F = 14.52, $p < 0.001$). The litter layer was completely absent at the 2017 burnt site, but averaged 37.5 cm in height in the adjacent unburnt area (Figure 2.13). At the 2005 site, the standing litter layer reached an average of 44.3 cm on the burnt area and 41.8 cm on the unburnt area (Figure 2.13). At the 1974 site, it was 54.1 cm above the peat surface, on average, which was significantly different to the other sites (Figure 2.13; Table 2.3). Other combinations of sites were not significantly different (Table 2.3). The 2017 burnt site was not included because it did not have a standing litter layer.

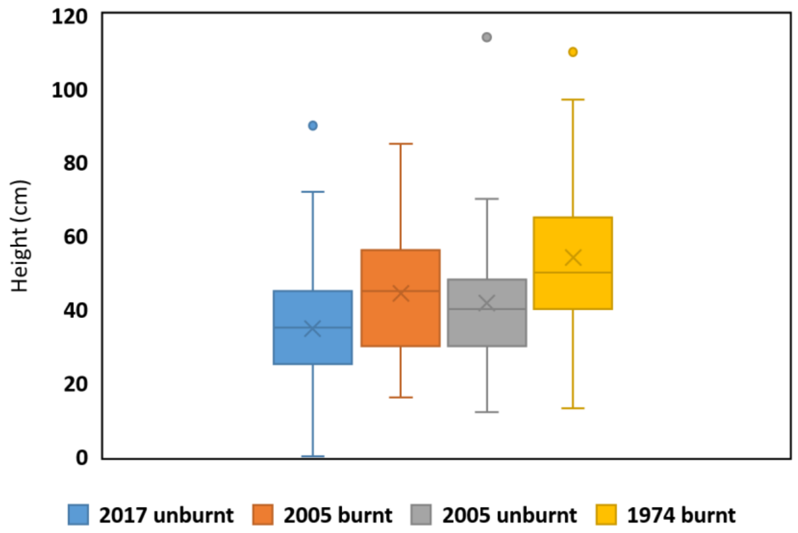


Figure 2.13. Box plot summaries of the height of the standing *Empodisma* litter at all sites it was present. Box plots show the median, upper and lower quartiles, and outliers. Means are marked by a cross.

Table 2.3. Tukey HSD pairwise comparisons of the height of the *Empodisma* standing litter layer between sites. Values in bold are significant ($p < 0.05$)

Site 1	Site 2	*p*
2017 unburnt	2005 burnt	0.133
2017 unburnt	2005 unburnt	0.570
2017 unburnt	1974 burnt	**0.000**
2005 burnt	2005 unburnt	0.919
2005 burnt	1974 burnt	**0.019**
2005 unburnt	1974 burnt	**0.003**

2.3.6 Environmental measures in *Sporadanthus*-dominated areas

The nutrient data indicate that areas where *Sporadanthus* is present are richer in nutrients. While not statistically significant, N, P, and K concentrations were all higher in surface peat collected from the *Sporadanthus*-dominated area than the neighbouring *Empodisma*-dominated area (Table 2.4). Foliar N and δ^{15}N levels were significantly higher from foliage growing in the Sporadanthus-dominated area, and P concentrations were higher but not significant (Table 2.5). The water table was significantly deeper in the *Sporadanthus*-dominated zone (mean = 16.3 cm) compared to the *Empodisma*-dominated zone (mean = 10.3 cm; t test, $p = 0.003$).

Table 2.4. Nutrient levels found in surface peat (0-5 cm) taken at the 1974 burn site from areas where *Sporadanthus* is dominant and where it is absent. Values in bold are significant ($p < 0.05$).

Vegetation type	**C (mg cm^{-3})**	**N (mg cm^{-3})**	**P (mg cm^{-3})**	**K (mg cm^{-3})**
Sporadanthus present	25.97 ± 2.35	0.419 ± 0.065	0.0067 ± 0.0014	0.0130 ± 0.0032
Sporadanthus absent	22.22 ± 0.73	0.357 ± 0.012	0.0042 ± 0.0008	0.0071 ± 0.0013
p (t test)	0.202	0.401	0.210	0.160

Table 2.5. Nutrient levels found in *Gleichenia dicarpa* foliage taken at the 1974 burn site from areas where *Sporadanthus* is dominant and where it is absent. Values in bold are significant ($p < 0.05$).

Vegetation type	**C (%)**	**N (%)**	**δ^{15}N (‰)**	**P (%)**	**K (%)**
Sporadanthus present	46.79 ± 0.09	0.855 ± 0.031	-14.55 ± 0.31	0.030 ± 0.002	0.342 ± 0.019
Sporadanthus absent	47.18 ± 0.2	0.775 ± 0.010	-16.89 ± 0.50	0.025 ± 0.001	0.440 ± 0.042
p (t test)	0.111	**0.039**	**0.004**	0.102	0.066

2.4 Discussion

Fire led to a temporary shift from an *Empodisma*-dominated community to *Gleichenia* dominance (Table 2.1; Figure 2.9 a, b). *Gleichenia* and the sedge species, *Machaerina* and *Schoenus*, are capable of vegetative resprouting from underground rhizomes and have been observed to dominate the early stages of recovery in similar studies (Clarkson, 1997; McQueen & Forester, 2000). In other studies, though, *Gleichenia* was slower to recover (Timmins, 1992; Johnson, 2001), possibly due to a lower water table which offered less protection from the lethal heat of fire. Both the 2017 and 2005 fires occurred during spring when the water table was likely to be high, enabling this vegetative response. *Empodisma*'s rhizomes are less likely than *Gleichenia*'s to provide protection from fire, and recovery is usually by the slower method of germination from seed dispersing onto the site from nearby unburnt vegetation (Clarkson, 1997). By 14 years, *Empodisma* had regained its dominance, leading to reduced percentage cover of *Gleichenia* (Table 2.1; Figure 2.9 a, b).

By 14 years, restiad bog vegetation had returned to approximate pre-burn species composition, although several differences in relative abundance remained. While *Empodisma* and *Gleichenia* resembled their previous cover, mānuka, *Epacris,* and the sedge species, *Machaerina* and *Schoenus,* were relatively more abundant (Table 2.1; Figure 2.9 c, d). The high cover of mānuka can be attributed to its serotinous release of seeds – a trait which is strongest in mānuka communities inhabiting sites with long histories of fire, such as restiad bogs of the North Island (Newnham *et al.*, 1995; Battersby *et al.*, 2017a). The higher cover of *Epacris* after 14 years (Table 2.1; Figure 2.9 c, d) is attributable to the fire-stimulated germination of dormant seed stored in the peat. This hypothesis is supported by an experiment which found *Epacris* seedlings to emerge at an average density of 3143 ± 452 seedlings m^{-2} from surface peat (0-5 cm depth) collected from Kopuatai (see Chapter 4). The increase in sedge cover can be explained by their significant increase in flower production following fire, leading to high numbers of seed set when conditions are conducive to seedling growth – i.e. light is more available. Despite previous reports of increased flowering of sedge species after fire in restiad bogs, and increased dominance, this is the first time such an effect has been demonstrated quantitatively. Clarkson (1997) observed *Machaerina teretifolia* and *Schoenus brevifolius* in flower six months after fire at Whangamarino. Timmins (1992) discussed how *Machaerina* increased its dominance after fire at several sites around New Zealand including South Westland pakihi (Wardle, 1977; Merton, 1986), Moanatuatua (Matheson, 1979), and Kopuatai (de Lange, 1989), although this effect was attributed to their rhizomatous advantage. It is more likely that these increases are actually related to post-fire flowering responses, although the vegetative recovery ability is a necessary prerequisite for fire-stimulated flowering (Lamont & Downes, 2011).

The height structure of regenerating plant communities had largely resumed its previous form by 14 years, although some difference remained. The presence of *Epacris* at the 2005 burn site at lower heights (mean = 1.1 m) than on the adjacent unburnt area (mean = 1.9 m; Figure 2.9) indicates that it takes longer than 14 years to recover to the heights seen on the unburnt area. The average growth rate of *Epacris* growing on the burn was 0.08 m $year^{-1}$, which would suggest that another 10 years would be required to reach the average height on the unburnt area. Mānuka was not recorded in the sampling area adjacent to the 2005 burn, suggesting that all plants remaining from the last fire had died by that time. As mānuka appears to have a similar growth rate as *Epacris* (Figure 2.9 c), it would probably also reach its maximum height structure after approximately 25 years.

The long-term recovery trajectory following fire, particularly in *Sporadanthus*-dominated areas, remains mysterious. Comparing the results from the current study to a survey done at approximately the same location 20 years post-fire (Figure 2.14; de Lange *et al.,* 1999) shows that mānuka and *Sporadanthus* have grown taller by 45 years (Figure 2.9 e), but also suggests regeneration of other species, namely *Gleichenia, Machaerina,* and *Epacris*, within the past 25 years. This may, however, be a result of different sampling methods and slightly different sampling areas between the two surveys. Based on the data from the 2017 and 2005 burn sites, the sedge and shrub species tend to increase their dominance only following disturbance. After some period without fire, they become less common (Table 2.1; Figure 2.9). However, the high abundance of *Schoenus,* mānuka, and *Epacris* at the 1974 burn site (Table 2.1; Figure 2.9 e) contradicts this. Mānuka, in fact, has a higher cover at this site than in any other sampling area (Table 2.1). These patterns may relate to differences in fire history. Based on the view that *Sporadanthus* is a fire-sensitive species (Dickinson, 1974; Newnham *et al.*, 1995; de Lange *et al.*, 1999), it may be assumed that the sites still dominated by *Sporadanthus* were burnt less often during periods of land clearing than areas currently dominated by *Empodisma*. Where burning was repetitive, *Sporadanthus,* mānuka and *Epacris* may not have had time to recover to mature plants by the time of the next fire, leading to their decline at these sites (cf. Noble & Slatyer, 1980). Prior to the most recent fire of the mid 1970s, the *Sporadanthus*-dominated sites may have been burnt relatively less and have more mature plants and rich seed banks to contribute propagules to the regenerating community, resulting in the higher abundances of these species detected here. It is also possible that mānuka and *Epacris* have retained their dominance at the 1974 burn site by regenerating in patches of lower restiad cover. Although the current data on the *Empodisma* canopy and its standing litter layer do not support this (Figure 2.9; Figure 2.13), the cover may have been more patchy several years ago.

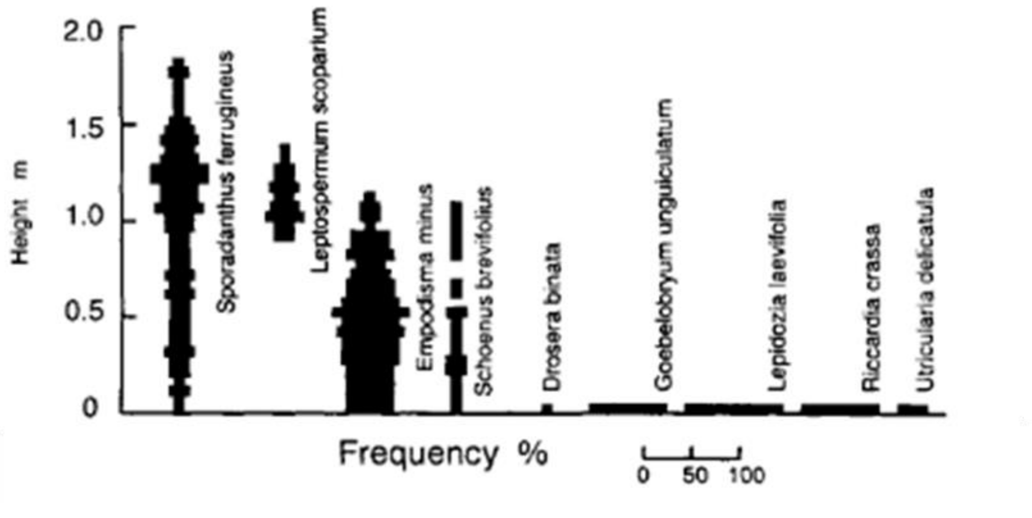


Figure 2.14. Height frequency diagram showing structure and composition at the 1974 burn site in 1995 (de Lange *et al.*, 1999).

Sporadanthus, once established, appears to alter both community structure and nutrient cycling. At the 1974 burn site, several species reached greater heights when growing in *Sporadanthus*-dominated vegetation than in adjacent vegetation lacking *Sporadanthus* (Figure 2.10). This can be explained for *Empodisma* and *Gleichenia* by the way they use the tall *Sporadanthus* plants as support structures. However, this same explanation does not apply to mānuka and *Epacris* (Figure 2.10). While it is plausible that the shrubs are growing taller to access sunlight, alternatively the difference in height is due to nutrient enhancement facilitated by *Sporadanthus*. Peat and foliage comparisons both suggest that nutrients are more abundant on *Sporadanthus*-dominated areas compared to adjacent areas where it is absent (Table 2.4; Table 2.5). The higher uptake of the heavier ^{15}N isotope by *Gleichenia* could indicate a lower P limitation, i.e. more plant-available P, in the *Sporadanthus*-dominated area because where P is limited, plants tend to show discrimination against the heavier isotope (Fry *et al.*, 2000; McKee *et al.*, 2002; Clarkson *et al.*, 2005). Clarkson *et al.* (2009) demonstrated that *Sporadanthus* and *Empodisma* have different mechanisms for obtaining nutrients. *Empodisma*'s cluster roots occupy the surface 5 cm and are well-adapted to preferentially receive N from rainwater, whereas *Sporadanthus* occupies a deeper root zone and receives most of its nutrients via mineralisation at greater depths (Clarkson *et al.*, 2009). Compared to an *Empodisma*-dominated system which relies on rainfall for nutrients, the nutrients that *Sporadanthus* incorporates into its biomass from deeper peat layers, and eventually deposits as litter, may be significant for plant growth. Water level measurements taken at the 1974 burn site also indicate that the water table is deeper in the *Sporadanthus*-dominated zone. The cause of this is likely related to greater biomass deposition where *Sporadanthus* is present. Greater exposure to oxygen, however, may cause higher rates of aerobic decomposition, leading to an increase in available nutrients. Essentially, these findings suggest that *Sporadanthus* can increase the fertility of a site by transporting nutrients from deeper layers of peat to the surface. This potential ecological engineering role of *Sporadanthus* has not been suggested before and further research is required to confirm this hypothesis.

Peat formation recovered within 14 years. The cluster roots of *Empodisma* had recovered by 14 years post-fire, indicating that peat formation of that area had been restored. The standing litter layer of *Empodisma*, which is thought to play an important role in controlling the water balance at Kopuatai (Campbell & Williamson, 1997), had also reached pre-fire levels by 14 years (Figure 2.13). The litter layer was significantly higher at the 1974 burn site than at all other sites (Table 2.3) due to the presence of *Sporadanthus* at that site, which *Empodisma* uses as a support to grow taller.

2.5 Conclusion

In conclusion, fire at Kopuatai Bog caused changes in species composition and structure, which largely return to pre-fire levels by 14 years. Persisting differences related to the higher cover of (a) the sedge species, which this study reveals increase their dominance via fire-stimulated flowering; (b) mānuka, which becomes more abundant via serotiny; and (c) *Epacris*, which recovers from a peat seed bank. These findings demonstrate that restiad bog communities are more responsive to fire than previously thought. The mechanisms controlling recovery in *Sporadanthus*-dominated areas are less clear, although may relate to the spatially variable history of burning at Kopuatai. Comparison of plant communities and environmental properties between areas or "patches" where *Sporadanthus* is present and adjacent areas where it is absent revealed that *Sporadanthus* may be enhancing nutrient availability by pumping nutrients from deeper peat layers.

Chapter Three

Effects of fire on the physical and chemical environment

3.1 Introduction

A single fire event can temporarily but substantially alter the physical and chemical environment at a site, usually resulting in conditions that lead to enhanced seedling recruitment, survival and growth (Whelan, 1995; Pyne *et al.*, 1996; DeBano *et al.*, 1998). Perhaps foremost is the removal of vegetation, greatly increasing light availability at the soil surface. The associated loss of shading and insulating qualities of the vegetation cover can also affect soil and air temperature regimes, generally leading to greater daily temperature fluctuations near the soil surface (Whelan, 1995; Geiger *et al.*, 2009). Fire necessarily results in a net loss of nutrients from an ecosystem as nutrients in biomass are volatilised and lost to the atmosphere or carried away as particulate matter by wind or in smoke (Christensen, 1994). Nutrients may also be volatilised from soil, particularly in intense fires or fires that burn into substrate layers (Christensen, 1994). Despite these losses, however, site fertility is typically enhanced following fire, primarily due to deposition of non-volatilised nutrients in ash but also from increases in mineralisation rates (Christensen, 1977; Pyne *et al.*, 1996; Neary *et al.*, 1999; Dikici & Yilmaz, 2006). Such alterations are thought to be responsible for various physiological responses of plants after fire such as often-observed increases in growth rates, flowering, and germination of soil-stored seeds (Gill, 1981; Bond & van Wilgen, 1996). The relative changes in light levels, temperature regimes, and nutrient availability vary, however, depending on properties of the pre-fire vegetation, soil, and landscape, as well as the fire itself (Neary *et al.*, 1999). New Zealand restiad peatlands are well known to be prone to natural burning and have long records of fire (Newnham *et al.*, 1995; McGlone, 2009; Perry *et al.*, 2014). Despite this, little research has been done on the fire-driven physical and chemical changes in these ecosystems.

The environmental effects of fire vary widely depending on site and vegetation properties, as well as characteristics of the fire itself (DeBano *et al.*, 1998; Neary *et al.*, 1999; Knicker, 2007). For example, fire intensity strongly influences the relative losses and gains in nutrient availability. Nitrogen (N) is the element most prone to volatilisation, with losses starting at ~200°C, and over half of the N content in organic matter being volatilised by 500°C (Neary *et* *al.*, 1999). Higher temperatures, in excess of 760°C, are needed to vaporise phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), and sodium (Na); so these elements are typically deposited in ash during low or moderate intensity fires (Neary *et al.*, 1999). Trace metals such as the micronutrients copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) can generally be expected to accumulate in soil, although a lack of studies limits our knowledge of their responses to fire, and results are variable (Pyne *et al.*, 1996; Certini, 2005; García-Marco & González-Prieto, 2008). Aside from volatilisation, nutrients may be depleted by convection in smoke columns, wind, leaching, or via conversion to insoluble oxidised forms (Raison *et al.*, 1985). Biogeochemical cycling can be impacted by post-fire changes in biological (e.g. microbial activity) or non-biological (e.g. by increased pH) processes, sometimes leading to increases in plant-available forms of certain nutrients, even if their total concentrations are unaffected (Neary *et al.*, 1999; Knicker, 2007). This is particularly common for N and P (Carballas *et al.*, 1993; Cade-Menun *et al.*, 2000; Knicker, 2007).

The impacts of fire on peat nutrient availability have not been measured in restiad bogs of New Zealand and are not well-known for peatlands, globally. The few studies that do address the effects of fire on nutrient availability in organic peat soils have been on degraded *Sphagnum*-dominated peatlands of the Northern Hemisphere (e.g. Wilbur & Christensen, 1983; Smith *et al.*, 2001; Dikici & Yilmaz, 2006; Wang *et al.*, 2015). Research into the links between fire and fertility in restiad bogs is necessary to support or disprove speculations in the literature that fire leads to nutrient increases in these ecosystems. For instance, “Fires release locked up nutrients within the bog vegetation back into the surrounding environment and provided these are not blown from the system, removed by flooding, or waterlogging, there is a brief period of nutrient enrichment” (de Lange, 1989, p. 92). This enrichment is hypothesised to facilitate temporary colonisation by exotic adventives and normally rare species (Clarkson, 1997; Norton & de Lange, 2003) which “take advantage of increased nutrient levels as well as higher light levels that occur in peatlands after fire” (Clarkson, 1997, p. 176).

In this chapter, I assess the impacts of fire on chemical and physical variables near the peat surface of a restiad bog. I set out to quantify the net changes in total and available nutrients, the increase in surface solar radiation, and the changes to daily temperature regimes over the course of a year. Measurements were taken at sites of various known burn dates, to determine the rates at which nutrient and light levels revert to pre-fire conditions. This will enable stronger inferences about the relative influence of nutrient, light, and temperature changes on post-fire changes in plant vegetative growth and reproduction, species diversity, and vegetation composition.

3.2 Methods

3.2.1 Site description

Environmental data were collected from three sites of known burn date (2017, 2005, 1974) within Kopuatai Bog, located in the Waikato region of the North Island of New Zealand. The 2017 and 2005 fires were extinguished quickly, leaving burn scars of less than 8,000 m^2 area. The 1974 fire burnt a significant, but unknown, portion of the approximately 100 km^2 bog area and is the last known event of a series of fires that swept across Kopuatai during conversion of the surrounding the area to agricultural land (Irving *et al.*, 1984; de Lange *et al.*, 1999). The 2017 (-37.3764, 175.5233) and 2005 (-37.447914, 175.53508) fires occurred in the "wire rush rushland" vegetation community type, which consists of a canopy up to approximately 1 m high dominated by the restiad *Empodisma robustum* (wire rush; henceforth *Empodisma*) with sedges *Machaerina teretifolia* (henceforth *Machaerina*), *Schoenus brevifolius* (henceforth *Schoenus*) and tangle fern *Gleichenia dicarpa* (henceforth *Gleichenia*) also present, and *Leptospermum scoparium* (mānuka) and *Epacris pauciflora* (henceforth *Epacris*) as occasional emergents (Reeves *et al.*, 2009; Chapter 2). The site within the 1974 burn area where sampling was carried out (-37.371175, 175.553673) is currently classified as "*Sporadanthus ferrugineus* rushland", due to its dominance of greater wire rush, *Sporadanthus ferrugineus* (henceforth *Sporadanthus*), in stands up to approximately 2.5 m tall. *Empodisma* and *Schoenus* are abundant amongst stands and mānuka and *Epacris* are occasional emergents (Reeves *et al.*, 2009; Chapter 2).

3.2.2 Light availability

The LAI-2200C Canopy Analyzer (LI-COR 2016, Lincoln, Nebraska, USA) was used to measure diffuse light availability beneath the plant canopy at the 2017 and 2005 burn sites and adjacent unburnt areas. Light measurements were taken during vegetation sampling at randomly determined points along a number of transects (see Chapter 2 for more detail). 36

measurements were made at the 2017 burn site (N_{burnt} = 18, $N_{unburnt}$ = 18) and 32 at the 2005 burn site (N_{burnt} = 18, $N_{unburnt}$ = 14). Diffuse irradiance under the canopy was calculated by the LAI-2200C as a fraction of light simultaneously measured by another sensor which has an unobstructed view of the sky. The output values range between 0% (complete obstruction of light by vegetation) to 100% (open sky). To mitigate scattering error, a scattering correction was applied to all measurements obtained under direct sunlight or non-uniform cloud cover (Kobayashi *et al.*, 2013). To determine whether light penetration differed between the four areas (2017 burnt, 2017 unburnt, 2005 burnt, 2005 unburnt), analysis of variance (ANOVA) was carried out, followed by post-hoc Tukey's honestly significant difference (HSD) tests.

3.2.3 Air temperature

To record air temperature near the peat surface, temperature dataloggers (Thermochron iButton, Sunnyvale, California, USA) were installed on the burnt and adjacent unburnt areas of the 2017 burn site. Four iButtons were installed on the burnt area and five on the unburnt area, with their positioning decided by randomly selecting a subset of vegetation sampling points (see Chapter 2 for detail). They were mounted on steel rods approximately 20 cm from the peat surface. To minimise the effects of radiative heating and chilling, radiation shields made from stacked plastic plates, three above the iButton and two below, were attached (Figure 3.1). The iButtons were programmed to record air temperature, to the nearest 0.5°C, every four hours from February 15 2019 to January 18 2020, giving 338 days of temperature measurements. Two-way ANOVAs were carried out to measure how the fire (burnt vs unburnt), time of year (month), and their interaction, affect daily maximum, minimum and average temperatures averaged across months.

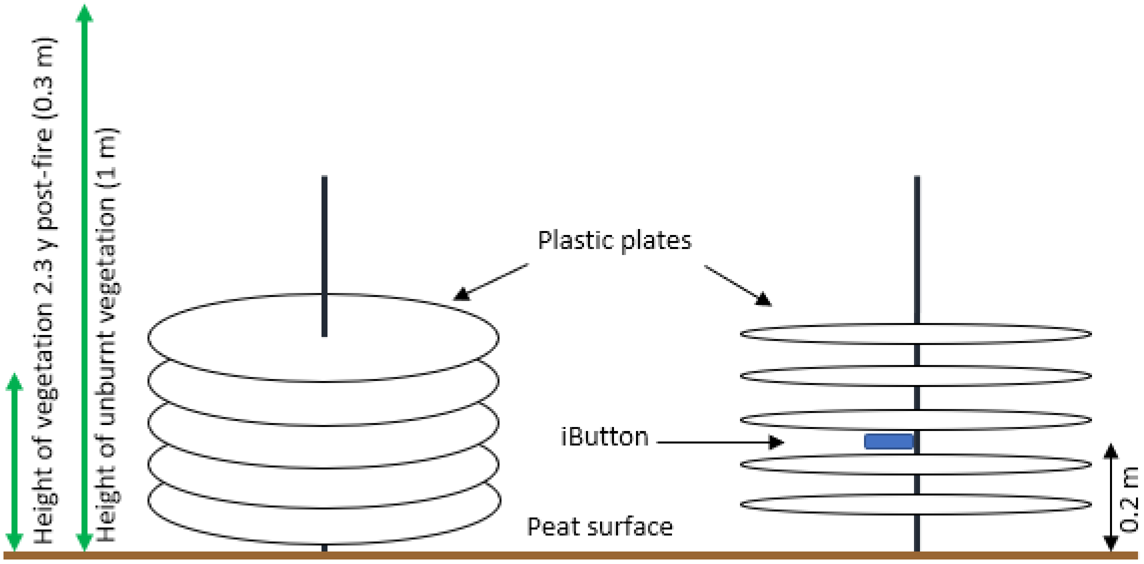


Figure 3.1. Deployment of temperature-recording iButtons in the field, showing white plastic plates acting as a radiation shield, and the relative heights of the iButtons and burnt and unburnt vegetation at the 2017 burn site at the time of instalment.

3.2.4 Peat properties – inherent site differences

To assess inherent site differences between the locations of the 2017, 2005, and 1974 fires, peat qualities were analysed in the top 5 cm of peat. At five random points at each site (this was restricted to the unburnt area at the 2017 burn site), surface peat decomposition status was assessed using the von Post scale (von Post & Granlund, 1926). This involved squeezing a handful of peat and matching visual attributes such as the colour of the water and peat structure and texture to a von Post rating from 1 (little to no decomposition) to 10 (complete decomposition). At each point, two peat samples were collected using a cylindrical stainless-steel corer (6 cm diameter, 5 cm height). The first core was dried at 105°C and bulk density determined gravimetrically. The second core was divided in half vertically. 10 g fresh weight of peat was taken from one half, mixed with 25 ml of distilled water and left for one hour before reading with a standard pH meter. The second half was dried at 55°C for 48 hours and analysed for C, N, P, and K (see peat nutrient section below). To assess differences in sites, ANOVAs were performed on each peat quality, followed by post-hoc Tukey’s HSD tests.

To characterise the site of the 2017 fire, the water table level was monitored over a period of 11 months from February 14 2019 to January 19 2020. This involved installing a dip well containing an automatic pressure transducer (INW level scout, Seametrics) programmed to take water level readings every 30 minutes. These measurements were correlated to rainfall readings taken from an eddy covariance tower in the centre of Kopuatai.

3.2.5 Peat nutrients

To determine how fire affected nutrient availability, nutrients in surface peat samples (0-2 cm depth) were compared between samples collected two weeks after the 2017 fire, two years after the 2017 fire, and from the adjacent unburnt area. A depth of 2 cm was chosen to maximise the chances of detecting any changes due to ash deposition which occurred at the peat surface.

Two-week post-fire sampling involved collection of surface scrapes (approximately 0-3 cm depth) from 10 random points along a single transect which ran north-south through the centre of the burn. These were frozen for two years until the analysis time, after which they were defrosted and subsampled to 2 cm depth. The later set of samples was collected approximately two years (26 months) post-fire on January 19 2020. Sampling was randomised by choosing a random set of 10 vegetation surveying points (see Chapter 2) from both the burnt area and the unburnt area. At each peat sampling point, two samples were taken using a cylindrical stainless-steel corer (6 cm diameter, 5 cm height).

In the lab, the first set of samples collected two years after fire was dried at 105 °C and bulk density determined gravimetrically. For the samples collected two years post-fire, which were of unknown volume, average bulk density from the samples collected two years post-fire was used later to convert nutrient concentrations to mg cm^3. Like the two-week post-burn samples, the second set of samples were cut horizontally to bring the depth to 2 cm from the surface, after which they were dried at 55°C for 48 hours.

Samples were then ground to a fine powder in a ball mill. Sub-samples were analysed at the University of Waikato Stable Isotope Unit for C and N concentrations by an Elementar Isoprime 100 analyser. Other elements of interest, including P, S, Na, Mg, K, Ca, Fe, Mn, Cu, and Zn, were analysed by ICP-MS at the Waikato Mass Spectrometry Facility following digestion into an aqueous solution. The digestion process involved ashing 0.5 g of representative dried ground sample at 450°C, following Yafa & Farmer (2006). The ashed samples were then transferred to 50 ml Falcon tubes and 1 ml of HNO_3 (65%) was added. The samples were then digested on a heater block for two hours with the lids loosely attached to minimise evaporation. Following this, type one water was added up to 50 ml, diluting each solution to 2% HNO_3. Each solution was then filtered using a 0.45 micron filter before being analysed by ICP-MS. To determine significance of nutrient differences between the samples collected two weeks post-fire, two years post-fire and from the unburnt area, ANOVAs were carried out for each nutrient, followed by post-hoc Tukey's HSD tests.

3.2.6 Foliar nutrients

Foliage samples from two common bog species, *Gleichenia dicarpa* (tangle fern) and *Machaerina teretifolia* (bog sedge), were collected from burnt and adjacent unburnt areas at the 2017 burn site (16 months post-fire) and the 2005 burn site (14 years post-fire). At the 1974 burn site (45 years post-fire), *Machaerina* was uncommon so only *Gleichenia* was collected. The 1974 burn site also lacked a comparable unburnt area. Five samples were taken from each sampling area by randomly selecting a number of vegetation sampling points (see Chapter 2) and collecting foliage samples from the nearest *Gleichenia* and *Machaerina* plants. An effort was made to select young-looking green foliage to control the effect of plant tissue age on nutrient levels (Field & Mooney, 1983).

Foliage samples were dried immediately upon return from the field at 55°C for 48 hours. Stems were removed from *Gleichenia* and sheathing bracts were removed from *Machaerina* culms after which the dry foliage was ground to a fine powder in a ball mill. Sub-samples were analysed in the same way as peat for total C and N, and $\delta_{15}N$ was also analysed by a fully automated Europa Scientific 20/20 isotope analyser. Other elements of interest (P, S, Na, Mg, K, Ca, Fe, Mn, Cu, Zn) were analysed by ICP-MS. The plant tissue digestion process involved weighing a 200 mg sub-sample of dried ground foliage into a Falcon tube and adding 1 ml of HNO_3 (65%) and 0.4 ml of H_2O_2 (30%). This was left to pre-digest overnight. The next day, the Falcon tubes were heated on a heating block at 80°C for one hour with the tube caps loosely attached. This was followed by 30 minutes of cooling, another 0.4 ml addition of H_2O_2, and another 30 minutes of re-heating. This last step was repeated twice more. Finally, the solution was brought to 50 ml (2% HNO_3) by adding type one water. 15 ml of solution was then filtered using a 0.45 micron filter and analysed by ICP-MS.

Nested ANOVAs were used to test the effects of fires on foliar nutrients. Burnt or unburnt areas were nested within the 2017 and 2005 sites. The 1974 burn site data was not included in these analyses as it lacked an unburnt area. T tests were also carried out to determine within site differences between foliar nutrient levels from burnt and unburnt areas.

3.3 Results

3.3.1 Light availability

At the time of sampling (16 months post-fire at the 2017 burnt area), diffuse light availability was significantly higher in the 2017 burn area (mean = 19.5%) than the adjacent unburnt area (mean = 0.1%) or either the 2005 burnt (mean = 0.2%) or unburnt (mean = 0.1%) areas (Figure 3.2).

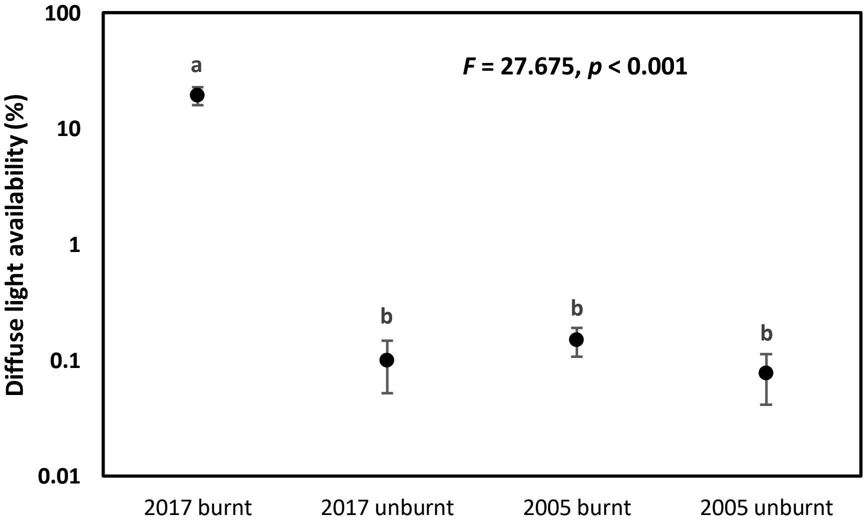


Figure 3.2. Mean diffuse light availability at the peat surface of the 2017 burnt site (approximately 16 months post-fire) and adjacent unburnt site, and the 2005 burnt site (approximately 14 years post-fire) and adjacent unburnt site. ANOVA results are displayed. Points with the same value above them are not statistically different based on Tukey's HSD test at $p < 0.05$. Error bars represent one standard error.

3.3.2 Air temperature

Mean daily air temperatures taken over 11 months within the 2017 burn area exceeded those in the unburnt area by an average of 1.4°C (Figure 3.3). Two-way ANOVA found a strong effect of the burn ($p < 0.001$) and time of year ($p < 0.001$) but no interaction effect ($p = 0.249$). Mean monthly maximum air temperatures were an average of 3.9°C higher on the burnt than the unburnt area throughout the year (Figure 3.3). There was a significant effect of the burn ($p < 0.001$) and of time of year ($p < 0.001$), but no significant interaction ($p = 0.102$). Mean monthly minimum temperatures differed between burnt and unburnt areas by an average of 0.6°C over the year and were significantly affected by the burn ($p = 0.013$) and the time of year ($p < 0.001$). While minimum temperatures were higher on the burnt area during warmer months (October – March), they were lower during colder months (May – August) (Figure 3.3). However, this interaction between time of year and burn was only marginally significant ($p = 0.067$). The number of air frosts recorded (minimum temperature < 0°C) was 61.5 on the burnt area and 58.6 on the unburnt area.

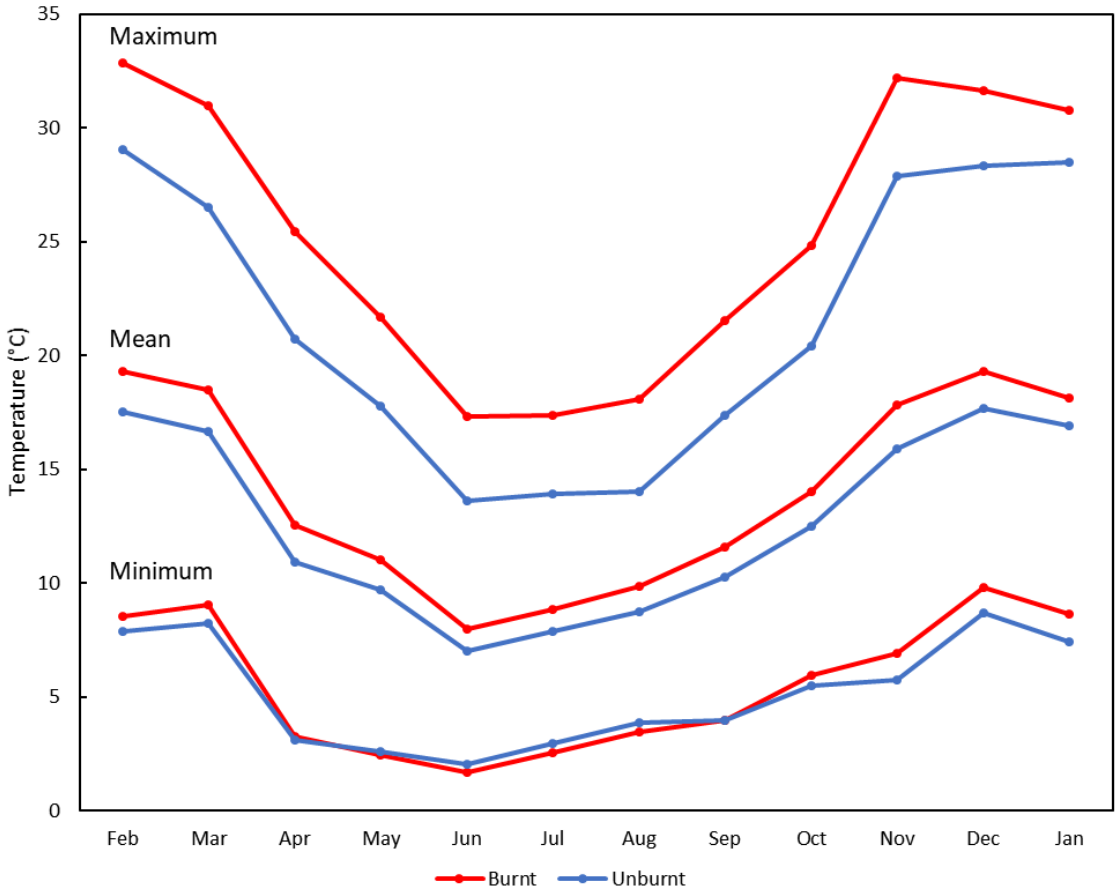


Figure 3.3. Mean monthly maximum, minimum, and mean air temperatures from the 2017 burnt and adjacent unburnt area from February 2019 to January 2020.

3.3.3 Peat properties – inherent site differences

ANOVAs performed on 0-5 cm deep peat samples revealed that the 2017 site was more fertile than the 2005 and 1974 burn sites (Table 3.1). Compared to other sites, the site where the

2017 fire occurred had a higher average von Post rating, bulk density, and N, P, and K concentrations, although K concentrations did not significantly differ to the 2005 burn site (Table 3.1). The 1974 site appears to be the most nutrient-poor, although nutrient levels did not significantly differ compared to the 2005 site (Table 3.1). There were no significant differences in pH between sites (Table 3.1).

Table 3.1. Mean values and ANOVA results of physical and chemical properties of peat (0-5 cm depth) collected from all three sites. The data summarised here is from the unburnt area only at the 2017 burn site, whereas at the 2005 site, site comparison samples were taken from both the burnt and unburnt areas. Values followed by the same number by row are not statistically different based on post-hoc Tukey's HSD tests at $p < 0.05$. *p* values in bold are significant ($p < 0.05$).

Peat property	**2017 burn site (unburnt area)**	**2005 burn site**	**1974 burn site**	***p* value (ANOVA)**
Von Post	3.4 a	2.2 b	2.0 b	**< 0.001**
Bulk density (g cm^{-3})	0.088 a	0.049 b	0.056 b	**0.003**
pH	4.30	4.47	4.48	0.189
C (mg cm^{-3})	34.89 a	22.92 b	24.72 ab	**0.020**
N (mg cm^{-3})	1.195 a	0.434 b	0.397 b	**0.001**
P (mg cm^{-3})	0.028 a	0.010 b	0.006 b	**0.001**
K (mg cm^{-3})	0.033 a	0.027 ab	0.010 b	**0.033**

3.3.4 Peat nutrients

ANOVA found significant differences between time since fire in P, S, Ca, Mg, K, Na, Mn, Cu and Zn (Table 3.2). Post-hoc Tukey HSD tests revealed that these differences were all due to higher concentrations in peat collected two weeks post-fire compared to peat collected two years post-fire or from the unburnt area (Table 3.2). Concentrations of N and Fe were not significantly different (Table 3.2). C:P and N:P levels were significantly higher two weeks after the fire, reflecting the higher levels of P immediately after the fire (Table 3.2).

Table 3.2. Mean values ± one standard error and significance levels (*p*, ANOVA) of the measured properties of peat (0-2 cm depth) from the Kopuatai 2017 burn site. Values sharing the same letter are not statistically different at $p < 0.05$. Values in bold are significant ($p < 0.05$)

	Time since fire			
	2 weeks (n=10)	**2 years (n=10)**	**Unburnt (n=10)**	***p* (ANOVA)**
N (mg cm^{-3})	0.621 ± 0.032 *a*	0.712 ± 0.077 *a*	0.764 ± 0.135 *a*	0.544
P (mg cm^{-3})	0.025 ± 0.002 *a*	0.016 ± 0.002 *ab*	0.016 ± 0.003 *b*	**0.028**
S (mg cm^{-3})	0.055 ± 0.007 *a*	0.028 ± 0.003 *b*	0.030 ± 0.005 *b*	**0.002**
Ca (mg cm^{-3})	0.209 ± 0.023 *a*	0.064 ± 0.006 *b*	0.074 ± 0.008 *b*	**< 0.001**
Mg (mg cm^{-3})	0.136 ± 0.016 *a*	0.052 ± 0.004 *b*	0.054 ± 0.005 *b*	**< 0.001**
K (mg cm^{-3})	0.089 ± 0.010 *a*	0.033 ± 0.004 *b*	0.038 ± 0.003 *b*	**< 0.001**
Na (mg cm^{-3})	0.106 ± 0.007 *a*	0.056 ± 0.006 *b*	0.047 ± 0.004 *b*	**< 0.001**
Fe (mg cm^{-3})	0.045 ± 0.005 *a*	0.065 ± 0.005 *a*	0.065 ± 0.013 *a*	0.214
Mn (µg cm^{-3})	12.765 ± 2.328 *a*	0.673 ± 0.114 *b*	1.275 ± 0.361 *b*	**< 0.001**
Cu (µg cm^{-3})	0.123 ± 0.008 *a*	0.067 ± 0.007 *b*	0.073 ± 0.015 *b*	**0.001**
Zn (µg cm^{-3})	1.417 ± 0.214 *a*	0.420 ± 0.045 *a*	0.449 ± 0.040 *a*	**< 0.001**
C:N	49.75 ± 2.69 *a*	45.87 ± 3.01 *a*	46.06 ± 4.25 *a*	0.662
C:P	1341 ± 158 *a*	2058 ± 182 *ab*	2405 ± 383 *b*	**0.024**
N:P	27.66 ± 3.92 *a*	45.92 ± 4.81 *b*	52.22 ± 6.24 *b*	**0.006**

3.3.5 Foliar nutrients

Nested ANOVAs performed on the foliar nutrient data from the 2017 and 2005 burnt and unburnt sites found that fire (nested within site) altered several nutrient levels (Table 3.3). Fire significantly affected $\delta^{15}N$, Mn, and Zn levels in both *Gleichenia* and *Machaerina*, while N, Na, and Cu were significantly affected in *Gleichenia* only, and S, Mg, K, Ca, and Fe were significantly affected in *Machaerina* only (Table 3.3). C and P levels were not significantly affected by fire in either species (Table 3.3).

Several nutrients were higher in foliage from the 2017 burn site than in that from the adjacent unburnt area (Figure 3.4). In both species, $\delta^{15}N$ levels (Figure 3.4 b) were significantly higher in the 2017 burnt area compared the unburnt area (t test, *p*(*Gleichenia*) = 0.002, *p*(*Machaerina*) = 0.004), whereas the differences at the 2005 site were insignificant ($p > 0.05$). Similarly, Mn concentrations (Figure 3.4 j) were significantly higher in foliage from the 2017 burnt area compared to the unburnt (*p*(*Gleichenia*) < 0.001, *p*(*Machaerina*) < 0.001), while differences at the 2005 site were insignificant ($p > 0.05$). Foliar Zn concentrations (Figure 3.4 l) were also significantly higher in samples from the 2017 burn area compared to the unburnt area (t test, *p*(*Gleichenia*) < 0.001, *p*(*Machaerina*) < 0.001). In *Machaerina* only, Mg ($p < 0.001$), Ca (p = 0.003), and S (p = 0.016) concentrations were higher in samples from the burnt area compared to the unburnt area (Figure 3.4 g, h, d). The only significant differences where nutrient levels were lower on the burnt area were in *Gleichenia* for Cu (p = 0.043) and K (p = 0.028) (Figure 3.4 k, f).

There were notably less significant differences between nutrient concentrations of foliage collected from the 2005 burnt area and the adjacent unburnt area, and none that appeared in both species (Figure 3.4). The significant differences that were found were all in *Machaerina* and were due to higher nutrient concentrations on the burnt area. They include K (p = 0.023), Fe (p = 0.021), Cu (p = 0.025), and Zn (p = 0.018).

Foliar levels of most nutrients from the 1974 burn site were similar to those found at the 2005 burn site (Figure 3.4). Possible exceptions to this were in $\delta^{15}N$ (Figure 3.4 b), K (Figure 3.4 f), and Cu (Figure 3.4 k) which were lower in the foliage samples from the 1974 burn site.

Table 3.3. Nested ANOVA testing effects of fire (burnt or unburnt) nested within site (2017 or 2005) on *Gleichenia dicarpa* and *Machaerina teretifolia* foliar nutrients. Values in bold are signficant ($p < 0.05$).

	Gleichenia		***Machaerina***	
	F	***p***	**F**	***p***
C	3.200	0.069	1.130	0.347
N	3.788	**0.045**	2.284	0.134
$\delta^{15}N$	11.949	**0.001**	15.900	**< 0.001**
P	0.467	0.635	3.181	0.069
S	1.655	0.222	5.202	**0.018**
Na	4.015	**0.039**	2.294	0.133
Mg	2.133	0.151	51.089	**< 0.001**
K	3.304	0.063	5.931	**0.012**
Ca	1.185	0.331	4.871	**0.022**
Fe	1.239	0.316	4.812	**0.024**
Mn	35.752	**< 0.001**	114.532	**< 0.001**
Cu	4.955	**0.021**	3.387	0.059
Zn	36.126	**< 0.001**	29.212	**< 0.001**

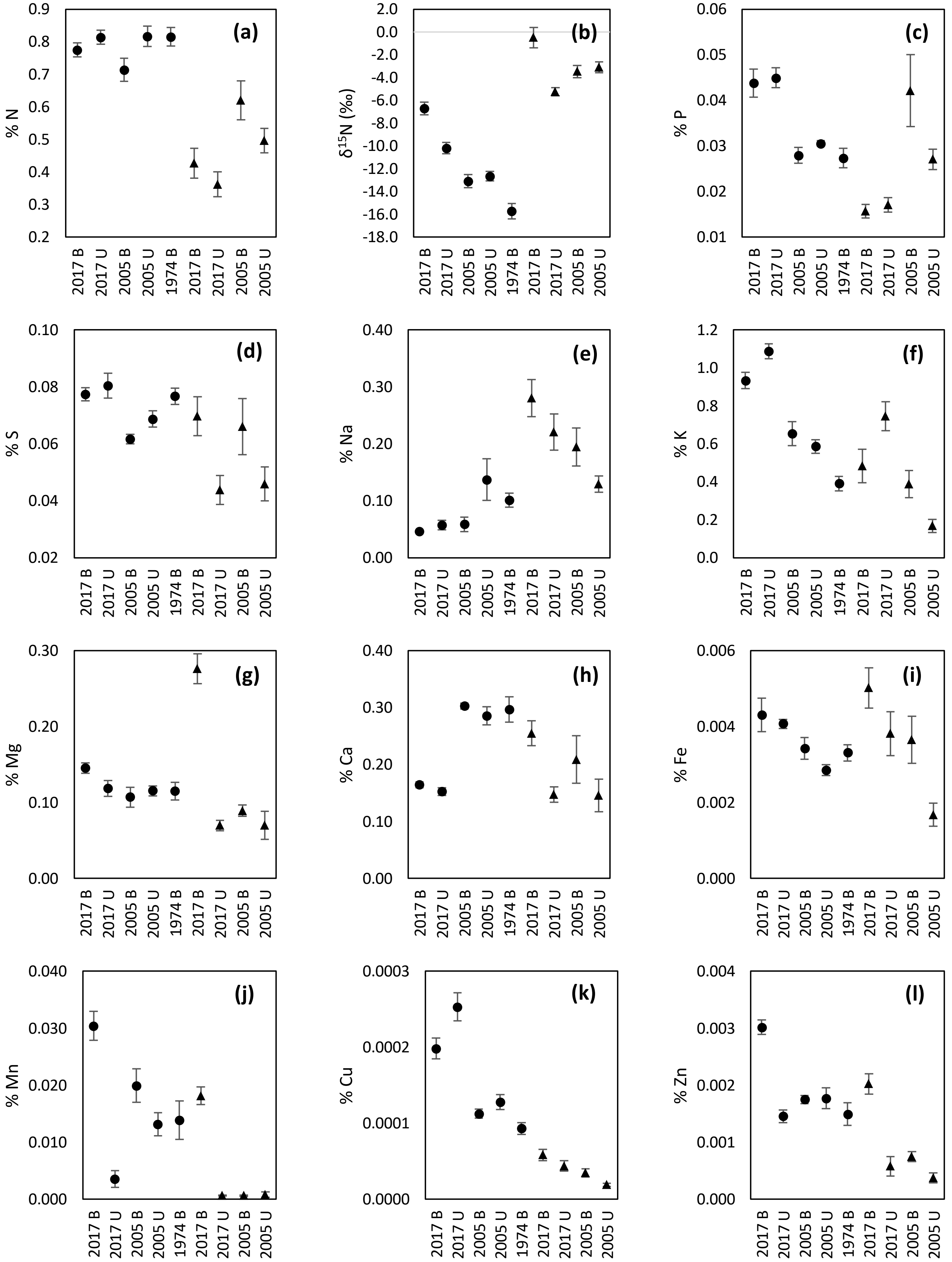


Figure 3.4. Nutrient concentrations *in Gleichenia dicarpa* (●) and *Machaerina teretifolia* (▲) foliage samples from sites burnt (B) in 2017, 2005, and 1974 and adjacent unburnt (U) sites (except for the 1974 burn site). Vertical bars represent one standard error.

3.3.6 Water table

The water table at the 2017 burn site averaged 25.8 cm below the peat surface (range 8.8 to 44.0 cm) over the course of the 11-month recording period.

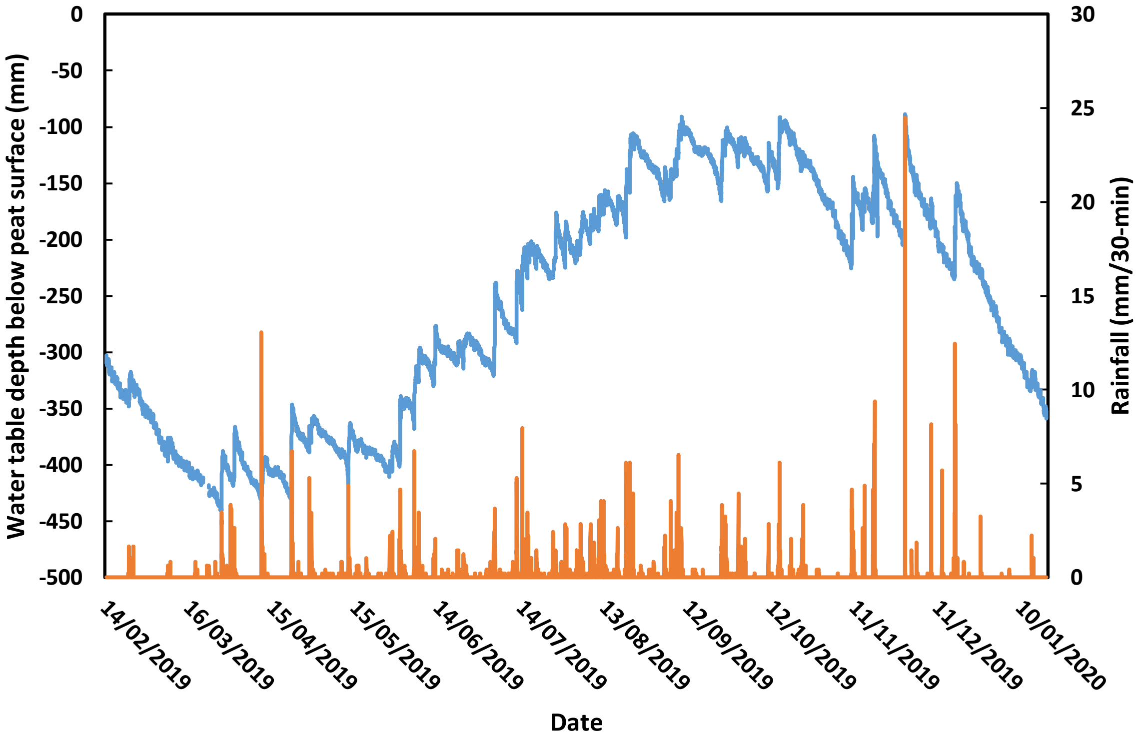


Figure 3.5. Relative water table depth (blue) and rainfall (orange) at the 2017 burn site at Kopuatai over 11 months.

3.4 Discussion

3.4.1 Light

Light was the variable most affected by the 2017 fire at Kopuatai Bog, increasing from virtual darkness (mean = 0.1%) under the *Empodisma* canopy to 19.5% diffuse light availability. Because the 2017 fire removed all above-ground biomass, except for a few standing dead shrubs (see Chapter 2), the diffuse light availability immediately following fire and before regrowth of *Gleichenia* is likely to have been near 100%. This shift from almost complete darkness to complete exposure is a greater change than would occur following fire in other ecosystem types such as forests. While light availability in New Zealand temperate old-growth forests is low, it is still greater than that found under the *Empodisma* canopy at Kopuatai. Using the same technology as in this study, Fritz and Lusk (2020) found understorey light in

45 old-growth forest stands across New Zealand to range between 0.6% and 7.0%. The almost complete removal of vegetation, which occurred at Kopuatai, would also be less likely to occur in a forest, as standing or fallen trees would impede light penetration to the ground.

As the *Empodisma* canopy regenerates, the disparity between burnt and unburnt light environments eventually disappears—a point which light data from the 2005 burn site suggests occurs within 14 years (Figure 3.2). By this time, the height of the live and dead *Empodisma* layers were similar to that in the unburnt area (see Chapter 2). Studies of fire recovery at two other Waikato restiad bogs, Whangamarino and Moanatuatua, found that vegetation had recovered to near pre-fire height and cover by 5.5 and 11.5 years, respectively (Clarkson & Stanway, 1994; Clarkson, 1997), and Norton and de Lange (2003) found that elevated levels of surface radiation still persisted 4.4 years after an experimental fire in Whangamarino wetland. From this information, it is likely that the enhanced light conditions following fire in restiad bogs last between five and ten years.

The light environments found here illustrate how inhibiting the dense *Empodisma* canopy is for seedling recruitment under normal conditions. The enhanced light levels after fire would greatly enhance the chance for seedlings to grow to maturity. Several restiad bog species exploit this opportunity by timing reproduction events to fire. For instance, mānuka is triggered by fire to release seeds from its canopy (Battersby *et al.*, 2017a), *Epacris pauciflora* synchronously germinates after fire from a peat seed bank (see Chapter 4), and the sedge species, *Machaerina teretifolia* and *Schoenus brevifolius*, greatly increase their flower and seed production efforts (see Chapter 2). The germination response of *Epacris* may actually be in response to changes in light (Borthwick *et al.*, 1954; Pons, 2000), as has been shown for two of the most common European heath species, *Calluna vulgaris* and *Erica tetralix* (Pons, 1989). Enhanced diurnal temperature fluctuations, as detected at the 2017 burn site (Figure 3.3), may also be a cue for germination, as may be enhanced nitrate levels (Hilhorst & Karssen, 2000), which often increase in soil following fire (Pyne *et al.*, 1996). Smoke and heat can also stimulate germination in certain fire-adapted species (Keeley & Fotheringham, 2000), although smoke is apparently unimportant at Kopuatai (see Chapter 4). The fire-stimulated flowering response in the sedge species may be related to any or a combination of the three environmental factors measured – light, nutrients, and temperature fluctuations (Pyke, 2017).

3.4.2 Air temperature

Diurnal temperature fluctuations near the peat surface were strongly affected by removal of the vegetation canopy by burning. The finding that maximum (daytime) temperatures were consistently higher throughout the year on the burnt area was an expected outcome which can be explained by the higher levels of solar radiation reaching the peat surface (Figure 3.2). This is supported by Norton and de Lange's (2003) observations that, following fire in a restiad bog, daily maximum peat temperatures declined in step with light availability.

Minimum (night-time) temperatures, however, are more complex. While mean monthly minimum temperatures were highest on the burnt area during warm months (October – March), they were lowest on the burnt area during cool months (May – August), compared to the unburnt area (Figure 3.2). This pattern probably relates to the lack of insulative vegetation on the burnt site and seasonal variation in day length. When soils are heated, some heat energy is transferred by conduction to deeper soil layers and some is re-emitted as longwave radiation to the atmosphere (Geiger *et al.*, 2009). During the night, the supply of solar radiation ceases, leading to soil cooling as more heat is emitted than received. It appears that during warm months, exposed peat on the burnt site absorbed more heat energy during the day and, over the relatively short summer nights, retained some of this. In contrast, the unburnt areas received less heat energy due to shading by plant cover, leading to cooler temperatures at night. The opposite effect, which was found during cooler months, is likely related to the lower amount of incoming solar radiation during winter days, resulting in weaker heating of surface peat and air. During long winter nights, both sites would have emitted a lot of heat to the atmosphere, but this effect was probably greater on the recently burnt area which lacked insulative canopy cover (Coulson *et al.*, 1993; Geiger *et al.*, 2009). These findings contribute to the current knowledge on how fire affects diurnal temperatures in restiad bogs. Norton and de Lange (2003) identified that daily maximum peat temperatures at 10 cm depth were enhanced after fire in agreement with these air temperature results, but their methods prevented them from detecting the seasonal effects that this study has identified.

The higher temperature fluctuations detected here may play a role in promoting plant productivity and/or stimulating germination of peat-stored seeds. Increased daily temperatures are thought to enhance growth rates for species which have growth limited by temperature (Whelan, 1995). Adams and Anderson (1978) found that plant productivity in a recently burnt grassland site was nearly double that in an adjacent unburnt site – a response that they related to differences in soil temperatures. This link was correlative though, and the study lacked replication – common problems in fire ecology research that make it difficult to generalise about the effects of fire on productivity (Whelan, 1995). There is, however, more direct evidence for daily temperature range shifts triggering germination. Auld and Bradstock (1996) established that increased soil temperatures after fire may exceed thresholds for breaking physical seed dormancy. This has been detected empirically in shrub species of fire-prone Australian sclerophyll vegetation (Santana *et al.*, 2010) and South Africa fynbos (Brits, 1986; Pierce & Moll, 1994). Further research would be required to determine the relative effects of light and temperature on germination from the Kopuatai peat seed bank.

3.4.3 Peat nutrients

The peat nutrient trends after the 2017 fire support suggestions that fire in a restiad bog causes a temporary but significant increase in nutrient concentrations (e.g. de Lange, 1989; Timmins, 1992; Clarkson, 1997). The finding that total N levels in peat were not enhanced following fire can be attributed to its low volatilisation temperature of about 200°C, resulting in high loss to the atmosphere and minimal deposition in ash (White *et al.*, 1973; Pyne *et al.*, 1996; DeBano *et al.*, 1998). Although not statistically significant, the peat N content two weeks after fire (0.62 mg cm^{-3}) was in fact lower than that after two years (0.71 mg cm^{-3}) and that from the unburnt area (0.76 mg cm^{-3}). This may be due to the volatilisation of some N from surface layers of peat. It is likely that surface peat reached a sufficient temperature for this to occur as an experimental "cool" fire at Whangamarino produced peat surface temperatures which, at times, exceeded 300°C (Norton & de Lange, 2003). After N, S is considered to be the next most sensitive element to fire due to its volatilisation temperature of 375°C (DeBano *et al.*, 1998). Norton and de Lange (2003) measured air temperatures exceeding 700°C in the path of the flames at Whangamarino, suggesting that S volatilisation is likely to have occurred at Kopuatai. However, peat S concentrations at Kopuatai were almost twice as high after the fire (Figure 3.2). In other studies, burning has been reported to remove only 20-40% of the S in the aboveground biomass, which may explain the results obtained for Kopuatai (DeBano *et al.*, 1998). The increase in peat P after fire can be explained by its reasonably high volatilisation temperature of 774°C and the fact that only 60% of total

P is lost when organic matter is totally combusted, leading to substantial deposits in ash (Raison *et al.*, 1985; DeBano *et al.*, 1998). The increases in K, Mg, Ca, Na, Zn, Cu, and Mn were expected due to their high temperature thresholds, leading to deposits in ash.

Post-fire concentrations of the most important nutrients still fell within the typical range for restiad bogs of New Zealand. Total N and P concentrations were within the expected range for bogs (Clarkson *et al.*, 2004b). Due to the loss of N to the atmosphere rather than deposition in ash, C:N ratios were unaffected by fire. Although the ratios of C:P (1341) and N:P (27.7) were lower two weeks after the fire compared to two years after the fire, they still fell within the typical range expected for bogs which is 533-4221 for C:P and 20.6-81.6 for N:P (Clarkson *et al.*, 2004b). These comparisons should, however, be interpreted with caution as I assessed nutrients in the top 2 cm whereas the values described for New Zealand bogs and swamps were obtained from 5 cm or 7.5 cm depth cores (Clarkson *et al.*, 2004a).

These findings are also similar to fire and nutrient studies in Northern Hemisphere bogs. For instance, Wilbur and Christensen (1983) reported that post-fire increases in the concentrations of most nutrients in the peat of an ombrotrophic bog lasted less than 12 months. The elevated peat nutrient levels after fire are soon drawn down due to uptake by vegetation or loss via leaching and run-off (Clay *et al.*, 2009a; Clay *et al.*, 2009b). Of these, uptake by rapidly recovering vegetation is the most likely mechanism. Leaching is probably less important, but may occur for certain soluble ions, such as orthophosphates and nitrates which are often made more abundant following fire (Christensen, 1994; Cade-Menun *et al.*, 2000). Surface runoff is unlikely as the water table level was not found to reach or exceed the peat surface at any time over 11 months of measurements at the 2017 burn site (Figure 3.5).

3.4.4 Foliar nutrients

The foliar nutrient results are not as straight-forward to interpret as the peat nutrient results, although overall there was a trend of higher nutrient content in foliage growing on the area burnt in 2017 than in the adjacent unburnt area. The differences between foliar nutrients at the 2005 burnt and unburnt areas are less (Figure 3.4), indicating that fertility had returned to pre-fire levels by this time.

The finding that peat fertility had recovered by two years (Table 3.2) but foliar nutrient levels were still elevated by approximately the same time (Figure 3.4) may reflect plant uptake of the previously more-available nutrients. An alternative explanation is that nutrient transformations led to higher levels of available forms, which were not detected by the total nutrient concentrations measured in peat. Fire often enhances the release of organically bound nutrients, converting them to plant-available inorganic forms. Ammonium (NH_4^+), for instance, tends to increase in soil as it is a chemical by-product of soil heating and microbial activity shortly after fire (Basher *et al.*, 1990; Pyne *et al.*, 1996). Nitrate (NO_3^-) levels also increase, resulting indirectly from mineralisation, decreased acidity, and increased ammonification (Pyne *et al.*, 1996). One of the most consistently reported effects of fire on soils is an increase in available P, most notably an increase of 100% following fire in a Northern Hemisphere ombrotrophic bog (Wang *et al.*, 2015). These transformations may be the direct outcome of fire's high temperatures or the result of fire-related elevated pH levels (Giardina *et al.*, 2000; Wang *et al.*, 2015). Increases in pH are a common effect of fire, due to the deposition in ash of basic cations, such as Ca^{2+}, Mg^{2+}, K^+, and Na^+, released during combustion (DeBano *et al.*, 1998; Cade-Menun *et al.*, 2000; Giardina *et al.*, 2000). While peat pH levels were not measured in this study, the levels of all metals assessed, except for Fe, increased in peat after fire (Table 3.2). The basic ions that these metals form likely contributed to an increase in pH at Kopuatai, such as the increase from 4.8 ± 0.1 before fire to 6.3 ± 0.4 post-fire detected in a restiad bog by Norton and de Lange (2003).

The less negative $\delta^{15}N$ levels found in both *Gleichenia* and *Machaerina* growing on the 2017 burnt area compared to the unburnt area suggest that P was more available in the soil. $\delta^{15}N$ is a heavier isotope of N which is less preferable to plants. In a P-limited system, which Kopuatai is likely to be (Verhoeven *et al.*, 1996; Clarkson *et al.*, 2005), not all N is assimilated and plant uptake will show discrimination against the heavier isotope, leading to strongly negative $\delta^{15}N$ values (Fry *et al.*, 2000; McKee *et al.*, 2002; Clarkson *et al.*, 2005). This relationship has been demonstrated by Clarkson *et al.* (2005) who found strong positive relationships between peat P concentrations and foliar $\delta^{15}N$ concentrations in mānuka and *Dracophyllum scoparium*. The higher (less negative) $\delta^{15}N$ values in *Gleichenia* and *Machaerina* tissues from the 2017 burn site could therefore indicate that P limitation in the soil has been relieved by fire. In a P-limited system, enrichment of P is likely to enhance plant productivity. This has been demonstrated recently by research relating volcanic P inputs at Moanatuatua

Bog to higher carbon accumulation rates in peat (Ratcliffe, 2019), presumably due to increased plant growth rates.

3.4.5 Peat properties – inherent site differences

The results of the 5 cm depth peat study imply that the site where the 2017 fire occurred is inherently more nutrient-rich than the other study sites (Table 3.1). Peat bulk density at the site of the 2017 fire, although still within the typical range for restiad bogs (Clarkson *et al.*, 2004a), was higher than at the other burn sites (Table 3.1). Its elevation suggests higher rates of decomposition (Boelter, 1969), which is supported by a high von Post rating (Table 3.1). The location of the 2017 fire is near the margin of Kopuatai and the site differences may, therefore, be caused by occasional nutrient inputs during flood events from the nearby Piako River – a pattern which has been recognised in other New Zealand peatlands (Blyth *et al.*, 2013; Douglas, 2019). While the 2005 burn site is also close to Kopuatai's margin, its peat properties were more similar to that at the central 1974 burn sampling site (Table 3.1), suggesting that this site is not affected by river inputs.

3.5 Conclusions

These findings provide evidence that fire causes several significant environmental changes in restiad bogs, making light and nutrients more available, and altering surface temperature regimes on daily and seasonal timescales. The environmental variable most affected by burning is light. As fire removes the densely shading *Empodisma* canopy, a shift occurs from an almost completely dark surface environment to one conducive to seedling recruitment. Therefore, light is probably the main driver of vegetation dynamics at Kopuatai, providing impetus for reproduction following fire (fire-stimulated flowering, serotiny, and seed bank germination). Germination responses are most likely triggered by light, although temperature changes and nutrient enhancements may also be implicated. Fire-stimulated flowering may be stimulated by any of the environmental variables. Increased fertility is probably most responsible for increased productivity following fire, as deposited nutrients are rapidly taken up.

Chapter Four

Role of the peat seed bank in post-fire regeneration

4.1 Introduction

It is common for species inhabiting fire-prone environments to enhance their regenerative success and take advantage of optimal resources and minimal competition by cueing reproductive processes to fire (Gill, 1981; Bond & van Wilgen, 1996; Lamont *et al.*, 2019). Such processes include mast flowering (Lamont & Downes, 2011; Pyke, 2017), promotion of seed release from serotinous cones (Battersby *et al.*, 2017a), and the germination of soil-stored seeds (Keeley & Fotheringham, 2000). These responses affect plant species' abilities to re-establish on a site after fire, ultimately controlling species composition.

The seeds of many plants have innate dormancy, enabling them to remain inactive until conditions are favourable for seedling growth. Suppression of germination may be caused by a thick seed coat which acts as a barrier to water or oxygen uptake, an inhibitor in the seed coat which needs to be leached, or the lack of some environmental stimulus (Keeley, 1995). Several fire-related changes may relieve the factors inhibiting germination of seeds stored in soil. The mechanisms may be directly fire-related such as a) fire-generated heat cracking the thick seed coat, b) chemicals in smoke or charred wood that break physiological dormancy (Keeley, 1987; Auld & O'Connell, 1991; Brown & Van Staden, 1997; Read *et al.*, 2000; Penman *et al.*, 2008), or indirectly such as via c) increased diurnal temperature fluctuations due to the removal of a pre-existing canopy, which can rupture the seed coat and increase permeability to water (Probert, 2000), or d) enhanced light availability which relieves physiological dormancy (Pons, 2000). Where germination is a direct consequence of fire or one of its components or by-products (e.g. heat, smoke, charates), it is considered a *fire-adapted* trait, whereas it is a *fire-related* trait if germination is triggered by more general environmental changes caused by fire (Lamont *et al.*, 2019).

Restiad bogs of New Zealand have a history of naturally recurrent fires (Newnham *et al.*, 1995; Perry *et al.*, 2014) yet, compared to many other fire-prone ecosystems around the world, the role of the seed bank in regeneration of these ecosystems is unknown. Seed bank dynamics have been well-studied in certain fire-prone ecosystems such as Australian heathlands and woodlands (Enright & Kintrup, 2001; Wills & Read, 2002) and Mediterranean-climate shrublands such as Californian chaparral (Zammit & Zedler, 1988) and South African fynbos (Pierce & Moll, 1994; Keeley, 1995). Much less is known about wetland, and particularly peatland, seed banks. Studies of peatland seed banks have so far been largely limited to the Northern Hemisphere, and have not been concerned with fire (e.g. McGraw, 1987; Jauhiainen, 1998; Egawa *et al.*, 2009). As most wetlands are not naturally prone to fire, this is not surprising. However, in view of the evidence of fire in New Zealand restiad bogs, it seems likely that peat seed banks will play some role in vegetation dynamics therein.

Several plant species that grow in New Zealand restiad bogs possess fire-related or fire-adapted traits which may enable them to persist in a frequently burnt ecosystem. These include serotinous release of seed from a canopy (Battersby *et al.*, 2017a), mass post-fire flower and seed production (see Chapter 2), and the possession of underground rhizomes which survive fire and subsequently resprout (Clarkson, 1997). However there has been no work on the potential role of dormant peat seed banks in restiad bogs. This knowledge gap prevents us from accurately predicting the effects of fire (and changes to the local fire regime) on vegetation composition in these ecosystems.

Vegetation surveys at Kopuatai, New Zealand’s largest remaining bog, revealed that cover and occurrence frequency of some species increase after fire (see Chapter 2). This was particularly true of the heath *Epacris pauciflora*, despite it not being documented as a fire-adapted species. Several other Ericaceae elsewhere have been shown to germinate in response to primary and secondary fire-related cues. For instance, both heat and smoke exposure promoted strong germination responses in the Australian species *Epacris impressa* (Enright & Kintrup, 2001; Penman *et al.*, 2008), *Epacris tasmanica* (Gilmour *et al.*, 2000), and *Epacris stuartii* (Keith, 1997) while two European heath species, *Calluna vulgaris* and *Erica tetralix,* are thought to germinate in response to post-fire increases of light availability (Pons, 1989). It is likely, therefore, that *Epacris* regenerates from a peat seed bank at Kopuatai. Several other bog species may also be present in the peat seed bank. Johnson (2001) detected a post-fire increase in abundance of the forked sundew, *Drosera binata*, in a southern New Zealand bog, a response that he attributed to a “large and well-distributed seedbank”. He also suggested that recolonisation in the restiad *Empodisma minus,* and the sedges, *Machaerina* *rubiginosa,* and *Schoenus maschalinus,* is at least partly due to recovery from a peat seed bank (Johnson, 2001). These speculations have not been tested, but if they are correct, it is likely that close relatives of these species at Kopuatai – *Empodisma robustum, Machaerina teretifolia* and, *Schoenus brevifolius* – also have dormant peat seed banks capable of germinating quickly after fire.

The aim of this study was to establish a) whether there is a viable peat seed bank at Kopuatai, and b) whether its germination is enhanced by fire-related cues. Determining the contribution of a peat seed bank to post-fire regeneration will add to our current understanding of fire ecology and enable better predictions to be made on post-fire vegetation dynamics.

4.2 Methods

4.2.1 Sample collection

Peat samples were collected from a site in the northeast of Kopuatai Bog (GPS coordinates: -37.371175, 175.553673) in the Waikato region of the North Island of New Zealand. The site was reportedly last burnt in approximately 1974 when an extensive fire affected a large portion of the bog (Irving *et al.*, 1984; de Lange *et al.*, 1999). Reports of this fire are corroborated by aerial photographs from 1975 which show streaky patterns that can be interpreted as the result of recent burning (see Chapter 2). Up until the mid-1970s, large-scale fires originating from land clearing for development were a relatively common occurrence at Kopuatai, and more recent aerial photographs do not display the same patterns. The vegetation at this site is dominated by the restiad species *Empodisma robustum* (henceforth *Empodisma*) and *Sporadanthus ferrugineus* (henceforth *Sporadanthus*), the tangle fern *Gleichenia dicarpa* (henceforth *Gleichenia*), sedges *Machaerina teretifolia* (henceforth *Machaerina*) and *Schoenus brevifolius* (henceforth *Schoenus*), *Leptospermum scoparium* (mānuka) and *Epacris pauciflora* (henceforth *Epacris*). See Chapter 2 for a more detailed vegetation description.

Peat collection was incorporated into the sampling plan for concurrent vegetation surveys (see Chapter 2). A 50 m x 50 m sampling area was established, with a base tape running east-west. Eight 50 m transects ran north from the base tape at random distances. At ten random distances along each transect, vegetation sampling was carried out using a point intercept method, totalling 80 points. At each point along six of these transects, a soil core (8 cm diameter, 5 cm depth) was extracted, totalling 60 points. The total surface area of peat collected was 0.302 m^2 and the total volume was 0.015 m^3. A depth of 5 cm was chosen to conform with previous seed bank studies (e.g. Enright & Kintrup, 2001; Wills & Read, 2002; Egawa *et al.*, 2009) and because viable seeds are typically concentrated at the surface and reduce in density with depth (Benoit *et al.*, 1989; Jauhiainen, 1998; Csontos, 2007).

4.2.2 Experimental treatment

All 60 cores were teased apart by hand and coarse roots and rhizomes removed, after which the peat was mixed thoroughly and then divided by wet weight into 20 approximately equal replicates. Homogenisation of the peat maximised our chances of detecting any effects of treatments, by minimizing variation between replicates. Of the 20 samples, five were treated with heat, five with smoke, five with heat and smoke, and five were left untreated as a control.

The heat treatment was applied prior to potting. Peat samples were spread in a thin (2-3 cm) layer in aluminium trays and placed in an oven preheated to 100°C, until the peat reached 70°C. This was reduced from Read et al.'s (2000) methods which involved heating soil samples in a 120°C oven until they reached 80°C. The reduction was made because, while soil temperature during a moderate intensity fire has been reported to be approximately 80°C (Auld & O'Connell, 1991), peat moisture content at Kopuatai of close to 90% by volume (Campbell & Williamson, 1997) would restrict the transmission of heat. Samples being treated with both heat and smoke were heated first. Following heating, samples were prepared by spreading the peat to a depth of approximately 2 cm over the surface of 5 cm of sterile potting mix in plastic germination trays (34.5 x 29.5 cm).

The smoke treatment was applied by exposing trays to smoke for 30 minutes, following Gilmour et al. (2000). A bee smoker was used to generate the smoke, by burning bee smoker pellets composed of 100% untreated wood. Previous research has found that smoke-stimulated germination is independent of the type of plant material used to generate smoke (Brown & Van Staden, 1997). Smoke was pumped directly into a large plastic tent containing the trays. At all times during the treatment, the tent was filled with thick smoke. After 30 minutes, trays were removed from the tent and lightly misted.

Following treatment, all 20 trays were arranged in a randomised order on benches in an isolated section of the University of Waikato glasshouse. Every two weeks the order of the trays was re-randomised. To prevent contamination from wind-borne seeds, all trays were covered with fine white mesh. Trays were watered for six minutes twice daily by an automatic watering system and were also regularly checked and watered by hand when the peat was unevenly moist. Automatic ventilation and evaporative cooling were set to limit the maximum air temperature to around 28°C, while minimum temperature was not controlled. During the experiment, mean monthly maximum air temperatures in the enclosure ranged from 27.0 to 28.6°C and mean monthly minima from 15.0 to 17.2°C. Trays were checked for germinants every 2 days during the first five weeks, and once a week henceforth. New seedlings were tagged with the date they were first observed and left to grow until they could be identified. The experiment commenced on Friday 13 December 2019 and concluded on Friday 27 March 2020, totalling 105 days.

4.2.3 Data analysis

To determine whether germination differed between treatments, seedling density and species richness were analysed by one-way analysis of variance (ANOVA). Post-hoc multiple comparisons of means were performed by Tukey's honestly significant difference (HSD) tests to determine differences between pairs of treatments. The same tests were performed on seedling densities of the three most abundant germinant species, *Epacris, Sporadanthus,* and *Empodisma*. Emergence rates across treatments of all seedlings and of the most common species were investigated by plotting cumulative seedling densities over the duration of the experiment.

Differences in composition among treatments was tested by permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis similarity index. This was done using the vegan package of R (Oksanen *et al.*, 2010). A Spearman's rank-order correlation was used to determine the relationship between the total number of germinants of each species and percentage cover of each species in the standing vegetation.

4.3 Results

4.3.1 Seedling density and species richness

A total of 1236 germinants were recorded from the 20 sample trays over the 105-day duration of the experiment. The density of emergent seedlings differed significantly among treatments (Figure 4.1a, Table 4.1). Post-hoc comparisons found that, compared to the control, the smoke treatment did not affect seedling density ($p = 0.180$; Figure 4.1a, Table 4.1). Both of the heated treatments, however, produced significantly fewer germinants than the control ($p(\text{Heat}) < 0.001$, $p(\text{Smoke \& Heat}) < 0.001$; Figure 4.1a, Table 4.1), suggesting that the heat treatment was lethal to many seeds.

Species richness differed significantly among treatments ($p < 0.001$; Figure 4.1b). The highest species richness was in the control and the lowest was in the heat and smoke & heat treatments, once again indicating damage to seeds during the heat treatment (Table 4.1).

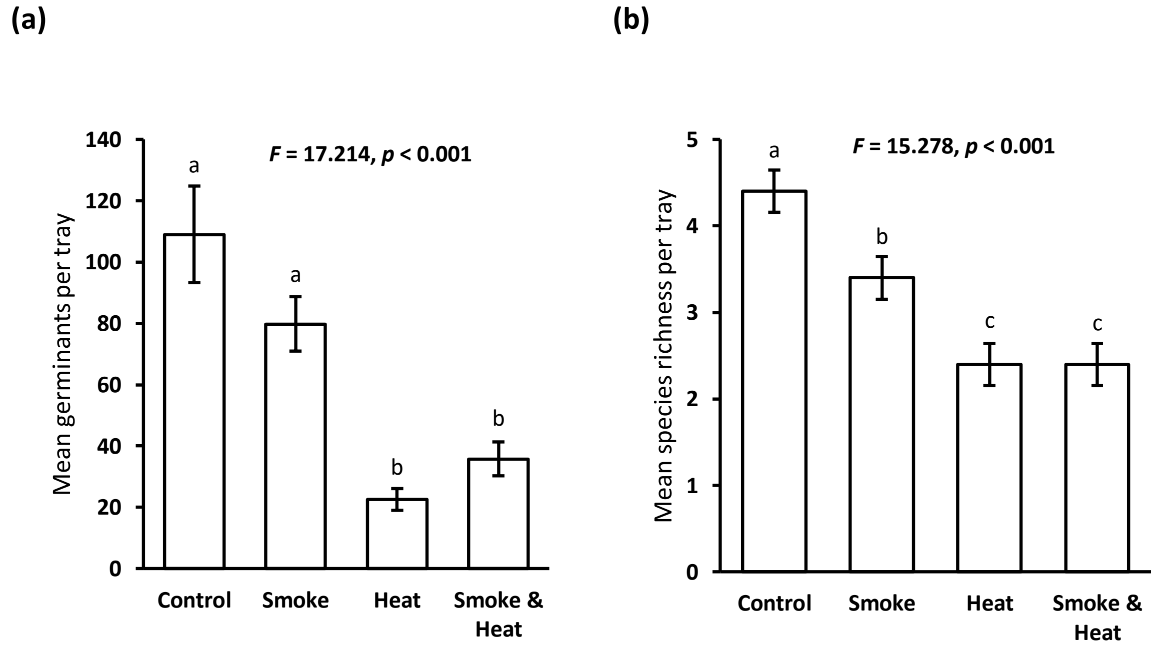


Figure 4.1 (a-b). Graphs showing (a) mean seedling density and (b) mean species richness per replicate tray of emergent seedlings from peat subjected to different treatments (± one standard error). The results of one-way ANOVAs are displayed. Shared letters indicate no significant difference between treatments based on Tukey's HSD test at $p < 0.05$.

Table 4.1. Total number of germinants per treatment, mean germinant density (± one standard error) per square metre of bog surface area, total number of germinant species per treatment, and the number of unique species which occurred in one treatment only. Density values followed by the same letter (by column) are not significantly different (ANOVA and Tukey's HSD test: *P* > 0.05).

Treatment	**Total no. of seedlings**	**Mean density (± SE) m^{-2}**	**Total no. of species**	**Unique species**
Control	545	7228 ± 1040 *a*	6	2
Smoke	399	5292 ± 590 *a*	5	1
Heat	113	1499 ± 234 *b*	3	0
Smoke & Heat	179	2374 ± 371 *b*	3	0
All	1236	4098 ± 601	8	N/A

4.3.2 Species composition

Seedlings of eight species emerged during the experiment. Of these, *Epacris, Sporadanthus,* and *Empodisma* were present in all treatments. *Epacris* was the most abundant germinant, making up 77% of the total seedling count at 948 individuals. The second most abundant species was *Sporadanthus* at 221 germinants (17.9%), followed by *Empodisma* at 43 (3.5%), mānuka at 17 (1.5%), and *Machaerina* at 2 (0.2%) (Table 4.2). The forked sundew, *Drosera binata*, and non-natives *Cyperus eragrostis* (tall flatsedge) and *Cirsium vulgare* (bull thistle), were each recorded once, making up less than 0.1% of total emergents (Table 4.2).

The trend of overall seedling densities being highest in the control and smoke treatments was replicated by the most common germinant species. Emergence of *Epacris* was significantly reduced by heating, but unaffected by smoke (Table 4.2). *Sporadanthus* had significantly more emergents in the control than any other treatments, and less in both heated treatments (Table 4.2). *Empodisma* seedling density did not differ significantly among treatments, but this is probably a reflection of small sample size (Table 4.2). Mānuka was present only in the control and smoke treatments, suggesting sensitivity to high temperatures (Table 4.2). *Machaerina* was recorded once in the heat treatment and once in the smoke treatment (Table 4.2).

Table 4.2. Total seedling density and individual species density per treatment and significance of differences. Where ANOVA found a significant difference ($p < 0.05$), shared letters across rows indicate no significant difference (Tukey's HSD test: $P > 0.05$).

Species	**Family**	**Total**	**% of total**	**Control**	**Smoke**	**Heat**	**Smoke & Heat**	***p***
Epacris pauciflora	Ericaceae	948	76.7%	388 *a*	321 *a*	93 *b*	146 *b*	**<0.001**
Sporadanthus ferrugineus	Restionaceae	221	17.9%	120 *a*	66 *b*	14 *c*	21 *c*	**<0.001**
Empodisma robustum	Restionaceae	43	3.5%	18	8	5	12	0.287
Leptospermum scoparium (mānuka)	Myrtaceae	19	1.5%	17	2	0	0	
Machaerina teretifolia	Cyperaceae	2	0.2%	0	1	1	0	
Drosera binata	Droseraceae	1	<0.1%	1	0	0	0	
*Cyperus eragrostis**	Cyperaceae	1	<0.1%	0	1	0	0	
*Cirsium vulgare**	Asteraceae	1	<0.1%	1	0	0	0	
All species		1236		545 *a*	399 *a*	113 *b*	179 *b*	0.000

*Non-native species.

4.3.3 Time course of emergence

The time course of emergence was similar between the control and the smoke treatments, whereas emergence in the heat and smoke & heat treatments began 10-20 days later and then proceeded at a slower rate (Figure 4.2a). This overall pattern was replicated by *Epacris* emergence rates, reflecting the abundance of *Epacris* seedlings and their influence on total seedling trends (Figure 4.2b). Emergence of *Epacris* seedlings continued throughout the experiment, although the rate had declined to near zero by 100 days, except perhaps in the heat treatment (Figure 4.2b). The initial emergence rates of *Sporadanthus* were similar between the control and smoke treatments, but tapered off earlier in the latter (Figure 4.2c). Lower rates of emergence were recorded in the heat and heat & smoke treatments and onset was delayed by about ten days in both. Heat treated *Empodisma* samples displayed a delayed onset of germination by about 20 days (Figure 4.2d). No new mānuka emergents were observed after 18 days in the smoked treatment and 30 days in the control (Figure 4.2e). This compares to the two restiad species and *Epacris,* which plateaued after approximately 60 days and 100 days, respectively (Figure 4.2b-d). Overall, the main effect was that heat slightly delayed germination and reduced the rate of germination.

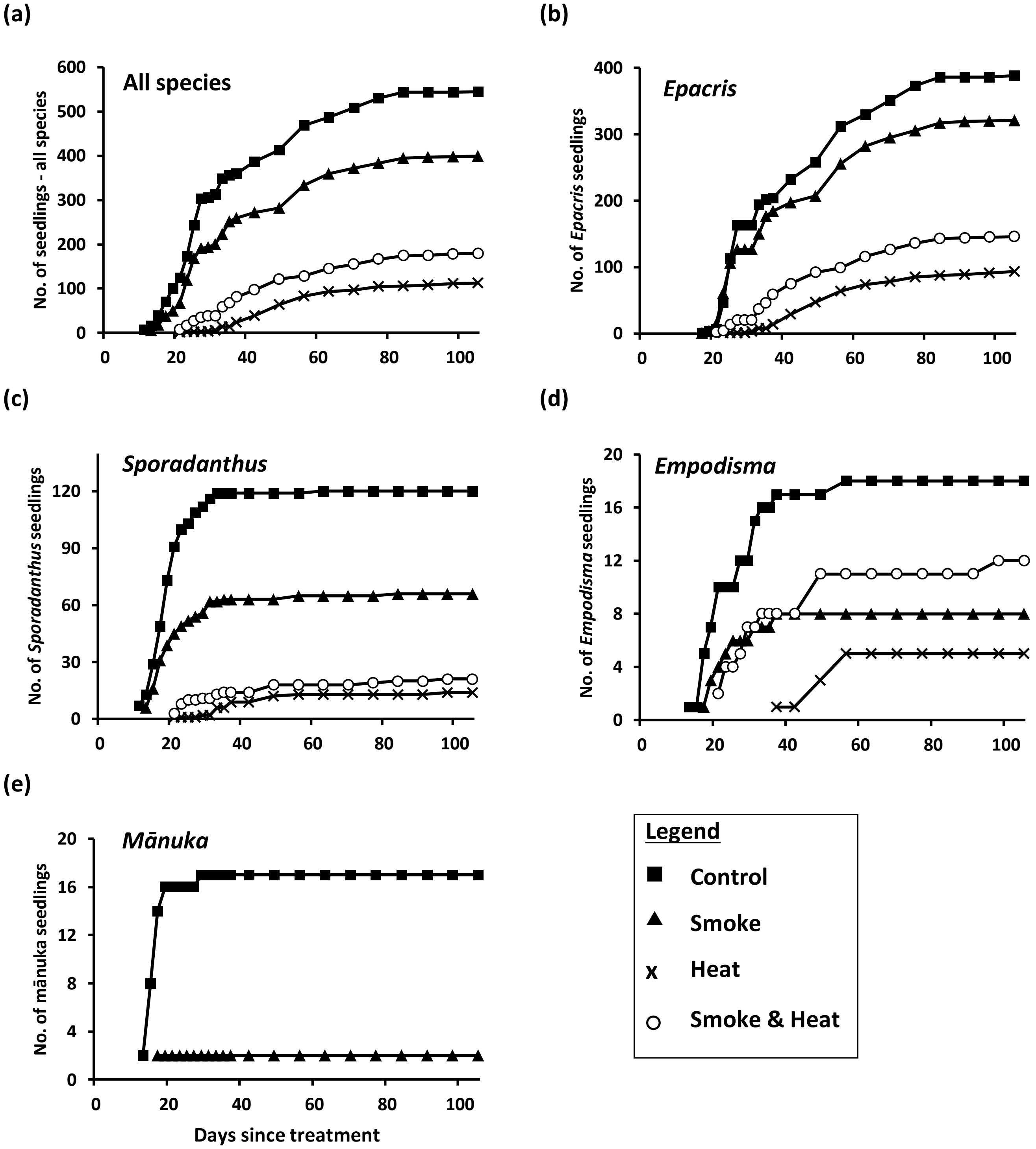


Figure 4.2 (a-e). Cumulative seedling density for (a) all species, (b) *Epacris pauciflora*, (c) *Sporadanthus ferrugineus*, (d) *Empodisma robustum*, and (e) *Leptospermum scoparium* (mānuka) for each treatment (■, control; ▲, smoke; **x**, heat; O, smoke & heat).

4.3.4 Species composition between treatments

PERMANOVA found significant differences in species composition between treatments (Table 4.3). The only insignificant pairwise differences were between the control and smoke treatments and between the heat and smoke & heat treatments.

Table 4.3. PERMANOVA results showing differences in species composition between all treatment pairs. Significant differences are in bold ($p < 0.05$)

Treatment 1	Treatment 2	F	R^2	p
All	All	9.15	0.632	**0.001**
Control	Smoke	1.94	0.195	0.148
Control	Heat	18.69	0.700	**0.009**
Control	Smoke & Heat	9.30	0.538	**0.010**
Smoke	Heat	17.42	0.685	**0.007**
Smoke	Smoke & Heat	6.97	0.466	**0.018**
Heat	Smoke & Heat	1.53	0.160	0.222

4.3.5 Species composition compared to collection site

Based on the Spearman's rank-order correlation, there was no significant correlation between species composition of the standing vegetation at the collection site and species composition of emergent seedlings ($r_s = 0.399$, $p = 0.254$). The most notable difference in rank order was that of *Epacris* which was the sixth most common species in the field in terms of percentage cover but the single most abundant germinant species (Table 4.4). While *Epacris* made up 11.3% cover at the collection site, the number of germinants across all treatments equated to 3143.3 seedlings m^{-2} (or 5146 in the control treatment). *Empodisma*, which was the most prevalent species in the field, was only the third most abundant germinant in the experiment. Species reasonably abundant in the standing vegetation but absent from the germination experiment included *Gleichenia* and *Schoenus* (Table 4.4). *Sporadanthus*, mānuka, and *Machaerina* did not differ much in terms of rank order between standing vegetation and germinants (Table 4.4). *Machaerina* was only recorded twice which corresponds with its low abundance in the field (Table 4.4).

Table 4.4. Comparison table between percent cover of standing vegetation at the collection site (ordered from most abundant), the total number of seedlings per species from all treatments, and their equivalent seedling density per m^2 of bog surface area.

Species	% cover at collection site	Total number of seedlings	Mean seedling density (± SE) m^{-2}
Empodisma robustum	96.3	43	142.6 ± 32.7
Sporadanthus ferrugineus	48.8	221	732.8 ± 143.4
Leptospermum scoparium (mānuka)	31.3	19	63.0 ± 25.2
Gleichenia dicarpa	28.8	-	-
Schoenus brevifolius	15	-	-
Epacris pauciflora	11.3	948	3143.3 ± 451.7
Machaerina teretifolia	5	2	6.6 ± 4.6
Drosera binata	-	1	3.3 ± 3.3
*Cyperus eragrostis**	-	1	3.3 ± 3.3
*Cirsium vulgare**	-	1	3.3 ± 3.3

*Non-native species

4.4 Discussion

4.4.1 Does Kopuatai peat contain a viable seed bank?

This study found that a seed bank of considerable size accumulates in the surface peat of a New Zealand restiad bog. The highest, and therefore most reliable, density of 7228 ± 1040 seedlings m^{-2} was found in the control treatment. This value fits into the range of seedling densities reported in seed bank studies of other types of fire-prone ecosystems, which are most often in the same order of magnitude. For instance, in a south-eastern Australian heathland, heat treated samples gave the highest seedling density of 4575 m^{-2} (Wills & Read, 2002), and heat- and smoke-treated soil samples from a dry sclerophyll forest in New South Wales yielded 2887–7578 germinants m^{-2}. Soil seed bank densities in South African fynbos have been reported to range from 1683 to 4518 seeds m^{-2} (Pierce & Cowling, 1991). Higher densities of 6510-12,148 seedlings m^{-2} germinated from fire-prone Scottish *Calluna* heathland soil (Mallik *et al.*, 1984), and of 8000-25,000 seedlings m^{-2} from Californian chaparral soil (Zammit & Zedler, 1988). Lower densities of 50-769 and 760-1734 seeds m^{-2} have been found for Australian woodland and scrubland, respectively (Meney *et al.*, 1994; Wang, 1997). Compared to these reports, the densities obtained from Kopuatai peat are moderately high. The Kopuatai seed bank, however, is dominated by a single species, *Epacris pauciflora,* without which, the control treatment seedling density would be 2082 m^{-2}.

4.4.2 Is the seed bank directly fire-stimulated?

The heat treatment which was intended to simulate the passage of fire was either too hot and/or the exposure too long, resulting in lower mean germination responses of all species in the heated treatments (heat, heat & smoke) compared to non-heated treatments (control, smoke). Therefore, little can be concluded regarding germination responses to heat. The three most abundant germinants, however (*Epacris, Sporadanthus,* and *Empodisma),* all showed some germination, albeit at lower levels, in the heated treatments, suggesting some intra-specific variation in heat tolerance of these species' seeds.

Treating peat with various heat treatments may have yielded more informative results. The specific heat treatment in this study involved wet heat of moderate temperature and reasonably long duration. Seeds can differ substantially in the optimum intensity and duration of heat to promote germination, and some studies have found that short exposure to high temperature is better at stimulating germination than prolonged exposure at moderate temperature (Keeley & Fotheringham, 2000; Gashaw & Michelsen, 2002). As this study has shown, heat shock too intense or prolonged can also kill seeds. To determine more precisely what the optimum and lethal heat treatments are, several authors have treated samples with a range of heat intensities and durations (e.g. Enright & Kintrup, 2001; Wills & Read, 2002; Thomas *et al.*, 2003); an approach which could be adopted in future restiad bog seed bank studies.

A lack of knowledge on how much heat is transferred to peat layers during fire in restiad bogs also limits our ability to accurately simulate fire in an experiment. Except for Norton and de Lange's (2003) report that surface temperatures "rarely exceeded 300°C" during an experimental fire, little is known on how hot surface layers of peat get during fires in restiad bogs, although temperatures can be expected to decrease rapidly with depth (Schimmel & Granstrom, 1996; Gashaw & Michelsen, 2002). If future studies into New Zealand bog seed banks are carried out, experimental measurements of temperatures reached by the uppermost 5 cm of peat during fires would be useful for developing methods.

The smoke treatment was more conclusive, demonstrating that seeds stored in peat at Kopuatai do not respond to the fire-related cue of smoke. *Sporandanthus*, however, showed a significant decline in germination response in the smoke treatment compared to the control

(Table 4.2), potentially indicating that smoke alone is harmful to *Sporadanthus* seeds. This may also be the case for mānuka (Table 4.2), although germination levels were too low to test this statistically. Any interactions between heat and smoke were masked by the negative effect of the heat treatment. However, mean seedling densities of *Epacris, Sporadanthus,* and *Empodisma* were all higher (but not significantly) in the smoke & heat treatment compared to the heat treatment (Table 4.2). This potential interaction effect would require further experimentation to clarify, using a more suitable heat treatment.

4.4.3 Is the seed bank indirectly fire-stimulated?

The high seedling densities in the control indicate that germination is cued by some environmental difference between the glasshouse and the bog surface, particularly in *Epacris*. By responding to cues such as light and temperature, species increase their chances of finding favourable growing conditions but their germination is not strictly dependent on fire which may provide some benefits during long fire-free periods (Probert, 2000).

The most apparent environmental change resulting from fire at Kopuatai is light availability. Light measurements under the canopy at Kopuatai found that negligible amounts of light typically reach the peat surface (see Chapter 3), whereas in the glasshouse, light penetration was largely unimpeded. Removal of canopy vegetation by fire also leads to higher daily maximum temperatures, and potentially lower minimum temperatures during winter (see Chapter 3). Globally, germination of many plant species is cued by increased light availability, or changes in light spectral quality, as a result of disturbance (Pons, 2000). Peat surface light availability in restiad bogs is significantly enhanced for about four years after fire (Norton & de Lange, 2003). The frequency of light is also probably affected, due to the removal of a canopy of vegetation containing chlorophyll pigments which absorb red light (660 nm) more effectively than far red light (730 nm) (Pons, 2000). Either or both of these changes may be enough to stimulate germination, or they may act complimentarily with another change such as temperature (Pons, 2000; Probert, 2000).

Enhanced daily temperature fluctuations in sites opened up by fire are known to stimulate germination in a wide number of species (Brits, 1986; Pierce and Moll, 1994). This has been detected in several species growing in fire-prone South African fynbos vegetation which emerge in pulses to form even-aged stands following fire (Brits, 1986; Pierce & Moll, 1994).

4.4.4 Implications of the seed bank for plant ecology

The *Epacris*-dominated peat seed bank is substantially different in composition to the *Empodisma*-*Sporadanthus*-dominated standing vegetation at the site of collection (r_s = 0.399, *p* = 0.254;Table 4.4). Seed bank dominance by few species and incongruencies between seed banks and aboveground vegetation are commonly found in this type of study (e.g. McGraw, 1987; Wills & Read, 2002). There are a number of possible explanations for these findings. Firstly, dormancy in some species may not have been broken by the treatments applied. This is unlikely for *Epacris* which was highly abundant in the control treatment, but it is likely that for other species, particularly *Empodisma* which is dominant in the standing vegetation but poorly represented by germinants, germination may be higher under the right heat treatment. Secondly, certain species may have been absent from the peat seed bank at the time of sampling due to the long period of approximately 45 years since fire (cf. Noble & Slatyer, 1980). For instance, the sedges, *Machaerina* and *Schoenus*, display fire-stimulated flowering in which they produce a high number of seeds in the first few years after fire (see Chapter 2), after which production declines. This is especially common in resprouters as they allocate resources to the production of fire-resistant underground organs at the expense of seed production (Bond & Midgley, 2001) and may explain why *Schoenus* has 15% cover in the field but was not observed as a germinant from the peat. Mānuka growing at Kopuatai is serotinous and it’s low representation in the seed bank may be due to its minimal release of seeds during inter-fire periods. Third, species with uneven distributions in the field may not have been detected due to insufficient sampling intensity.

This study demonstrates that *Epacris* has a large peat seed bank which is released from dormancy by some environmental cue, likely relating to changes in light and/or temperature. As light and temperature regimes are both altered by fire, this research successfully validates the hypothesis advanced in Chapter 2 that *Epacris* increases its dominance after fire via germination from the peat seed bank. While it may not be as fire adapted as other *Epacris* species in Australia which have enhanced germination in response to heat and/or smoke (Keith, 1997; Gilmour *et al.*, 2000; Enright & Kintrup, 2001; Penman *et al.*, 2008), its response to more general cues is still advantageous in frequently burnt restiad bog environments, enabling it to take advantage of the space and resources available on recently burnt sites.

Empodisma is widespread in the standing vegetation at Kopuatai and may be more common in the seed bank than is suggested by the control treatment germinants. *Empodisma* regenerates after fire mostly by seed and occasionally by resprouting, germinating within weeks after fire (Clarkson, 1997; Wagstaff & Clarkson, 2012). Such rapid recolonisation may be due to recovery by fire-stimulated germination, which a more appropriate heat treatment might detect.

The abundant emergence of *Sporadanthus* from the seed bank (Table 4.2) is somewhat surprising, considering its depiction in the literature. It is regarded as a particularly fire-sensitive species and its loss from several sites, including large areas of Kopuatai, has been attributed to increases in fire frequency since European settlement (Dickinson, 1974; de Lange, 1989; Newnham *et al.*, 1995; de Lange *et al.*, 1999). While its close New Zealand relative, *Sporadanthus traversii,* has been reported to establish after fire from seeds remaining in a seed bank, the slow recovery rate of *Sporadanthus ferrugineus* has led to speculation that it has no seed bank and is only able to recover from freshly deposited seeds (Clarkson, 1997; de Lange *et al.*, 1999)—an idea not supported by my experimental results (Table 4.2). It is possible that the loss of *Sporadanthus* from many places is due to multiple fires which occurred in close succession, with the second occurring before the seed bank could re-establish itself (Noble & Slatyer, 1980).

Mānuka populations at Kopuatai are highly serotinous, releasing few seeds in the absence of fire (Battersby *et al.*, 2017a), so its poor representation in the peat seed bank was an expected result. This research corroborates other studies reporting mānuka's lack of an effective seed bank (Mohan *et al.*, 1984; Bond *et al.*, 2004) and the inability of heat to enhance its germination (Battersby *et al.*, 2017b).

As discussed above, the sedges, *Machaerina* and *Schoenus*, are both resprouting species which only seed heavily after fire. It is therefore unsurprising that there was little germination of these species; although it is possible that a more appropriate heat treatment may have yielded different results. Similarly, there was no emergence of *Gleichenia* as a germinant, despite its abundance in the standing vegetation (Table 4.4). While soil stores of angiosperm seeds are more common, at least some fern species form viable "spore banks", available to colonise an area after disturbance (Penrod & McCormick, 1996; Ramírez-Trejo *et al.*, 2004; Esaete *et al.*, 2014). As *Gleichenia* is a widely distributed species at Kopuatai (28.8% cover), its absence as a peat germinant suggests that this is not the case for this species.

While known to grow at Kopuatai (Irving *et al.*, 1984, and see Chapter 2), *Drosera binata* was not recorded in the aboveground vegetation at the sampling site, so its single occurrence as a germinant in the control treatment is notable. This finding lends some support to Johnson's (2001) suggestion that an increase in abundance of this species following fire in a southern New Zealand bog was due to recovery from peat-stored seed. In a Japanese peatland, *Drosera rotundifolia*, despite being uncommon in standing vegetation, was found to have a dense seedbank which was stimulated to germinate when exposed to increased light penetration and temperature fluctuations (Egawa *et al.*, 2009). Germination of *Drosera glanduligera,* in the soil seed bank of an Australian *Eucalyptus* woodland, was promoted by heat and smoke (Enright & Kintrup, 2001). Further research is required to determine the role of a seed bank for *Drosera* species in New Zealand peatlands.

4.5 Conclusion

While previously, the role of the peat seed bank in restiad bogs was largely speculative, it is now clear that at least some species are capable of recovering from seed stored in peat and are stimulated to do so by environmental changes associated with fire, likely increases in light availability and/or temperature fluctuations. What remains unclear is the role that heat plays in stimulating germination. Further research should involve several heat treatments to accurately determine optimum germination responses. Ideally, peat samples should also be collected from more than one site and from sites of various time since last burn as this can influence seed production. Overall, this study has contributed to our knowledge of the links between fire and vegetation dynamics in New Zealand restiad bogs. Combined with knowledge of other life history traits, and information on how species interact with one another and with the physical environment, this information can enable more accurate predictions on plant community dynamics following fire or in the absence of fire.

Chapter Five

Conclusions

5.1 Introduction

This study set out to enhance the current understanding of the role of fire in driving restiad bog vegetation dynamics. This involved comparing measurements on species composition and structure, nutrient levels, light penetration, and near-surface temperature regimes between sites burnt at different times. Two reproductive responses were also assessed – fire-stimulated flowering, and post-fire germination from a peat seed bank. The results of this research contribute to a more complete understanding of the processes shaping plant community structure and composition at Kopuatai Bog, which are summarised here.

5.2 Immediate effects of fire

The immediate effects of fire at Kopuatai were to increase resource availability and alter the surface microclimate. Photo evidence from two weeks post-burn show complete combustion of herbaceous biomass and litter. This resulted in deposition in ash of many nutrients, including P, S, Ca, Mg, K, Na, Fe, Mn, Cu, and Zn, which were previously tied up in biomass. N levels did not increase in surface peat, suggesting that N in pre-existing vegetation had been volatilised, rather than deposited. These nutrient increases, particularly in P, may contribute towards temporary increases in plant productivity and also enable non-bog species to briefly colonise a burnt site. An important effect of fire was to create a bare peat surface fully exposed to sunlight. This is a substantial difference to the negligible amounts of light that penetrate an intact *Empodisma*-dominated community.

5.3 Short-term effects of fire (days to years)

The initial vegetation regeneration was dominated by "resprouters", capable of vegetative recovery, although "seeders" were abundant as small seedlings by 16 months post-fire. *Gleichenia, Machaerina,* and *Schoenus* rapidly re-established in the 2017 burn area via resprouting. *Empodisma, Epacris* and mānuka, although slower to recover, were common by 16 months post-fire, but it was too soon for this to be reflected in percent cover. Fire-stimulated flowering responses were found in *Machaerina* and *Schoenus* approximately two years post-fire.

The nutrient pulse was short-lived, with total nutrient levels in peat declining to pre-fire levels within two years. This decline presumably reflects uptake by regenerating vegetation which is supported by elevated levels of some foliar nutrients 16 months post-fire. Foliar nutrient data also suggests increases in plant-available nutrient forms. Notably, elevated levels of ^{15}N isotope in foliage collected 16 months post-fire indicate that P was more available (Clarkson *et al.*, 2005).

Within the period of sampling at the 2017 burn site, the surface microclimate was still strongly affected by fire. As the *Empodisma* canopy had not recovered, insolation was still high. This caused elevated daytime temperatures close to the peat surface on the burnt area. The impact on minimum temperatures, however, depended on season, with lower minima recorded on the burn during the coldest months of the year and higher minima during warmer months.

5.4 Medium-term effects of fire (decade)

By 14 years post-fire, environmental effects of burning were no longer detectable and the plant community had largely returned to its pre-fire condition, although some differences in species dominance and structure remained. Vegetation apparently takes longer than 14 years to recover to pre-fire structure, particularly for *Epacris* which was still shorter than in the unburnt area by this time. In terms of species dominance, *Machaerina, Schoenus*, mānuka, and *Epacris* had higher percent cover on the burnt area than the neighbouring unburnt area. The increase in mānuka can be explained by its well-documented serotinous response to fire. The strong fire-stimulated flowering responses measured in *Machaerina* particularly, but also in *Schoenus*, are likely responsible for the increase in cover of these species. Results from the germination experiment demonstrate that *Epacris* recruits new seedlings after fire from a peat seed bank, germination likely being stimulated by increased light. Although *Epacris* did not require fire-related cues for germination, the role of heat in promoting germination of other species, such as *Empodisma* and *Sporadanthus*, was unclear.

Empodisma had regained its former role as the most dominant species by 14 years. Height measurements indicate that this was sufficient time for recovery of the standing litter layer, dense enough to block out sunlight. The prevalence of *Empodisma* cluster roots and the recovery of the litter layer indicate that peat formation has resumed by this point too.

5.5 Long-term effects of fire (multi-decade)

The long-term recovery trajectory following fire, particularly in *Sporadanthus*-dominated areas, remains mysterious. Based on the findings described above, it was predicted that species that cue reproduction to fire would eventually decline in dominance after long periods without burning. Consistent with this pattern, species such as *Machaerina* and *Gleichenia* had low cover by 45 years post-fire, relative to more recently burnt sites. Percent cover of mānuka, and *Epacris,* however, were relatively high. It is unclear whether the abundance of these species is a result of recruitment after the 1974 fire or whether regeneration has occurred since then. As this site lacked a comparable unburnt site, this was impossible to clarify.

5.6 Summary

This research identified two previously undescribed reproductive responses to fire – fire-stimulated flowering in the sedge species and seed bank germination in *Epacris* – which led these species to become more dominant following burning, persisting even after 14 years. As seedling success is severely restricted by low light levels during inter-fire periods, I suggest that a dramatic increase in light availability is the most important driver of post-fire vegetation dynamics at Kopuatai, leading to selection for species which can respond to the window of opportunity afforded by the post-fire reduction in *Empodisma* cover.

5.7 Further research

Further experimentation involving various temperature treatments could resolve the possible role of heat in germination of some species, particularly for the restiads. To determine the effects of fire-related cues on germination of less common species, it may be more appropriate to treat seeds collected from plants rather than to treat peat.

This research demonstrates more clearly the links between fire and some of the most common vascular plants at Kopuatai Bog. The effect of fire on non-vascular bog species and species which are less common or absent from my study sites remains unclear. This research gap is important to fill, especially to ensure appropriate protection of threatened species.

An incidental finding, unrelated to the fire-associated aims of this thesis, is evidence that *Sporadanthus* may alter nutrient cycling within Kopuatai. Further research is required to back up the very tentative evidence provided in Chapter 2 for this hypothesis.

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