The role of the peat seed bank in plant community dynamics of a fire-prone New Zealand restiad bog

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Abstract New Zealand restiad bogs have histories of natural fire, which is reflected in the presence of plant species with adaptations such as serotiny and fire-stimulated flowering. The possibility of fire-cued germination has not been investigated in restiad bogs, despite its widespread occurrence in other fire-prone environments, globally. We performed a glasshouse experiment to assess the role of peat seed banks in post-fire regeneration at Kopuatai Bog in northern New Zealand. Peat samples collected were either (a) heated until they reached 70 °C, (b) exposed to wood smoke for 30 min, (c) heated and smoked consecutively, or (d) left untreated. The emergence of vascular plants was then monitored for 105 days in a glasshouse. Mean seedling density was highest in the control treatment (7228 ± SE 1040 m^{-2}); it was lowest in the heated samples, suggesting that the heat treatment may have been excessive. Smoke did not significantly increase emergence. *Epacris pauciflora* accounted for 76.7% of total seedlings, consistent with our hypothesis based on vegetation surveys that this species relies on synchronous post-fire seed bank germination. *E. pauciflora* was most abundant in the control, suggesting that emergence is in response to some disturbance-related cue other than heat or smoke. The restiad *Sporadanthus ferrugineus* was abundant in the control and smoke treatments. Its emergence following heating was reduced, but still considerable enough to cast doubt on its classification as a fire-sensitive species. In contrast, the dominant peat-forming restiad *Empodisma robustum* showed low levels of emergence. Our overall findings demonstrate that substantial quantities of viable seed are stored in the upper peat layers of a restiad bog and are capable of germinating in response to disturbance-related environmental changes. These findings contribute to our understanding of restiad peatland plant community dynamics, particularly explaining the mechanism behind increased *E. pauciflora* dominance post-fire.

Key words: fire-cued germination, Kopuatai, peatland, seedling emergence, wetland.

INTRODUCTION

Peatlands have high climate change mitigation value as efficient carbon storage ecosystems – they contain almost one-third of the world's soil organic carbon despite covering only 3% of Earth's land surface (Dunn & Freeman 2011). In a recent IPCC report, Jia et al. (2019) recommended their protection against threats, such as fire and drainage, which can lead to carbon sink reversal and the short-term release of carbon stored over several millennia. This view of fire as a threat is appropriate for the globally widespread *Sphagnum*-dominated peatlands which do not naturally burn frequently (Kuhry 1994; Sillasoo et al. 2011), and for drained or otherwise degraded peatlands which can burn underground for years. However, it may be a less useful view of intact Restionaceae-dominated (restiad) peatlands within Australasia where recurring fire is an important natural driver of vegetation dynamics (Newnham et al. 1995; Whinam & Hope 2005; Hope et al. 2019),

selecting for fire-adaptive plant traits (Clarkson 1997; Norton & De Lange 2003; Battersby et al. 2017). Prior to human arrival in New Zealand ca. 700 years BP, the site-specific fire return interval was approximately 100 years at our study site, Kopuatai Bog (Newnham et al. 1995; Perry et al. 2014).

Synchronous germination from a soil seed bank is a common strategy of re-establishment following disturbance (Warr et al. 1993). To date, the majority of seed bank studies concerned with fire have focussed on highly flammable grasslands (Morgan 1999; Ghebrehiwot et al. 2012), shrublands (Keeley & Fotheringham 1998; Wills & Read 2002), and sclerophyll forest ecosystems (Read et al. 2000; Penman et al. 2008). Similar responses might be expected in restiad bogs, which burn frequently. Flammability is partly a result of waterlogging and nutrient-poor tissues, which lead to slow decomposition and the accumulation of fine, well-aerated fuel loads >15 T ha^{-1} (Whinam & Hope 2005; Goodrich et al. 2015). In addition, the high polyphenol and lignin contents of *Empodisma* tissues may increase flammability (Kuder et al. 1998; Küçük & Aktepe 2017). Furthermore, *Empodisma*-dominated bogs have been described as

'wet deserts' because the low dense canopy creates a barrier to evaporation, resulting in high sensible heat fluxes creating an above-canopy microclimate more typical of arid environments (Campbell & Williamson 1997), which may favour the spread of fire.

However, to date there has been no research on post-fire emergence from seed banks of Australasian restiad-dominated peatlands, despite charcoal particles in cores indicating a long history of fire (Newnham *et al.* 1995; Whinam & Hope 2005; Hope *et al.* 2019). Recently, Trezise *et al.* (2021) documented the germination of 48 native species, including *Empodisma minus*, from the soil seed banks of *Gleichenia*-dominated heathy peatlands of the Fleurieu Peninsula of South Australia. Their study site, however, was not a true restiad bog in that restiad species were only a small component of the vegetation and the system was not isolated from groundwater nutrient inputs. Thus, it remains unclear what role peat seed banks play in the vegetation dynamics of New Zealand's restiad peatlands which are classified as endangered ecosystems (Holdaway *et al.* 2012).

Rapid regeneration after fire offers the benefits of growth during a period of decreased competition, higher light availability and a potential 'ashbed effect' of enhanced fertility (Bond & Van Wilgen 1996; Lamont *et al.* 2019). This may be especially important in New Zealand restiad-dominated peatlands where seedling development is usually restricted by a dense canopy of *Empodisma robustum* that admits <0.5% of light to the peat surface (Wilson 2020). Cueing of germination to fire is therefore likely to greatly increase seedlings' chances of survival (Gill & Groves 1981).

Common plants native to Aotearoa/New Zealand restiad peatlands express a range of mechanisms for persistence in frequently burnt environments. These include serotiny in *Leptospermum scoparium* (Battersby *et al.* 2017), fire-stimulated flowering in *Corybas carsei* (Norton & De Lange 2003) and *Machaerina teretifolia* (Wilson 2020), and rhizomatous resprouting in *Gleichenia dicarpa* (Clarkson 1997). Post-fire increases in abundance of *Drosera* and *Epacris* species in these ecosystems are suspected to reflect synchronous germination from a peat seed bank (Johnson 2001; Wilson 2020), although this hypothesis has not been tested.

Synchronous seedling emergence is regulated by seed dormancy and germination cues that seeds receive due to changes associated with fire (Keeley & Fotheringham 2000; Finch-Savage & Leubner-Metzger 2006). In certain species, dormancy may be broken by fire-cues cracking the impermeable seed coat, or germination promoted directly by chemicals in smoke (Auld & O'connell 1991; Brown & Van Staden 1997; Read *et al.* 2000; Penman *et al.* 2008). Fire may also promote germination indirectly,

through the increased diurnal temperature fluctuations (Probert 2000) and enhanced light availability (Pons 2000) in the post-fire environment.

We conducted a glasshouse experiment using peat from a large intact restiad bog in New Zealand, to determine (a) whether there is a viable peat seed bank and (b) whether emergence is enhanced by fire-related cues. This will enable improved predictions of post-fire vegetation dynamics and inform conservation management of restiad bog plant ecosystems, which have been greatly reduced in extent since European settlement of New Zealand. Knowledge of germination may also have a practical application for peatland restoration by assisting in the propagation of species that are notoriously difficult for growers to germinate, such as those belonging to the Restionaceae and Ericaceae families (Langkamp 1987; Meney & Dixon 1988).

METHODS

Site description

Peat was collected from Kopuatai Bog, a 100 km^2 restiad bog in northern New Zealand (Figs 1, 2). Kopuatai is classified as a domed bog due to the accumulation of peat over the past ~11 000 years (Newnham *et al.* 1995) creating a convex dome raised above the local topography. The raised surface elevation has the effect of isolating the peatland from the influence of groundwater, making it an ombrotrophic ecosystem entirely reliant on rainfall for nutrient inputs. While horticultural peat harvesting occurs in the nearby Torehape Bog (Clarkson *et al.* 2013), and *Sphagnum* harvesting is a 5 million dollar industry for New Zealand (Plant and Food Research 2020), there is no commercial harvesting at Kopuatai Bog. Essentially unmodified, except at its margins, Kopuatai Bog is the largest remaining raised bog in New Zealand (McGlone 2009).

The main plants found at Kopuatai are listed in Table 1. Vegetation is dominated by the jointed wire rush, *Empodisma robustum*, which forms a dense intertwined canopy of dead and living stems, typically up to ~0.8 m high (Goodrich *et al.* 2017). Spatial variations in plant community composition are thought to be influenced by nutrient availability and fire history (Irving *et al.* 1984). Phenological information available for local species is limited. However, it is known that *Leptospermum scoparium* at Kopuatai is highly serotinous, only releasing seed abundantly after fire (Battersby *et al.* 2017). Similarly, the local sedge species, *Machaerina teretifolia* and *Schoenus brevifolius*, express fire-stimulated flowering (Wilson 2020) and can be expected to deposit seed abundantly only for a few years post-fire. *Empodisma robustum* at Kopuatai Bog produces large quantities of seed in summer, specifically December and January (Sharp 1995). Fruiting times for other common species, such as *Sporadanthus ferrugineus* and *Epacris pauciflora*, are undocumented. Of the species listed in Table 1, *Machaerina*, *Schoenus*, and *Gleichenia* are documented as resprouters, capable of rapid regrowth from fire-protected rhizomes (Clarkson 1997; Wilson 2020). *Empodisma* is reported to

Fig. 1. Satellite image of Kopuatai Bog, situated in the Hauraki Plains of the North Island. Source: Google Earth.

Fig. 2. An aerial view of Kopuatai Bog. Except for the margins and *Sporadanthus*-dominated patches such as at the back left of this photo, the vegetation is dominated by *Empodisma robustum*. Photo credit: Georgie Glover-Clark.

Table 1. Common plants at Kopuatai Bog. Species listed here were present in at least 40% of quadrats within one or more vegetation types, as surveyed by Irving *et al.* (1984)

Species	Family
Seed-bearing plants	
Dracophyllum lessonianum	Ericaceae
Drosera binata	Droseraceae
Drosera spatulata	Droseraceae
Empodisma robustum	Restionaceae
Epacris pauciflora	Ericaceae
Leptospermum scoparium	Myrtaceae
Machaerina teretifolia	Cyperaceae
Schoenus brevifolius	Cyperaceae
Sporadanthus ferrugineus	Restionaceae
Ultricularia delicatula	Lentibulariaceae
Spore-bearing plants	
Campylopus acuminatus var. *kirkii*	Dicranaceae
Goebelobryum unguiculatum	Acrobolbaceae
Gleichenia dicarpa	Gleicheniaceae
Lycopodiella lateralis	Lycopodiaceae
Lycopodiella serpentina	Lycopodiaceae
Sphagnum cristatum	Sphagnaceae

More recent but less quantitative surveys have been done by Wildlands (2016). Lichens and soil-surface algaes have not been studied in detail, although Irving *et al.* (1984) noted that *Cladia* and *Cladonia* lichen species were common in some areas.

regenerate occasionally by resprouting but predominantly by seed (Clarkson 1997; Wagstaff & Clarkson 2012).

As determined by charcoal fragments in peat cores taken from a location in Kopuatai Bog approximately 4 km south of our collection site, the fire return interval (the average interval between two successive fire occurrences at the same place) was approximately 100 years during the pre-human period of 1850–700 BP (Newnham *et al.* 1995). Kopuatai thus appears to have naturally burned more frequently than most other New Zealand ecosystems, especially forests which probably had return times of one or two millennia at that time (Ogden *et al.* 1998). Electrical storms, although not frequent in NZ, ignited occasional fires on the eastern sides of both the North and South Islands of New Zealand during drought years in pre-human times (Ogden *et al.* 1998; Christian *et al.* 2003). Volcanism was a more localized and less frequent source of ignition, initiating large-scale burns somewhere in the central North Island every 300–600 years (Lowe 1988; Ogden *et al.* 1998; Ratcliffe *et al.* 2020). The relatively high fire rate for northern New Zealand peatlands is thought to be due to the flammability of the *Empodisma* canopy, which is composed of fine, dry, well aerated plant material that is slow to break down. Furthermore, North Island bogs tend to burn more regularly than South Island bogs, probably because of a summer rainfall minimum throughout much of the north, compared to the more uniform rainfall patterns in the south (Perry *et al.* 2014). Following human arrival in the area c. 700 BP, the estimated fire frequency at Kopuatai increased to 1 in 78 years, although it was probably higher than this during the 20th century when fire was commonly associated with surrounding land development practices. A 1974 report to the then managing body, the Hauraki Catchment Board, described how Kopuatai experienced a major fire every 3–5 years during this time (Harris 1974). Since the 1970s, however, Kopuatai has not had any large-scale fires, primarily because of cessation of new wetland drainage activities, but also because of regulated fire management. Recently, lightning-initiated fires occurred at Kopuatai in

2005, 2017, and 2020. As per the current fire management policy, which sees fire as a threat to the conservation values of the site, these were promptly extinguished so had small spatial extents.

Peat was collected from a 50 × 50 m area in the northeast of Kopuatai (−37.3712, 175.5537). This site was probably last burnt in 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 patterns evident in aerial photographs from 1975 consistent with recent burning (see Wilson 2020). The vegetation at this site is dominated by the restiads *Empodisma robustum* and *Sporadanthus ferrugineus*, the fern *Gleichenia dicarpa*, the sedges *Machaerina teretifolia* and *Schoenus brevifolius*, the small tree *Leptospermum scoparium* and the shrub *Epacris pauciflora*. As all of these species belong to different genera, they will be referred to by their genus names henceforth.

Sample collection

Peat sampling was incorporated into concurrent vegetation surveys which used a point intercept method to assess vegetation structure and composition (see Wilson 2020). A 50 m × 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 10 random distances along each transect, vegetation sampling was carried out using a point intercept method. At each point along six of these transects, a soil core (8 cm diameter, 5 cm depth) was extracted, totalling 60 cores. We only sampled from six transects to ensure collection could be completed in a day. The total surface area of peat collected was 0.302 m² and the total volume was 0.015 m³. While viable seeds have been found at depths of up to 50 cm in a Northern Hemisphere bog (Jauhiainen 1998), 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; Trezise *et al.* 2021) and because viable seeds are typically concentrated at the surface and become scarcer with increasing depth (Benoit *et al.* 1989; Jauhiainen 1998; Csontos 2007). Based on the present rate of peat accumulation in northern Kopuatai of 2.6 mm y⁻¹, a 5-cm depth correlates to approximately 19 years (Newnham *et al.* 1995). Samples were collected on 11 December 2019. At this time of year, surface peat is likely to contain freshly deposited seeds of *Empodisma* and possibly other species for which phenology is unknown. It is unlikely to contain substantial amounts of seed of *Leptospermum*, *Machaerina*, or *Schoenus*; which have seed production or release linked to fire. Samples were treated the following day after collection, with peat field moisture content retained through all steps.

Experimental treatment

The regeneration pattern of many seeders, involving synchronous seedling emergence following burning but minimal emergence during fire-free periods, is regulated by seed dormancy and/or germination requirements (Keeley & Fotheringham 2000). 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 promote germination (Auld & O'connell 1991; Pérez-Fernández *et al.* 2006; Nelson *et al.* 2012; Liyanage & Ooi 2015), or indirectly such as via (c) increased diurnal temperature fluctuations which can rupture the seed coat and increase permeability to water (Probert 2000), or (d) enhanced light availability which relieves physiological dormancy (Pons 2000).

We homogenized the peat from our 60 cores to maximize our chances of detecting any effects of treatments by minimizing other sources of variation between replicates. The cores were teased apart by hand and coarse roots and rhizomes were removed, after which the peat was mixed thoroughly and then divided by wet weight into 20 approximately equal 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 to 2–3 cm depth in aluminium trays and heated simultaneously in an oven preheated to 100°C, until the peat reached 70°C as measured in two randomly selected trays by analogue thermometers. 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 based on an assumption that, while soil temperature during a moderate intensity fire has been reported to be approximately 80°C (Auld & O'connell 1991), the high water content of peat at Kopuatai (Campbell & Williamson 1997), would slow heating during natural fires there. Without any available information on surface peat temperatures in restiad peatland fires, we considered that 70°C was appropriate. Samples being treated with both heat and smoke were heated first. All samples were prepared for the glasshouse by spreading the peat to a depth of approximately 2 cm over the surface of 5 cm of sterile Tui brand all-purpose potting mix in 0.103 m² plastic germination trays (35 × 29.5 cm).

The smoke treatment was applied by exposing trays to smoke for 30 min, following Gilmour *et al.* (2000). A bee smoker was used to generate the smoke, 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 1.8 m³ sealed plastic bag containing the trays. At all times during the treatment, the bag was filled with thick smoke. After 30 min, trays were removed from the tent and lightly misted with water.

Following treatment, all 20 trays were arranged in a randomized order on benches in a closed section of the University of Waikato glasshouse. Every 2 weeks, the order of the trays was re-randomized. To prevent contamination from air-borne seeds, all trays were covered with fine white mesh. Trays were watered for 6 min twice daily by an automatic watering system and were also regularly checked and watered by hand when the peat was unevenly moist. Automatic ventilation was set to limit the maximum air temperature to around 28°C, while minimum temperature was not controlled. During the experiment, mean daily maximum

air temperature in the enclosure was 27.9°C and mean daily minima was 16.3°C. Trays were checked for seedlings every 2 days during the first 5 weeks, and once per week thereafter. New seedlings were tagged and labelled with the date they were first observed and left to grow until they could be identified. Non-vascular plants were not recorded. The experiment commenced on 13 December 2019 and concluded on 27 March 2020, totalling 105 days.

We used a LAI-2200C Canopy Analyser (LI-COR 2016, Lincoln, NE, USA) to quantify light environments in the glasshouse. Six measurements were taken beneath the mesh covering the seedling trays, at randomly spaced points on two transects run along the benches. The LAI-2200 calculates diffuse irradiance as the proportion of light simultaneously measured nearby by another sensor with an unobstructed view of the sky. Light was found to be $26.1 \pm 0.6\%$ of that outside the glasshouse, which is roughly comparable to the average light availability of $19.5 \pm 3.4\%$ measured at a site at Kopuatai that was burnt approximately 2 years prior (Wilson 2020).

Data analysis

To determine whether seedling emergence 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 emergent species, *Epacris*, *Sporadanthus*, and *Empodisma*. Emergence rates across treatments were investigated by plotting cumulative seedling densities over the duration of the experiment.

Differences in composition among treatments were tested by permutational multivariate analysis of variance (PERMANOVA) using the Bray–Curtis similarity index. This was done using the vegan package within R (Oksanen *et al.*

2010). To see how representative the seed bank was of the above-ground plant community, a Spearman rank-order correlation was carried out between the total number of emergent seedlings of each species and percentage cover of each species in the standing vegetation. This non-parametric correlation was used because of intractable non-normality, including some zero values.
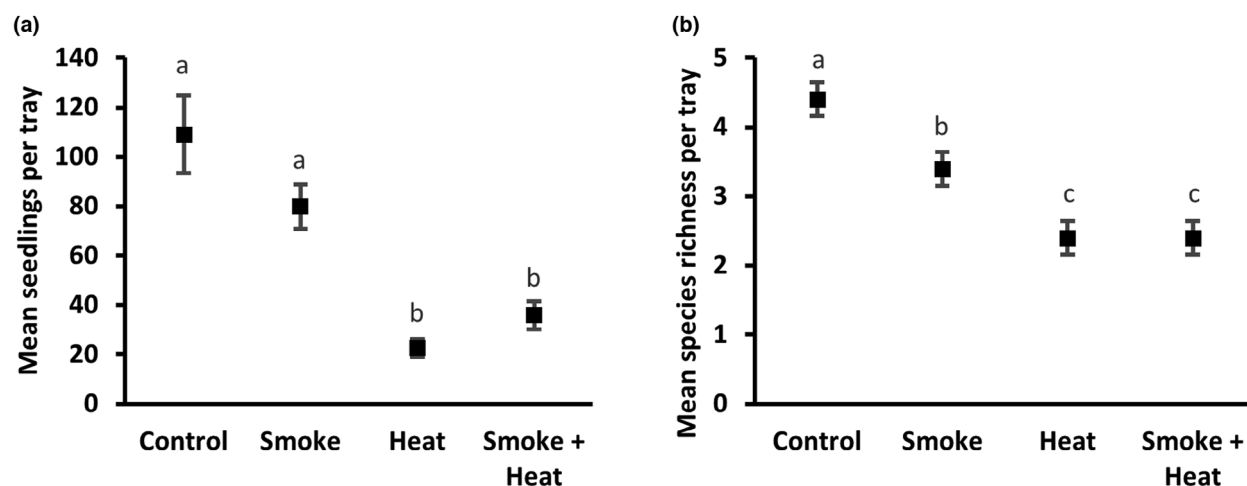
RESULTS

Seedling density and species richness

A total of 1236 seedlings were recorded from the 20 sample trays over the 105-day duration of the experiment. The density of emergent seedlings differed significantly among treatments (Fig. 3a, Table 2). Post-hoc comparisons found that, compared to the control, the smoke treatment did not affect seedling density ($P = 0.18$; Fig. 3a, Table 2). Both of the heated treatments, however, produced significantly fewer seedlings than the control (p(Heat) < 0.001, p(Smoke + Heat) < 0.001; Figure 3a, Table 2), suggesting that the heat treatment killed many seeds.

Species richness differed significantly among treatments ($P < 0.001$; Fig. 3b). Richness was highest in the control, and lowest in the two heated treatments, once again indicating damage to seeds during the heat treatment (Table 2).

Species composition

Seedlings of eight species emerged during the experiment. Of these, *Epacris*, *Sporadanthus* and *Empodisma*

Fig. 3. (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 2. Total number of emergent seedlings per treatment, mean seedling density ($\pm$ one standard error) per square metre of bog surface area, total number of emergent species per treatment and the number of unique species which occurred in one treatment only

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

Density values followed by the same letter (by column) are not significantly different (ANOVA and Tukey's HSD test: $P > 0.05$).

were present in all the treatments. *Epacris* was the most abundant emergent seedling, making up 77% of the total seedling count at 948 individuals (Table 3). The second most abundant species was *Sporadanthus* at 221 seedlings (17.9%), followed by *Empodisma* at 43 (3.5%), *Leptospermum* at 17 (1.5%) and *Machaerina* at 2 (0.2%). The forked sundew, *Drosera binata*, and non-natives *Cyperus eragrostis* (tall flatsedge) and *Cirsium vulgare* (bull thistle), were each recorded once.

No species departed markedly from the overall trend of emergence being highest in the control and smoke treatments. Emergence of *Epacris* was significantly reduced by heating, but unaffected by smoke (Table 3). *Sporadanthus* was significantly more abundant in the control than in any other treatment, and least in both heated treatments. *Empodisma* seedling density did not differ significantly among treatments, but this is probably a reflection of small sample size. *Leptospermum* was present only

in the control and smoke treatments, suggesting sensitivity to high temperatures. *Machaerina* was recorded once in the heat treatment and once in the smoke treatment.

Time course of emergence

While the patterns of emergence were similar between the control and smoke treatments, the heat treatment caused a 10- to 20-day delay in emergence and a reduction of total seedlings (Fig. 4a). This overall pattern was closely paralleled by *Epacris*, reflecting the abundance of *Epacris* seedlings (Fig. 4b). *Epacris* also emerged over a longer period than the less common species (Fig. 4b–e), with *Epacris* seedling counts plateauing after ~80 days compared to *Empodisma* (~60 days), *Sporadanthus* and *Leptospermum* (both ~40 days). The heat treatment caused emergence delays in the restiad species (Fig. 4c,d). Overall, the main effect was that heat slightly delayed the onset of emergence and reduced the rate and total number of seedlings.

Species composition between treatments

PERMANOVA found significant differences in species composition between treatments (Table 4). The only insignificant pairwise differences were between the control and smoke treatments and between the heat and smoke + heat treatments.

## Species composition compared to collection site

No significant correlation was found between species composition of the standing vegetation at the collection site and species composition of seedling communities in the experiment ($r_s = 0.40$, $P = 0.25$). The

Table 3. Total seedling density and individual species density per treatment and significance of differences

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	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.

Where ANOVA found a significant difference ($P < 0.05$), shared letters along rows indicate no significant difference (Tukey's HSD test: $P > 0.05$).
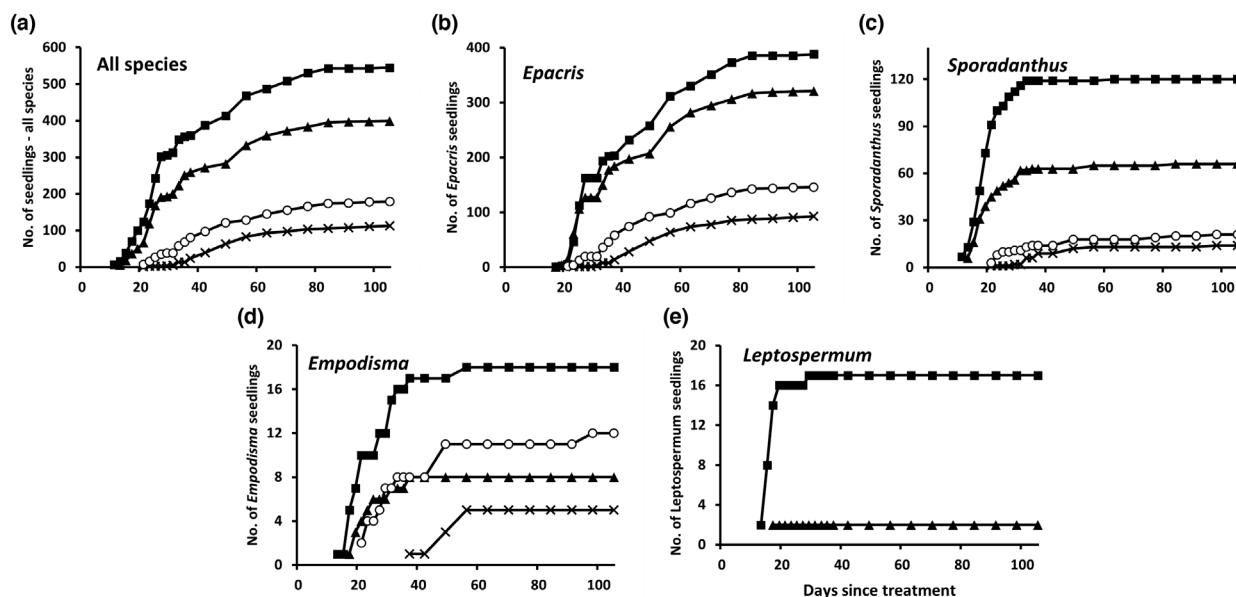
Fig. 4. (a–e). Cumulative seedling density of (a) all species, (b) *Epacris pauciflora*, (c) *Sporadanthus ferrugineus*, (d) *Empodisma robustum* and (e) *Leptospermum scoparium* in each treatment (■, control; ▲, smoke; **x**, heat; ○, smoke + heat). Note the differences in y-axis scales.

Table 4. PERMANOVA results showing differences in species composition between all treatment pairs

Treatment 1	Treatment 2	F	R^2	p
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

Significant differences are in bold ($P < 0.05$). The overall effect of treatment on species composition was highly significant ($F = 9.15$, $R^2 = 0.632$, $P = 0.001$).

most notable difference in rank order was that of *Epacris* which emerged in far greater numbers than any other species, despite ranking only sixth in terms of percentage cover in the field (Table 5). While *Epacris* made up 11.3% cover at the collection site, the number of seedlings across all treatments equated to 3143 m^{-2} (or 5146 m^{-2} in the control treatment). *Empodisma*, which was the most prevalent species in the field, was only the third most abundant seedling in the experiment. Species that were common in the standing vegetation but failed to emerge in the experiment included *Gleichenia* and *Schoenus* (Table 5), although *Gleichenia* gametophytes may have been overlooked due to their visual similarity to liverworts growing in the trays. *Sporadanthus*, *Leptospermum* and *Machaerina* emerged roughly in proportion to their abundance in the standing vegetation (Table 5). Only

Table 5. 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 ($\pm$ SE) m^{-2}
Empodisma robustum	96.3	43	142.6 $\pm$ 32.7
Sporadanthus ferrugineus	48.8	221	732.8 $\pm$ 143.4
Leptospermum scoparium	31.3	19	63.0 $\pm$ 25.2
Gleichenia dicarpa	28.8	-	-
Schoenus brevifolius	15.0	-	-
Epacris pauciflora	11.3	948	3143.3 $\pm$ 451.7
Machaerina teretifolia	5.0	2	6.6 $\pm$ 6
Drosera binata	-	1	3.3 $\pm$ 3.3
Cyperus eragrostis†	-	1	3.3 $\pm$ 3.3
Cirsium vulgare†	-	1	3.3 $\pm$ 3.3

†Non-native species.

two seedlings of *Machaerina* were recorded, which corresponded with its low abundance in the field (Table 5).

DISCUSSION

Kopuatai peat contains a viable seed bank

A seed bank of considerable size accumulates in the surface peat of a New Zealand restiad bog, with the highest density of 7228 $\pm$ 1040 seedlings m^{-2} found in the control treatment. This is a relatively high seedling density compared to studies using similar methods in other fire-prone ecosystems. For instance, Trezise *et al*. (2021) found 2649 native seedlings m^{-2} emerged from south Australian heathy peatland soil (5 cm depth), with no significant difference between a control and a heat + smoke treatment. Heat-treated soil samples (5 cm depth) from a south-eastern Australian heathland yielded seedling numbers equating to 4575 seedlings m^{-2} in the field (Wills & Read 2002), and heat- and smoke-treated soil samples (2.5 cm depth) from a dry sclerophyll forest in New South Wales bore 2887–7578 germinants m^{-2} (Read *et al*. 2000). Soil seed bank densities in South African fynbos have been reported to range from 1683 to 4518 seedlings m^{-2} (5 cm depth) (Pierce & Cowling 1991). Higher densities of 6510–12 148 seedlings m^{-2} germinated from naturally burnt Scottish *Calluna* heathland soil (2–3 cm depth) (Mallik *et al*. 1984), and 8000–25 000 seedlings m^{-2} from Californian chaparral soil (5 cm depth). The Kopuatai seed bank appears to be relatively well-stocked, although it is dominated by a single species, *Epacris pauciflora*.

Is the seed bank directly fire-stimulated?

The reduced emergence of all species in the heated treatments may mean the treatment intended to simulate the passage of fire was too intense. While this may have obscured any potential heat effect, high rates of emergence in the unheated samples (smoke, control) indicate that, particularly for *Epacris pauciflora*, heat was not required to break dormancy. The three most abundant emergents (*Epacris*, *Sporadanthus* and *Empodisma*) also showed some emergence, albeit at lower levels, in the heated treatments (Table 3) suggesting some intra-specific variation in heat tolerance of these species' seeds.

Treating the peat while wet may have contributed to low emergence. Physical dormancy, or hard-seededness, caused by an impermeable seed coat is a trait seen in only 17 families (Baskin *et al*. 2000, 2006; Horn 2004), none of which feature in this study. Therefore, it is likely all seeds were hydrated during the treatment. As seeds with elevated moisture contents have lower lethal temperature thresholds (Tangney *et al*. 2019), this is likely to have led to increased mortality. However, while wet heat is more damaging for seed survival, moist soils have a higher heat capacity than dry soils, and so can be expected to remain cooler in a fire. This may have implications for post-fire seedbank responses in the field where surface peat moisture contents vary seasonally.

Smoke did not enhance seedling emergence compared to the control (Table 3). As with the heat treatment, emergence may have been impacted by the seeds' moisture status (Turner *et al*. 2009; Long *et al*. 2010). For instance, Long *et al*. (2010) found that dry seeds germinated better than hydrated seeds in response to the smoke-derived compound karrikinolide. However, *Sporandanthus* showed a significantly lower emergence in the smoke treatment compared to the control (Table 3), which is potential evidence that smoke is harmful to *Sporadanthus* seeds. Interaction effects between heat and smoke require further experimentation.

Is the seed bank indirectly fire-stimulated?

The high rate of emergence in the control treatment indicates that germination is cued by some environmental difference between the glasshouse and the undisturbed peat surface of the bog, particularly for *Epacris*. The most apparent environmental change resulting from fire at Kopuatai is light availability – measurements under intact *Empodisma*-dominated canopies found that negligible light typically reaches the peat surface (Wilson 2020), whereas the peat in our experimental treatments received an estimated 26% of full sunlight. The spectral quality of light at the peat surface may also be affected by fire, due to the removal of a canopy of vegetation containing chlorophyll pigments which absorb red light more effectively than far red light (Pons 2000). However, this is unlikely to be the main germination trigger at Kopuatai where the *Empodisma* canopy consists largely of dead plant matter. Globally, these disturbance-related changes in light environments cue germination in many species (Pons 2000) and it is likely that light plays a role in seedling emergence from New Zealand restiad bog seed banks. While effects are likely to be greatest at the peat surface, a previous study has found that, in some species, seeds buried up to 8 cm deep can be stimulated by 5 min of red light exposure at the soil surface (Benvenuti *et al*. 2001).

Removal of canopy vegetation by fire also leads to higher daily maximum temperatures, and lower minimum temperatures during winter (Wilson 2020). These enhanced temperature fluctuations are known to stimulate germination in a large number of species including several growing in fire-prone South African

fynbos vegetation which emerge in pulses following fire to form even-aged stands (Brits 1986; Pierce & Moll 1994). It is unlikely to be the stimulant for germination in this study, however, due to properties of the glasshouse reducing thermal amplitude compared to an open field site.

Implications for plant community dynamics of New Zealand restiad bogs

The main species growing at the collection site all emerged as seedlings in the experiment (Table 5). There were, however, notable differences between the restiad-dominated vegetation site and the experimental seedling communities which were dominated by *Epacris* (Table 5). There are several possibilities for such incongruencies which are common in this type of study (e.g. McGraw 1987; Wills & Read 2002). Firstly, certain species in the peat seed bank may not have received an appropriate stimulus (or stimuli) to promote germination – although, as this study did not involve any species known to undergo physically dormancy, it is unlikely that a different heat treatment would have yielded better results than the control (Baskin *et al.* 2000, 2006; Horn 2004). Secondly, the methods used to measure vegetation composition differ between the field (point intercept method) and the glasshouse (individual seedling counts). This may have implications for species such as *Empodisma* which can occupy a large area via vegetative growth from a single plant (Clarkson & Clarkson 1984; Sharp 1995). Conversely, a large number of *Epacris* seedlings may not necessarily lead to a large number of mature *Epacris* plants if rates of seedling mortality are high. Thirdly, contribution to the seed bank depends on variable rates of seed production and release. This may be related to fire-timed reproductive efforts, such as fire-stimulated flowering or serotiny. For instance, seed banks of species such as *Machaerina* and *Schoenus*, which flower profusely after fire at Kopuatai and at minimal rates when undisturbed (Wilson 2020), may have been depleted during the 45 years elapsed since the last known fire at the site (cf. Noble & Slatyer 1980). Fire-stimulated flowering is especially common in resprouters, which allocate resources to the production of fire-resistant underground organs at the expense of seed production during fire intervals (Bond & Midgley 2001); this may explain why *Schoenus* has 15% cover in the field but did not emerge from peat samples during our experiment. Finally, species with patchy or uncommon distributions in the field may not have been detected due to insufficient sampling intensity.

The overrepresentation of *Epacris pauciflora* seedlings in our experiment, relative to the species' abundance in the standing vegetation (Table 5), indicates that recovery from a seed bank is this species' primary method of post-disturbance regeneration. As hypothesized, seed bank recovery is the mechanism by which *Epacris pauciflora* can increase its dominance after fire, as detected at a historical burn site at Kopuatai bog by Wilson (2020). While some Australian species of *Epacris* are more specifically adapted to fire, in that their germination is enhanced by exposure to heat and/or smoke (Keith 1997; Gilmour *et al.* 2000; Enright & Kintrup 2001; Penman *et al.* 2008), *Epacris pauciflora* evidently responds to a more general disturbance-related cue which offers the same benefits of early colonization.

Following fire in New Zealand bogs, *Empodisma* is capable of re-establishing itself as the dominant cover species within approximately 4.5 years (Clarkson 1997). This is despite its lack of traits that might be expected to enable rapid recolonization: it is a poor resprouter (Timmins 1992; Clarkson 1997) and, according to our results, has low emergence rates from the peat seed bank (Table 3). This species' ability to reclaim dominance may be due to vegetative expansion. Clarkson and Clarkson (1984) observed a circular patch (0.2 ha) of *Empodisma robustum* which they understood to have resulted from 'colonization and subsequent radial vegetative spread'. This asexual growth strategy dominates in stable ecosystems, enabling *Empodisma* to spread despite its thick canopy restricting seedling establishment (Sharp 1995). It may also give *Empodisma* a competitive advantage in the later stages of post-disturbance recovery, meaning it does not have to rely on early establishment to survive in an environment with a natural fire return interval of ~100 years (Newnham *et al.* 1995). Parallels can be drawn between this restiad bog ecosystem and that of the *Gleichenia microphylla*-dominated heathy peatlands in the Australian Fleurieu Peninsula. There, *G. microphylla* is capable of gaining dominance in the later stages of regeneration, probably via vegetative spread, thus overtopping and outcompeting most ground-stratum species (Trezise *et al.* 2021). Fire provides a period of reduced competition, which several species exploit by regenerating rapidly from soil-stored seed (Trezise *et al.* 2021).

The abundant emergence of *Sporadanthus* from the seed bank, including from the heat-treated samples (Table 3), seems at odds with its depiction in the literature as a particularly fire-sensitive species. 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 Chatham Islands 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 our experimental results (Table 3). It is possible that the loss of *Sporadanthus* from many places has been caused by multiple fires occurring in close succession, with the second occurring before the seed bank could re-establish itself (cf. Noble & Slatyer 1980).

Leptospermum at Kopuatai is highly serotinous, releasing few seeds in the absence of fire (Battersby *et al.* 2017), so its poor representation in the peat seed bank was an expected result. This finding corroborates other studies reporting *Leptospermum*'s lack of an effective peat seed bank (Mohan *et al.* 1984; Bond *et al.* 2004).

While abundant in the standing vegetation, the tangle fern *Gleichenia dicarpa* did not appear in any of our germination treatments. Similarly, an experimental study of seed/spore banks in south Australian heathy peatlands reported no emergence of *Gleichenia microphylla*, despite the dominance (44% cover) of this species in the standing vegetation (Trezise *et al.* 2021). These patterns may be due to the fern's reproduction mode. Viable 'spore banks' have been identified for at least some fern species (Penrod & Mccormick 1996; Ramírez-Trejo *et al.* 2004; Esaete *et al.* 2014), and it is possible that *Gleichenia* gametophytes were overlooked, especially as they look superficially similar to liverworts which were present. However, seed/spore bank recovery is much more common in angiosperms, and it is more likely that *Gleichenia* relies solely on resprouting for early regeneration as other studies have suggested (Walker & Boneta 1995; Clarkson 1997; Mcqueen & Forester 2000).

The single *Drosera binata* seedling in our study is not enough evidence to support Johnson's (2001) hypothesis that it is capable of rapid recovery via seed bank germination. However, several *Drosera* species overseas accumulate dense seed banks which respond to fire-related cues (Egawa *et al.* 2009, Enright & Kintrup 2001). Further research may require a different sampling approach, such as collecting seed rather than peat, due to *Drosera*'s paucity at Kopuatai (Irving *et al.* 1984).

Where plant reproduction events are linked to disturbance, alterations to the natural fire regime can influence local plant community dynamics. In managing these ecosystems, the potential impacts of current fire-suppression policy should be considered. However, consideration must also be given to the effects of climate change on fire regimes. Although rainfall at Kopuatai is predicted to change little during the 21st century, faster evapotranspiration due to rising temperatures will result in larger summer water deficits, making ignition and fire propagation more likely (Verbesselt *et al.* 2007). Furthermore, underground peat fires can be expected to become more common as drier conditions lead to lower water tables. Taking weeks to years to put out, peat fires can result in large carbon releases and the destruction of underground seed banks and the rhizomes of resprouting species. The year 2022 has already seen severe peat fires in two of New Zealand's remaining peat bogs, Awarua and Kaimaumau (De Graaf & Jensen 2022; Jackson 2022). Although the causes of these fires are pending investigation, hotter and drier conditions relating to climate change may have contributed to their severity. Improving our understanding of phenology as it is related to fire will assist with predicting how restiad peatland plant communities will respond to different fire regimes.

CONCLUSION

This experiment demonstrated that some species native to New Zealand restiad bogs can re-establish after fire by germination from the peat seed bank. *Epacris pauciflora* was by far the most common seedling, supporting our hypothesis that synchronous emergence from a well-stocked seed bank is the mechanism by which this species can increase its dominance after fire. The highest seedling density was in the control, indicating that germination is stimulated by some environmental change between the bog and the glasshouse. These changes may relate to increases in light availability and/or temperature fluctuations which are also associated with the post-fire environment and are common triggers for germination. The heat treatment we applied was probably too intense, so the role of heat (and a heat/smoke interaction) remains unclear. In general, fire treatments reduced seedling emergence, suggesting that there is a general disturbance response that cues germination, but perhaps fire cues are not as prominent in these peatland ecosystems as other disturbance effects.

Further research should involve different heat treatments and sampling from several locations with varying times since last burn. Seeds can differ substantially in the optimum intensity and duration of heat to promote germination and treating peat with various heat treatments may have yielded more informative results. For instance, some studies have found short exposure to high temperature to be better at stimulating germination than prolonged exposure at moderate temperature (Keeley & Fotheringham 2000; Gashaw & Michelsen 2002). In-field measurements of peat heat fluxes during fire would be instructive for future studies, as would data on the implications of peat moisture content for post-fire

germination. Future seed bank studies would also benefit from an improved knowledge of local species' phenology to determine whether the persistent seed bank or freshly deposited seed is being collected.

Overall, this study has added a new dimension to our understanding of how fire influences regeneration and plant community composition 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 of plant community dynamics under different fire regimes.

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AUTHOR CONTRIBUTIONS

Clara Renée Wilson: Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (lead); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Christopher H. Lusk:** Conceptualization (equal); methodology (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal). **David Ian Campbell:** Conceptualization (equal); funding acquisition (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal).

CONFLICT OF INTEREST

There are no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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