Proceedings of the
Linnean Society of New South Wales

Below-ground in grassy woodland: smoke, heat and fire effects on the soil seedbank of remnant Cumberland Plain Woodland in Western Sydney

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ABSTRACT

Cumberland Plain Woodland (CPW) is the original native vegetation of the shale soils in Western Sydney but now so reduced in extent that it has been declared a Critically Endangered Ecological Community. While the species composition of above-ground CPW is well documented, this is not the case for the below-ground seedbank. An investigation of the below-ground seedbank was undertaken for two sites of remnant CPW to determine species presence, growth form and numbers, and whether germination treatments of smoke, heat or fire affected species composition. Soil blocks taken in June 2001 were subjected to the following treatments: untreated controls, aerosol smoke, heat, smoke and heat, or fire. Seedlings were counted over July – November and left to grow on to allow identification where possible. A total of 10,436 seedlings appeared, of which 7,596 from 60 taxa were identified. The study showed that natives were present in the seedbank, were responsive to germination cues and outnumbered exotics both in species richness and number of seedlings.

Of the identified seedlings, 43 were native species and 17 were exotics. Native forbs, shrubs and grasses each had 10 or more species. Exotics were largely forbs and some grasses. 39% of the CPW groundcover and shrub indicator species appeared in the experiment. Germination treatments significantly increased total natives species richness; smoke alone gave a significant increase over the control, and heat or heat plus smoke gave further significant increases. Species richness of exotics did not respond to any of the germination treatments.

Seedlings numbers were dominated by natives, with 6,503 counted (5,011 identified as *Themeda triandra*). Exotics numbered 1,073 seedlings. Germination treatments significantly increased numbers of seedlings for native shrubs, and approached significance for total natives and for grasses. Numbers of exotic seedlings, while highest in the controls, did not vary significantly with germination treatments. Seedlings from 8 individual species responded to germination treatments in the same way over both sites; 4 were natives in which numbers of seedlings increased, and in a further 4 species (1 native, 3 exotic) numbers of seedlings decreased.

Natural History in all its Branches

E. Charles Morris (2025) Below-ground in grassy woodland: smoke, heat and fire effects on the soil seedbank of remnant Cumberland Plain Woodland in Western Sydney *Proceedings of the Linnean Society of New South Wales* **147**, 91-99.

Published on 27 December 2025 at https://openjournals.library.sydney.edu.au/index.php/LIN/index

Manuscript accepted for publication 10 December 2025

Keywords: Soil seedbank, grassy woodland, Cumberland Plain Woodland, germination cues, heat, smoke, fire

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ISSN 1839-7263

Species composition was significantly affected by heat and by site; but smoke effect only approached significance. Heat and smoke effects were consistent across the two sites. Plotting the nMDS analysis grouped the controls with the smoke treatment, which were separate from the treatments with a heat component. Analysis of species contributing to cumulative similarity showed that the number of native species was lowest in the controls, but this progressively increased over the smoke, heat, smoke and heat and fire treatments.

INTRODUCTION

Persistence of plant populations through recurrent disturbances is achieved by recruitment of new individuals from the seedbank, resprouting of survivors from the bud-and-tuber bank, a combination of these two, or by dispersal of seed in from surrounding sites (Keith 1996). The seedbank may be held in the canopy or stored in the soil. This study reports on a study of the seedbank at remnant sites of Cumberland Plain Woodland (hereafter CPW).

CPW is a grassy woodland in Western Sydney which was extensively cleared for agricultural use from the time of European settlement onwards (Figure 1). It has Critically Endangered Conservation status under New South Wales and Commonwealth legislation (Tozer et al. 2015). Attempts by Greening Australia to restore CPW onto former agricultural sites have been going on for several decades. The initial approach was to revegetate with tube stock of 20 CPW trees, seven shrubs and two groundlayer species (Davies and Christie 2001). However, the majority of floral diversity is found in the groundlayer of CPW (French et al. 2000). The NSW Scientific Committee report on indicative CPW species lists 13 trees, 17 shrubs and 85 groundlayer species (Office of Environment and Heritage 2010). The tree planting restoration undertaken under-represented the shrublayer, and ignored the high number of groundlayer species. While the planted canopy trees and some shrubs have persisted and grown at the revegetated sites, the missing shrub and groundlayer species have not reappeared (Wilkins et al. 2003; Nicols et al. 2010; Nicols and Morris 2024). Investigation of the soil seedbank of pasture and pasture revegetated with canopy trees has shown that the seedbank of pasture and revegetated pasture was dominated by exotic species (half or more of total), and by exotic seedlings (three quarters of total) if germination is induced. Native shrub and tree species which were present in adjacent remnants of CPW, were notably absent from the seedbank of pasture and revegetated areas, indicating seed limitation as the cause of the absence in the above-ground vegetation (Morris 2022).

To overcome seed limitation of native shrubs and trees, reseeding with native species is required. Having sourced appropriate seeds in the quantities needed, it is important to know whether pre-treatment of seeds or application of other treatments at sowing will assist germination and establishment (Gibson-Roy and Delpratt 2015). Fire-related cues of smoke, heat, or their combination have been shown to successfully stimulate germination of CPW native species in field and in ex situ trials (Hill and French 2004; Morris and de Barse 2013; Morris and Gibson-Roy 2018).

Another element of successful restoration is to identify both the species that need to have propagules added, and their growth form and place in the vegetation structure. Good quality CPW remnants have tree and shrub canopies, and groundlayer (Tozer et al. 2015). There is a need to investigate the seedbank of good quality CPW remnants, to establish what species are present. Establishing suitable benchmarks for CPW restoration should include both the above-ground vegetation, and the below-ground propagule bank. Restoration works that wish to re-introduce missing species also need to look at the growth form of added species to ensure sufficient coverage of tree, shrub and groundlayer species.

This study set addressed the following questions:

1. What species were present in the seedbank of remnant CPW, across what growth forms and native/exotic divide?
2. How did species richness, seedling numbers and species composition respond to fire-related treatments?

Figure 1. Cumberland Plain Woodland remnant showing the predominant grassy groundlayer where the majority of floral diversity is found (Conservation Woodland, Australian Botanic Garden, Mt Annan, D. Benson, December 2020).

METHODS

Site descriptions

The experiment was conducted on soil taken from two western Sydney sites: Nurragingy Reserve (NR), a 90 ha passive recreation reserve containing remnant CPW vegetation in an urban setting managed by Blacktown City Council; and Clarendon Paddocks (CP) on Western Sydney University's Hawkesbury Campus at Richmond, similar in size to Nurragingy and surrounded by agricultural land. Remnant CPW vegetation at both sites has a well-developed canopy of trees (*Eucalyptus tereticornis, Eucalyptus moluccana* at both, *Eucalyptus fibrosa* at CP). A shrublayer was present at both sites (*Bursaria spinosa* the most frequent species), as was a groundlayer. Past uses of both sites include grazing, tree felling and illegal rubbish dumping. Monthly average rainfall ranges from 46–102 mm for the Blacktown area, with a yearly average of 877 mm. For Richmond monthly average rainfall ranges from 42–97 mm with a yearly average of 804 mm. Average temperature ranges are from 16.8–29.4°C in summer to 3.2–17.8°C in winter over both sites (https://www.bom.gov.au/climate/data). Neither site had been burnt in the 20 years preceding the study.

Experimental design

To estimate the species composition and size of the soil seedbank, soil blocks were taken from the field, germination treatments applied and seedlings counted and identified. Five germination treatments were used; 1. untreated controls; 2. aerosol smoke; 3. heat; 4. smoke + heat; 5. fire.

Soil sampling

At each site, two randomly-selected sub-sites (150 m x 5 m) were located, and six replicate soil blocks (330 x 280 mm) per treatment per sub-site were taken during late May to early June 2001. Straight lines 3 m apart were laid out and soil blocks were located every 3–5 m along lines. Prior to collection, ground cover vegetation was clipped from sample blocks, and a spade used to mark out and extract the soil block to a depth of 5 mm; the 30 blocks per subsite were returned to the glasshousehouse, randomly assigned into treatments and allowed to air-dry for two weeks prior to the application of treatments. The total surface area of the combined 120 soil blocks was 11.1 m^2.

Application of germination treatments

Aerosol smoke was generated by burning a mix of fresh and dry native plant material from the sites in a 44-gallon drum and smoke was piped to a 1.44 m^3 tent containing the soil blocks for one hour. Water was used to cool the connecting pipe; air temperature inside the tent did not exceed 6°C above ambient temperature. Three soil blocks per sub-site were smoked simultaneously in one application of the treatment; there were two smoke applications per sub-site. Fuel was changed between applications (Morrison and Morris 2000). Testing for any effect of smoke application on numbers of seedlings was by 2-way nested ANOVA: the smoke application term was not significant ($F_{4,35}$ = 0.35, P > 0.5).

Heat was applied to soil blocks by immersion in boiling water; this method was chosen to avoid any spontaneous combustion of soil organic matter that can occur if dry heat is applied to soil in an oven (J. Keeley pers. com.). Spontaneous combustion of soil organic matter can generate smoke, thus potentially confounding the heat and smoke treatment. Soil blocks were wrapped in muslin cloth (to maintain structural integrity) and immersed in 15 L of boiling water. The target was to exceed 60°C for up to 10 minutes, a minimum exposure to heat known to break dormancy in many Fabaceae (Auld and O'Connell 1991). Pilot trials on blocks containing thermocouples at 25 mm depth showed that temperature was raised to 59–89°C after 14–17 minutes immersion, so 20 minutes immersion was used to standardise the treatment. Temperature in soil blocks one hour after treatment was approximately 50°C, and 27°C after six hours. Soil blocks were treated individually, and the immersion bath washed and re-filled between applications. Heat treatments were applied 5–6 July. For the fire treatment, blocks were overlaid with 180 grams of dry and fresh litter (equivalent to 20 tonnes ha^{-1}) which was set on fire. Trials showed that this achieved temperatures of 61–71°C in the soil blocks. Because heat was applied by water, all remaining blocks were immersed in cold water as a procedural control for the wetting process (7–11 July). All remaining blocks were air dried for a further two weeks before applications of smoke to the smoke or smoke and heat blocks (25–31 July). Fire treatments were applied 8–10 August. All soil blocks were placed in a glasshousehouse which had a humidifier but was not temperature controlled; the temperatures recorded in the glasshousehouse house ranged from 3.8–43°C over the course of the experiment. Blocks were watered every second week. Observations of seedlings commenced on 18 July for the heat only treatment, and on 18 August for remaining treatments. The appearance of new seedlings tapered off in all treatments by 6 November, and observations were terminated by 30 November.

Floral identification

Emerging shoots were allowed to grow on to facilitate identification. As the focus of the study was the seedbank, seedlings were counted and identified; vegetative resprouts were not. A total of 68 taxa emerged from the soil blocks; eight species remained unidentified. Botanical nomenclature and assignation to a growth form (forb, grass, graminoid, climber, shrub, tree followed Harden (1990–93) updated by PlantNet (2023). Identified species were checked as to whether they were listed as indicator species on the NSW determination of CPW as a Critically Endangered Ecological Community.

A total of 10,436 seedlings appeared during the observation period, in comparable numbers from both sites (54% from Nurragingy, 46% from Clarendon; Table 2). About one-quarter of seedlings did not survive long enough to be identified; 7,596 survived to the end of observations and were identified.

Analyses

Analysis of treatment effects on species richness, seedling numbers of total natives and total exotics, and for each growth form group within natives and exotics was made using a one-way ANOVA, using site means as data. Subsequent comparison of means was made with the Student Newman Keul test. An alternative approach was used for analysing the numbers of seedlings for individual species. The experimental design allowed for an asymmetrical two-way mixed-model ANOVA in which the factorial combination of heat and smoke (main effects and interaction) could be tested, and fire could be compared to the other treatments as a planned comparison (fire vs the rest). Germination treatments (fixed factor), combined with site (random factor) and subsites were nested within. To tentatively identify any response of individual species to treatments, analysis was limited to any species that showed the same response to treatments over both sites (treatment x site interaction not significant). A response to treatments at only one site could be due to spatial variability in the seedbank between sites. Eight species having sufficient numbers of seedlings showing a similar pattern of response across both sites were analysed using the factorial design and planed comparison. This detection of significant differences between treatments must be regarded as tentative only, as spatial variability could still be the underlying causes of such differences.

Multivariate analysis of treatment and site effects was by two-way PERMANOVA of the 4th square root transformed data at the subsite level, with pairwise comparison of treatment effects. Similarity between treatments was taken from the PERMANOVA analysis. Data were shown graphically by non-metric MDS. SIMPER analysis was used to determine the species contributing to 75% cumulative similarity within treatments (Clark and Gorley 2001; Anderson et al. 2008).

RESULTS

Species richness

Natives made up 72% of identified taxa (43 species) and the remaining 28% (17 species) were exotic. Forbs were the most numerous growth form of natives (15 species), followed by native shrubs (12 species) and native grasses (10 species) (Appendix Table 1). Native graminoids (3 species), trees (2 species) and a climber (1 species) made up the remaining natives. Exotic species were predominantly dicot forbs (14 species), with 2 grass and 1 shrub species (Table 2).

Germination treatments significantly increased total species richness of natives ($F_{4,5}$ = 4.53; P = 0.007). The smoke treatment had significantly more native species than the control, and the remaining treatments, which all had a heat component, gave further significant increases (Figure 2; Appendix Table 3). The germination response of native shrubs approached significance, reflecting an increase if given the heat or smoke and heat treatments (Appendix Table 3). Species richness of the other native growth forms was less responsive to the treatments (Appendix Table 3). Exotic species richness was unresponsive to the germination treatments (Figure 2; Appendix Table 3).

Of the 56 species of ground cover and shrubs listed as CPW indicator species, 22 (39%) species appeared over the course of the experiment.

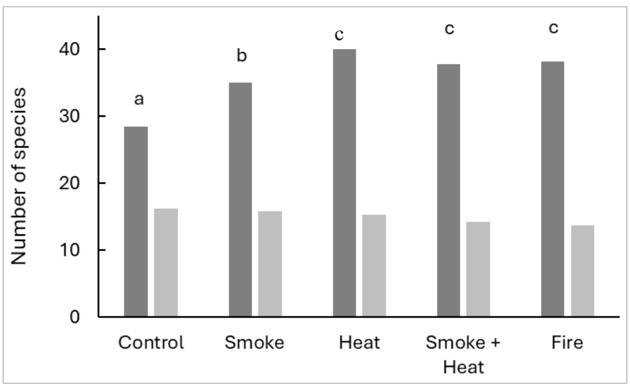

Figure 2. Mean total species richness of native (dark grey) and exotic (light grey) species in each treatment. Means labelled with different letters differ significantly at P <0.05. Data are mean per site.

natives	control	smoke	heat	smoke + heat	fire	total	%
trees	2	0	7	0	1	10	0.15
climbers	0	1	14	15	11	41	0.63
shrubs	18	29	113	146	75	381	5.84
forbs	93	177	302	219	208	999	15.32
graminoids	8	14	17	12	30	81	1.24
grasses	875	1,575	860	923	778	5,011	76.82
total	996	1,796	1,313	1,315	1,103	6,523	100
exotics							
forbs	276	128	79	79	29	591	55.1
grasses/graminoids	100	42	211	53	76	482	44.9
total	376	170	290	132	105	1,073	100
total identified						7,596	
total emerging						10,436	

Table 1: Numbers of identified seedlings by functional group in each of the treatments, for natives and exotics pooled over both sites. Percentage of seedlings in each group calculated as a proportion of native or exotic seedlings surviving during the experiment.

Total seedling numbers

Native species (n = 6,523) made up 85.8% of identified seedlings (Table 2; Figure 3), with one native grass (*Themeda triandra*) being the most numerous (n = 5,011). Other identified exotics (n = 1,073) were a lesser component, making up 14.1% of seedlings (Table 1; Figure 3).

Germination treatment effects approached significance for total native seedlings and for native grasses, and were significant for native shrubs (Appendix Table 4). Numbers of native grass seedlings peaked in the smoke treatment (*Themeda* response), and total native seedlings also peaked in this treatment (Appendix Table 4). In comparison, the significant response by shrubs reflected higher numbers of seedlings in the heat, and smoke and heat treatments (Appendix Table 4). For exotics, while seedlings numbers were highest in the control, and lower than the control in all other treatments, differences were not significant (Appendix Table 4).

Eight individual species showed responses to germination treatments that were consistent across the two sites. Five of these species were natives, and the response was positive for four of them (*Bursaria spinosa, Dichondra repens, Fimbristylis dichotoma, Themeda triandra*) and

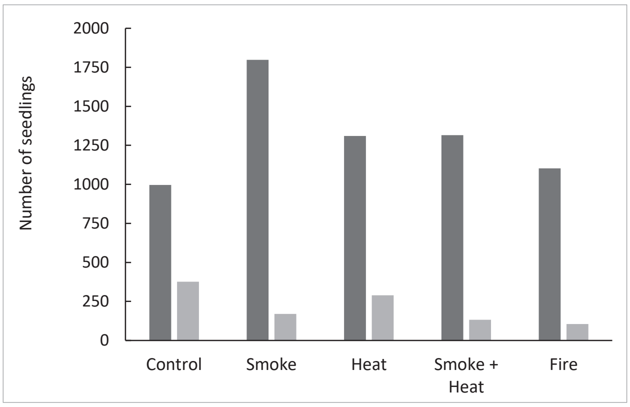

Figure 3. Total number of seedlings in each treatment for natives (black) and exotics (grey) in each treatment.

Species	Control	Smoke	Heat	Smoke + Heat	Fire	Response	Term	P
Bursaria spinosa	2.25	3.25	8.5	6.375	3.75	positive	Heat	< 0.025
**Conyza* sp.	44	17	7.5	11.5	0.5	negative	Fire	< 0.001
Dichondra repens	0	1	14	7	14.5	positive	Heat	< 0.005
Fimbristylis dichotoma	1	2.5	1	0.75	6.5	positive	Fire	<0.025
**Gamochaeta purpurea*	13.75	9.75	6.5	5	0.25	negative	Fire	0.05<P<0.10
Microlaena stipoides	21.5	23.75	11.25	10	4.25	negative	Fire	<0.005
**Senecio madagascariensis*	2.5	3	1	1	0	negative	Fire	<0.05
Themeda triandra	159	326.5	160	151.5	142.5	positive	Smoke	<0.05

Table 2. Species showing responses to germination treatments (Smoke, Heat, Smoke + Heat, Fire) at both sites; significant ANOVA Term and P given. Data are mean number of seedlings per soil block.

negative for one (*Microlaena stipoides*; Table 2). Three species were exotic; the response was significantly negative for two species *(*Conyza sp., *Senecio madagasariensis*) and approached significance for one *(*Gamochaeta purpurea;* Table 2).

Treatment effects on species composition

Species composition differed significantly amongst treatments (Pseudo-$F_{4,4}$ = 4.854, P(perm) = 0.001). In the factorial PERMANOVA comparing heat and smoke, there was a strong main effect of heat on species composition (Pseudo-$F_{1,11}$ = 5.56, P(perm) = 0.002, 999 permutations), while the smoke main effect only approached significance (Pseudo-$F_{1,11}$ = 1.98, P(perm) = 0.07, 999 permutations). There was a significant separation between the two sites in the nMDS plot (sites; Pseudo-$F_{1,11}$ = 6.12, P(perm) = 0.002, 999 permutations). Effects of heat and smoke were consistent across both sites, with separate but

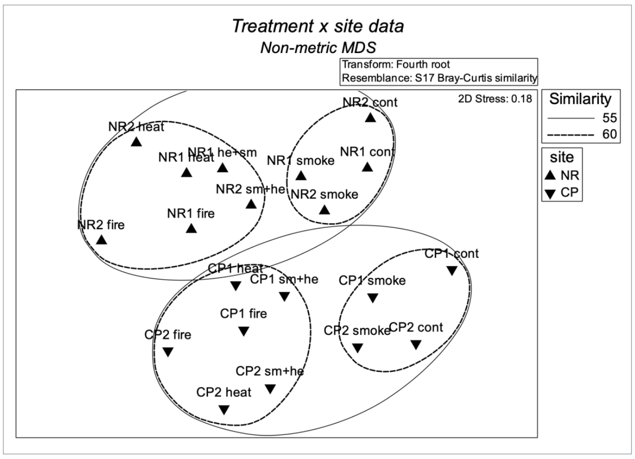

Figure 4. Ordination (nMDS) of treatments at each site. Labels shown for Nurragingy (NR); Clarendon (CP); control (cont); smoke; heat; smoke + heat (sm+he); fire.

Control			Smoke			Heat			Sm+He			Fire		
Species	Ab	%	Species	Ab	%	Species	Ab	%	Species	Ab.	%	Species	Ab	%
Themeda triandra	2.2	15	*Themeda triandra*	2.7	*15.8*	*Themeda triandra*	2.3	13	*Themeda triandra*	2.2	12	*Themeda triandra*	2.1	12
**Conyza* sp.	1.6	24	*Microlaena stipoides*	1.4	*24.4*	**Sisyrinchium micranthum*	1.6	22	*Paspalidium distans*	1.6	21	*Paspalidium distans*	1.6	23
Microlaena stipoides	1.4	33	*Paspalidium distans*	1.4	*32.6*	Unknown dicot	1.2	29	*Eragrostis. brownii*	1.3	30	*Dichondra repens*	1.2	30
Paspalidium distans	1.4	42	Unknown dicot	1.3	*39.7*	*Acacia buxifolia*	1.2	36	Unknown dicot	1.2	36	*Eragrostis. brownii*	1.1	37
Unknown dicot	1.2	50	*Wahlenbergia gracilis*	1.3	*46.4*	*Microlaena stipoides*	1.2	43	*Acacia buxifolia*	1.2	42	*Wahlenbergia gracilis*	1.2	44
Tricoryne simplex	1.1	57	**Conyza* sp.	1.2	*52.9*	*Dichondra repens*	1.2	49	*Microlaena stipoides*	1.1	49	Unknown dicot	1	50
**Gamochaeta purpurea*	1.2	64	*Tricoryne simplex*	1	*58.4*	**Gamochaetapurpurea*	1.1	56	*Dichondra repens*	1.1	55	*Acacia buxifolia*	1.1	56
**Senecio madagascarienis*	0.8	68	**Senecio madagascarienis.*	0.8	*63.5*	*Wahlenbergia gracilis*	1.2	61	**Conyza* sp.	1.1	61	*Microlaena stipoides*	0.9	67
**Sisyrinchium micranthum*	0.9	71	**Gamochaetapurpurea*	1	*68.4*	*Paspalidium distans*	1.2	67	*Bursaria spinosa*	1	66	*Fimbristylis dichotoma*	1	67
Bursaria spinosa	0.6	74	*Bursaria spinosa*	0.8	*72.9*	**Conyza* sp.	1	73	**Gamochaetapurpurea*	0.9	71	*Phyllanthus* sp.	0.8	72
**Facelis retusa*	0.6	77	*Fimbristylis dichotoma*	0.8	*77.4*	*Glycine clandestina*	0.9	78	*Wahlenbergia gracilis*	0.9	76	*Glycine clandestina*	0.8	77
Native species	5			7			7			9			10	
Exotic species	5			3			3			2			0	

Table 3. Species contributing up to 75% of the Bray-Curtis cumulative similarity for each treatment (fourth square root transformation). Numbers of native and exotic (marked *) species are shown for each treatment. Ab = average abundance; % = cumulative percentage.

approximately parallel trajectories for treatments on the plot (treatment x site interaction not significant; Pseudo $F_{4,8}$ = 0.839, P(perm) = 0.67; Figure 4). Similarity between treatments reflected the strong effects of site, heat, and lesser impact of smoke. There was a change in species composition from controls, grouped together with the smoke treatment on the nMDS plot, to a significantly different grouping of the treatments that had a heat, or smoke and heat components, at both sites (Figure 4; Appendix Tables 5, 6). Comparison of the contribution of individual species to cumulative similarity within treatments showed that the number of native species contributing increased, as germination treatments were added singly or in combination (Table 3). Eleven species (five native, five exotic and one unknown) contributed up to three-quarters of the similarity for the controls (Table 3). As treatments with germination cues were added, the number of species contributing to similarity remained constant, but the proportion of native species contributing increased. Smoke alone and heat alone each added two more species; the smoke heat treatment each added three more additional species, compared to controls. Fire added five more species (Table 3).

DISCUSSION

The inability to fully identify all taxa and seedlings in this study means that the proportion of native and exotic species reported for species richness and numbers of seedlings may be inaccurate. However, the proportion of unidentified taxa was low; native species would still constitute the majority of emergent taxa, even if all unidentified taxa were exotics. The same holds for numbers of seedlings; while a larger proportion of seedlings were unidentified than for taxa, even if all the unidentified seedlings were exotics, they would still be fewer than natives. Further limitations would be that the soil depth of the blocks did not adequately sample the deeper seedbank, and the temperatures achieved in the wet heat treatment may not have broken dormancy in some heat-cued species. The temperature threshold for mortality of seeds with physical dormancy is reduced if seeds are hydrated (Tangney et al. 2019). The germination of seeds may have varied between the wet heat treatment and unheated treatments because of this, rather than from other treatment effects on dormancy.

Limitations aside, an important feature of the seedlings at the two CPW remnant sites was that natives made up the majority both in species richness, and in seedlings. This has not been the case in a comparison of the seedbank of pasture, pasture planted with native trees, and remnant CPW (Morris 2022). In that study, while the majority of species in the remnant CPW seedbank were natives, numbers of seedlings were approximately equal for both natives and exotics. Methodology differed between the two studies, with soil being sieved and spread in trays in Morris (2022), whereas the current study applied treatments to otherwise undisturbed soil blocks taken from the field. If each of the two methods give accurate representation of at least the relative numbers of native and exotic species and seedlings, then the CPW remnants in this study apparently have both more native taxa and more native seedlings than exotics. Dominance of the seedbank by exotics in remnant grassy woodland has been observed elsewhere (Lunt 1997) and so to find sites where the exotic presence is reduced compared to natives shows that remnant stands of CPW can still have a majority native presence in the seedbank.

Importantly, the seedbank in the current study also contained native species from across the full range of growth forms and from the ground, shrub and tree layers. 39% of the native groundcover and shrub indicator species for CPW appeared in the experiment, from a total of only 11 m^{-2} area of soil sampled. Attempts to restore CPW by planting seedlings of overstorey trees on former pasture (Davies and Christie 2001; Wilkins et al. 2003) have not led to the reestablishment of shrub species which are largely absent from the seedbank of former pasture planted with native trees (native shrubs = 8% of native species and 1.4% of native seedlings; Morris 2022). The current study confirms that shrub species are present in the seedbank of good quality CPW remnants, making up 23% of native species and 5.8% of native seedlings.

Not only was there a wider range of native species and growth forms present at the two sites, native seeds responded positively to the germination cues, resulting in more native species appearing above-ground and in higher numbers than in the controls. Positive germination responses to fire-related cues were apparent in the analyses of species richness, numbers of seedlings, and species composition, and are well known from other studies (Hill and French 2004; Morris and de Barse 2013; Morris and Gibson-Roy 2018). Changes in the proportion of native and exotic species contributed to the decrease in similarity of the germination treatments compared to controls, across the range from single fire cues to both fire cues or actual fire. Natives were progressively added, and exotics were progressively excluded from the list of species contributing to similarity across the treatments. Positive responses of natives to the germination cues drove this trend. All the germination treatments increased species richness compared to controls, with the largest responses coming either heat, or from treatments with a heat component (heat plus smoke; fire). Looking at the growth forms, the largest response of native richness to germination cues was from shrubs, with a four-fold increase in species richness compared to controls. The number of natives seedlings was dominated by the flush of *Themeda triandra* in the smoke treatment, with a doubling of grass numbers compared to the control; the increase approached significance. A stronger and significant response of native seedlings came from the heat, or heat plus smoke treatments, with six- to- eight-fold significant increase compared to the control. Shrubs from the Fabaceae made up 6 of the 12 native shrub species identified, and the positive response of seeds from this family to heat shock is well known (Auld and O'Connell

1991). At the individual species level, *Bursaria spinosa* and *Themeda triandra,* both common and important native species, responded positively to fire-related cues of heat or smoke. *Themeda* plays an important role in maintaining soil nitrate at low levels via plant-soil feedbacks from its litter (Prober et al. 2005) and *Bursaria* is the dominant shrub species in CPW (Watson et al. 2009). The positive response of natives to germination cues contrasted with the lack of such a response from the exotics for species richness and numbers of seedlings. Negative effects of treatments were detected in the response of seedlings from individual species for two exotics; these species (**Conyza* sp., **Senecio madagascariensis*) are widespread and abundant in degraded CPW remnants or sites with previous agricultural land use (Morris and Sanders 2021). And for species composition, the germination treatments favoured natives and reduced exotic species contributing to similarity, compared to controls. If these effects translated to the field, use of fire should favour natives over exotics. Beneficial effects of fire on species richness and abundance of CPW native species have been observed after single fires in field experiments (Morris and de Barse 2013; Morris and Gibson-Roy 2018) and after two fires (Morris et al. 2016; Morris and Sanders 2021). An exception was a fire treatment that led to rapid growth of **Briza subaristata* on a plot where the pre-fire vegetation was dominated by *Microlaena stipoides* (Morris and Gibson-Roy 2018). Observations from a landscape scale survey that tested whether fire frequency affected trees or shrubs found that exotic shrub abundance was highest at low fire frequency, and was lowest at high fire frequencies (Watson et al. 2009). An extension of this study examined whether microhabitat or fire frequency affected species composition of the groundlayer in CPW remnants. As for the shrubs, abundance of exotic groundlayer species was highest at low fire frequencies (Watson and Morris 2020).

Returning to the questions posed at the beginning, this study showed that the soil seedbank under remnant CPW can contain a wide range of native species across a range of growth forms. In particular, species of native shrubs that have been absent from degraded sites used for revegetation by tree planting, were present in the remnants. Also present in the groundlayer of remnants were species of native ‘yams’, used for food by indigenous people (Watson and Morris 2020). A majority of species in the seedbank were natives, which responded positively to germination cues associated with fire. In comparison, exotics either did not respond to fire, or were negatively affected.

ACKNOWLEDGEMENTS

This work was undertaken by Peter D. Wood as part of an Honours program for the Bachelor of Landscape Management and Conservation at Western Sydney University. Acknowledgement is given to Peter for undertaking the work required for the project, and to Burhan Amiji, Pat Hanson and Peter Lister for technical assistance.

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APPENDIX

Native species	Growth form
Glycine clandestina	climber
Arthropodium minus	forb
Bulbine bulbosa	forb
Calotis cuneifolia	forb
Calotis lappulacea	forb
Commelina cyanea	forb
COMMELINACEAE	forb
Dichondra repens	forb
Murdannia graminea	forb
Opercularia diphylla	forb
Oxalis perennans	forb
Polymeria calycina	forb
Poranthera microphylla	forb
Solanum prinophyllum	forb
Tricoryne simplex	forb
Wahlenbergia gracilis	forb
Cyperus enervis	graminoid
Cyperus gracilis	graminoid
Fimbristylis dichotoma	graminoid
Aristida vagans	grass
Dichelachne parva	grass
Digitaria diffusa	grass
Eragrostis brownii sens. lat.	grass
Eragrostis leptostachya	grass
Microlaena stipoides var. *stipoides*	grass
Paspalidium distans	grass
Poa spp.	grass
Sporobolus creber	grass
Themeda triandra	grass
Acacia buxifolia	shrub
Acacia falcata	shrub
Acacia parramattensis	shrub
Bossiaea prostrata	shrub
Bursaria spinosa	shrub
Dillwynia spp.	shrub
Einadia hastata	shrub
Einadia nutans subsp. *linifolia*	shrub
Ozothamnus diosmifolius	shrub
Pea spp.	shrub
Phyllanthus spp.	shrub
Plectranthus parviflorus	shrub
Angophora spp.	tree
Eucalyptus spp.	tree

APPENDIX Table 1. Native species by growth form

Exotic species	Growth form
**Veronica arvensis aquatica*	forb
**Centaurium erythraea*	forb
**Conyza* species	forb
**Facelis retusa*	forb
**Gamochaeta purpurea*	forb
**Hypochaeris microcephala* var. *albiflora*	forb
**Hypochaeris radicata*	forb
**Lactuca serriola*	forb
**Richardia stellaris*	forb
**Romulea rosea var. australis*	forb
**Senecio madagascariensis*	forb
**Sisyrinchium micranthum*	forb
**Solanum nigrum*	forb
**Sonchus oleraceus*	forb
**Eleusine indica*	grass
**Setaria gracilis*	grass
**Gomphocarpus fruticosus*	shrub

APPENDIX Table 2. Exotic species by growth form

Treatments	Control	Smoke	Heat	Smoke + Heat	Fire	$F_{4,5}$	P
Total natives	4.75 a	5.83 b	6.67 c	6.2 c	6.37 c	4.33	**0.007**
Forbs	1.54	1.63	2.21	1.79	2.3	1.69	0.28
Grasses	2.5	2.79	2.46	3.17	2.38	1.96	0.24
Shrubs	0.42	0.71	1.58	1.58	0.96	4.33	0.069
Total exotics	2.71	2.63	2.54	2.38	2.29	0.07	0.99

APPENDIX Table 3. Mean species richness of natives (total, forbs, grasses, shrubs), and exotics (total) in each germination treatment. F-ratio and probability (P) of treatment effects are shown (significant P values shown in bold). Means followed by different letters are significantly different from each other (P < 0.05). Data are means per soil block.

Treatments	Control	Smoke	Heat	Smoke + Heat	Fire	$F_{4,5}$	P
Total natives	41.5	74.9	54.6	54.8	46	4.17	0.074
Forbs	3.8	7.3	12.6	9.2	8.7	0.48	0.75
Grasses	36.5	65.6	35.8	38.5	32.4	4.905	0.056
Shrubs	0.75a	1.21ab	4.70bc	6.08c	3.12ab	6.73	**0.03**
Total exotics	15.7	7.1	12.1	5.5	4.4	1.188	0.47

APPENDIX Table 4. Mean numbers of native (total, forbs, grasses, shrubs), and exotic seedlings (total) in germination treatments. F-ratio and probability (P) of treatment effects are shown. (significant P values shown in bold). Means followed by different letters are significantly different from each other (P < 0.05). Data are means per soil block.

Treatment	Control	Smoke	Heat	Smoke + Heat	Fire
Control	-	0.127	**0.017**	**0.037**	**0.023**
Smoke		-	**0.037**	0.15	0.053
Heat			-	0.1	0.06
Smoke + Heat				-	0.1
Fire					-

APPENDIX Table 5: Comparison of treatments after PERMANOVA: P(perm) of t values shown; values in bold P(perm) < 0.05. Bray-Curtis similarity, fourth-root transform of data. Unique permutations ranged 357 – 377.

	Control	Smoke	Heat	Smoke + Heat	Fire
Control	61.4				
Smoke	61.4	64.1			
Heat	50.2	55	60.3		
Smoke + Heat	53.1	60.2	60.7	59.9	
Fire	49.5	56.5	58.8	60.5	63.3

APPENDIX Table 6: Average similarity (%) of treatments within and between treatments (Bray Curtis, fourth square root transform)