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Observations of fire regime and overstorey tree canopy decline in karri forests

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Abstract

Background Frequent mild fire regimes have been associated with healthy and bushfire-safe forests, particularly under traditional Aboriginal management in Australia and the New World. In this study, we tested the hypothesis that karri (*Eucalyptus diversicolor*) forest tree canopy health (TCH) declines with time since fire (TSF) due to changes in soil chemistry that adversely impacts tree roots. We visually assessed the TCH of dominant and co-dominant trees at 66 sites in mature karri forests based on the extent and density of foliage, the extent of epicormic growth, and the extent of branch death. TSF ranged from two to 94 years. Fire regimes can influence tree health via soil chemistry conditions, so we sampled topsoil at each site.

Results A model based on TSF and soil exchangeable potassium content explained 63.9% of the variation in TCH with TSF explaining 56%. K content was an indicator of variation in soils and susceptibility to decline rather than a cause of decline. There was little evidence that changes in soil chemistry with TSF contributed to tree decline and no evidence that climate change was the primary driver of canopy decline.

Conclusion Karri tree canopy decline is likely caused by the physical effects of the accumulation of forest floor litter (or mulch) on tree roots and on soil microbiota via changed soil conditions such as temperature, moisture, aeration, insolation and penetrability. Other than gravel content, we did not measure soil physical factors, so this proposal requires further investigation. If the healthy functioning of tree roots is compromised by long periods of fire exclusion, then declines in tree canopy health may be exacerbated by drought events associated with climate change.

Keywords Fire regimes, Eucalypt forest, Tree health, Forest soils, Climate change

Resumen

Antecedentes Regímenes de fuegos frecuentes y moderados han sido asociados con bosques saludables y seguros contra incendios de arbustales, particularmente asociados con el manejo del fuego tradicional de aborígenes en Australia y el Nuevo mundo. En este estudio, probamos la hipótesis de que la salud del dosel (TCH) del karri (*Eucalyptus diversicolor*) declina a medida con el tiempo desde el último incendio, debido a cambios en la química del suelo que impacta de manera adversa las raíces de estos árboles. Determinamos visualmente la TCH de árboles dominantes y co-dominantes en 66 sitios en bosques maduros de kerri basados en la extensión y densidad del follaje, el grado de crecimiento epicórmico y la extensión de la muerte de ramas. El rango de variación de TCH varió de dos a 94 años. Los regímenes de fuego pueden influenciar la salud de los árboles a través de las condiciones químicas del suelo, por lo cual muestreamos el suelo superficial en cada sitio.

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Resultados Un modelo basado en TSF y el contenido de potasio intercambiable en el suelo explicaron el 63,9% de la variación en TC, con TSF explicando el 56%. El contenido de K fue un indicador de la variación en suelos y la susceptibilidad a la declinación más que la causa de la declinación. Hubo una muy pequeña evidencia de que los cambios en la química del suelo con TSF contribuyeron a la declinación de los árboles y ninguna evidencia de que el cambio climático fue un conductor primario de ella declinación de los doseles.

Conclusiones La declinación en el dosel del kerri es causado por los efectos físicos de la acumulación de broza (mulch) sobre las raíces en el suelo forestal y en la microbiota del suelo a través de cambios en las condiciones del suelo como temperatura, humedad, aireación, aislación y penetrabilidad. Salvo el contenido de grava, no medimos otros factores físicos del suelo, por lo que esta propuesta requiere de más investigaciones. Si el funcionamiento saludable de las raíces está comprometido por largos períodos de exclusión del fuego, entonces la declinación de la salud del dosel puede ser exacerbada por eventos de sequía asociados con el cambio climático.

Background

Declines in the health of forest trees have been attributed to exotic pests and diseases, native organisms, drought, disruption of hydrological processes and agricultural or urban pollution (Manion and Lachance 1992; Jurskis 2005; Matusick et al. 2013; Guegan et al. 2023). Drought and heat-waves associated with climate change have also been implicated in a process variously described as forest tree collapse, decline, dieback or die-off (e.g., Allen et al. 2010). Extended periods of below average rainfall have contributed to tree health declines in south-west Australian jarrah (*Eucalyptus marginata* Sm.) forests on shallow soils (Evans et al. 2013; Matusick et al. 2013, 2018; McGrath et al. 2023; Anderson et al. 2025). By contrast, karri (*Eucalyptus diversicolor* F.Muell.) trees in the higher rainfall regions of south-west Australia appear to have been relatively resilient to reduced rainfall to date (Evans et al. 2013). Nevertheless, there are potential interactive effects of drought and fire regime that may impact on karri forest tree health in the future.

In fire-prone forests, fire regimes can be harmful or beneficial to tree health. A regime of intense bushfires can cause widespread death and injury to trees, and fire exclusion can alter the structure and composition of forests (e.g. Harvest et al. 2008; Stanton et al. 2014; McCaw and Middleton 2015; Fairman et al. 2015; Williams et al. 2020; Hagmann et al. 2021). The exclusion of frequent mild fire has caused, or been associated with a decline in health of overstorey trees in a variety of Australian eucalypt forests (Jurskis and Turner 2002; Jurskis 2005, 2017; Harvest et al. 2008; Lewis 2020; Williams et al. 2022).

Various ecological histories and discussions of changes in biota and ecosystem function according to changing human management of forest fire have been published for Australia and North America (e.g. Hessburg and Agee 2003; Hessburg et al. 2005; Jurskis 2017; Stephens et al. 2018; Jurskis et al. 2020). Many studies have related tree crown decline to soil chemistry changes, especially of carbon, nitrogen and phosphorus, mediated by altered fire regimes (e.g. Jurskis 2005; Turner and Lambert 2005; Turner et al. 2008; Dijkstra and Adams 2015). A global assessment by Bobbink et al. (2010) identified that N accumulation in ecosystems can lower resistance of trees to pests and pathogens, increase their attraction to herbivores and increase their susceptibility to damage such as frosting, droughting or waterlogging by altering their physiology and biomass allocation. In a conceptual model of eucalypt decline, Jurskis and Turner (2002) proposed that a tree crown decline is associated with increased soil moisture and nitrogen status that stresses the roots. This pre-disposes trees to arbivores, parasites and diseases (Jurskis and Turner 2002; Turner and Lambert 2005; Jurskis 2005). Working in dry eucalypt forests of south-east Australia, Turner et al. (2008) reported increased levels of extractable mineral N and other soil chemistry changes in long unburnt forests. They hypothesised that this creates a poorer root environment, directly impacting tree health and increasing susceptibility to pests and pathogens. Close et al. (2009) proposed a model for premature decline in eucalypt forest trees in the long absence of fire based on reduced soil water availability due to mid-storey competition and less access to some nutrients that were immobilised in litter and midstorey biomass. Exclusion of mild fire and the subsequent accumulation of forest floor litter at various stages of decomposition (acting as mulch) can change topsoil moisture, aeration, chemistry, organic matter content and exposure to solar radiation and wind (Brockett et al. 2012; Horton et al. 2013; Agbeshie et al. 2022).

Whether the health of karri trees declines in the long absence of fire remains unclear. The purpose of this study was to test the hypothesis that karri tree canopy health declines with time since fire due to changes in soil chemistry that adversely impacts tree roots, hence tree crown health.

Methods

Study area

Karri forests are tall open sclerophyll forests with karri as the dominant or co-dominant overstorey species. Karri forests are restricted to the lower south-west of Western Australia. They mostly occur on podzoloic and red-brown loamy soils on granitic substrates in high rainfall areas (1000 mm – 1300 mm per annum). Karri can occur in pure stands or in association with other eucalypts including marri (*Corymbia callophyla* [Lindl.] K.D. Hill & L.A.S. Johnson) and occasionally jarrah, and in the cooler south-east of its range, the three tingle species (*E. brevistylis* Brooker, *E. jacksonii* Maiden, *E. guilfoylei* Maiden) (Bradshaw 2015). Mapping based on soils and landform has identified twenty three vegetation complexes associated with karri forests (Mattiske and Havel 1998). The region experiences a mild Mediterranean-type climate with warm dry summers and cool wet winters. Given the climate and seasonally flammable vegetation, fire is considered an integral part of the ecology of these forests (Christensen and Abbott 1989).

The current study builds on work by Burrows et al. (2023) who, in a space-for-time study, measured fuels at 72 sites in mature karri forests with different but known times since last fire, ranging from 1 to 92 years. At each site, they acquired measurements including overstorey and mid-canopy tree height, stocking and basal area, understorey height and cover, and fuel biomass and litter depth (LD). Some two years later, in February 2024, we carried out tree canopy health assessments and sampled topsoil at 66 of these sites. Of these, 56 were last burnt by prescribed fire and four were last burnt by wildfire. The type of fire on six sites is unknown. There are no fire intensity of fire severity data available but typically prescribed burns in karri forests are patchy and low intensity while wildfires are moderate to high intensity (McCaw and Middleton 2015). About 70% of the sites were unburnt for 12 + years. While three sites had been burnt four times in 33 years (mean fire interval ~ 8 years), the mean fire interval at other sites ranged from 11 to 33 + years.

Assessing canopy health

We conducted an initial reconnaissance of karri forests to calibrate the tree canopy health assessment method used by Forestry Corporation of New South Wales (Forestry Corporation 2020) in eucalypt forests in south-east Australia and to ensure consistent assessment amongst observers. This visual technique (Table 1) is similar to that used by others (e.g., Stone et al. 2003; Stone and Haywood 2006; Souter et al. 2010; Horton et al. 2013). Mistletoes and other parasites are not a symptom of canopy decline in karri forests as they are in many other Australian forests so that feature of the Forestry Corporation assessment was not relevant.

Mixed species stands, in addition to karri, included marri and in a few cases, red tingle (*E. jacksonii*). These species had denser foliage and less evidence of canopy decline than karri, so for consistency across sites, our assessment was restricted to karri. During the calibration phase, we saw trees in a range of canopy condition (Table 1) and were able to achieve consistent assessments amongst three observers.

We assessed the health of crowns of dominant and co-dominant trees within a 20 m radius of the centre point of sample sites used by Burrows et al. (2023). The centre point was marked with a wooden peg, which was sometimes difficult to locate due to thick vegetation, the peg being dislodged or removed, and inherent inaccuracy of the hand-held GPS device (Garmin Foretrex) in tall forests. The peg could not be located at six sites, so tree canopy health was assessed at the GPS coordinates (latitude and longitude) for the sites. Because of the relatively large scale of fire in these landscapes, this did not affect the 'time since fire attribution' for the site. The number of trees assessed at each site varied from three

Table 1 A summary of the criteria used to visually assess the crown condition of dominant and co-dominant karri trees (after Forestry Corporation 2020). Where canopy decline (CD) was assessed to be between classes, we rated condition as 0.5, 1.5, etc.

Canopy decline class	Description	Foliage	Dead branches
0	Healthy	Dense foliage at the end of fine branchlets	Few, with expected distribution for species and growth stages
1	Early signs of decline	Slightly thin foliage on the end of branchlets	Some death of branchlets
2	Moderate decline	Obvious epicormic growth and tatty/discolored foliage on branches	Obvious death of some fine branches
3	Severe decline	Contracting crown with mostly unhealthy foliage derived from epicormic growth on structural branches	Many structural branches dead
4	Terminal decline. Stand dying	Very sparse contracted epicormic crown mostly on larger branches	Many dead primary branches

to eight ($\bar{x}=4.2$ per site; ~ 300 trees assessed), reflecting variation in tree species composition and size, and stand structure. Assessments were made from directly beneath the canopies because the pendent foliage of eucalypts obscures an oblique view of symptoms of canopy decline. During summer 2024, individual trees at each site were assessed before an overall, integrated rating was assigned to the site. Foliage density, appearance and arrangement, the extent of epicormic foliage, and the extent of dead branches, were all considered for each tree (Table 1). Dead or broken branches or tops arising from normal processes of crown development and maintenance, or from prior physical events such as fires or storms, were disregarded. The condition of tree crowns assessed at a site were similar so we were able to derive a single crown health value for each site (Table 1). Photographic examples of early decline and severe decline are shown in Fig. 1.

Stand attributes, fire history, and rainfall

For analysis, we also incorporated the site-based data collected by Burrows et al. (2023) (see above). The fire history for each site from the 1970s was obtained from electronic and map-based records held by the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA). The available historical (1942–2024) annual rainfall observations for the town of Pemberton (34.45°S, 116.04°E) in the 'heart' of the karri forest region were acquired from the Australian Government Bureau of Meteorology (bom.gov.au/climate/data/).

Topsoil chemistry

At each site, 10 topsoil samples (each 10 cm deep × 5 cm diameter) were taken along a 20 m line transect through the centre of each plot, with a sample taken every 2 m. The 10 samples were bulked, mixed and a single sample of about 700 g was placed in a labelled calico bag. Soil chemical analysis was undertaken in the CSBP laboratories in Perth, Western Australia (CSBP 2023). The analyses included pH, organic and total carbon, total nitrogen, ammonium and nitrate N, total P and Bray II P, exchangeable Ca, Mg, K, Na and Al. Soil samples were also screened for gravel content (particles > 2 mm), expressed as a proportion of dry weight. Soils were air dried and passed through a 2 mm sieve. Organic carbon was estimated using the Walkley–Black method with a digestion of sulphuric acid and dichromate solution. Total carbon and total Nitrogen were estimated using a Leco analyser. Ammonium Nitrogen and nitrate nitrogen were extracted using 2 M KCl and measured calorimetrically. Total phosphorus was estimated from a Kjeldahl extract (sulphuric acid digest) and measured calorimetrically. Bray II P was extracted using ammonium fluoride and hydrochloric acid and measured calorimetrically. Exchangeable Ca, Mg, K and Na were extracted using ammonium chloride and barium chloride and then analysed using ICP. Exchangeable Al was extracted using 0.01 M calcium chloride and analysed using ICP (see CSBP 2023 for further detail).

Pests and diseases

The six least healthy (CD ≥ 2.5; Table 1) stands were visually inspected for insect and fungal damage and foliar nutrient deficiency (based on foliage colour) using a pair of Nocs Pro Issue 8 × 42 binoculars in June 2024. Recently fallen leaves were also inspected.

Data analysis

Litter depth as measured in the fuel accumulation study can be described as a logarithmic function of time since fire and basal area of karri, with an adjusted R^2 of 0.80 (Burrows et al. 2023). In the data analysis, we used



Fig. 1 Mature karri tree crowns showing early signs of decline (left—decline class 1.0) and severe decline (right—decline class 3.5)

modelled LD to account for the 2-year difference in LD between the fuel study and the current study, as well as the LD measured at the time of the fuel study.

Distance-based linear model (DISTLM) routines using Primer 6 (Anderson 2006) were used to explore the linear relationships between soil chemistry, various stand and fuel variables, TSF and karri canopy health condition. The routines examine alternative multivariate models describing the variation in a distance matrix constructed from the response variable for each sample. A Euclidean distance matrix was constructed for Canopy Decline (CD) after standardization of CD against its maximum value. The BEST procedure was used to select 'explanatory' variables according to Bayesian Information Criterion (BIC) values (Brewer et al. 2016). The selected explanatory variables were used to produce models for CD.

The soil and stand variables formed a multivariate 'cloud' describing distance between sites. We conducted a discriminant analysis using the Primer 6 CAP routine (Canonical analysis of principal coordinates) to find axes through the multivariate cloud that best discriminated among the a priori classifications of time since fire and litter depth. Soil and stand variables were normalised and a Euclidean distance matrix constructed between sites. Variables most correlated with the CAP axes were identified. In a post hoc analysis samples were categorized into those with CD $\leq$ 2.5 (early to moderate decline), and those with CD > 2.5 (severely decline) (Table 1). T-tests were conducted for each measured soil variable, assuming unequal variances.

Results

Canopy decline (CD)

CD at sample sites ranged from signs of early decline (1.5) to severe decline (3.5); none of the sampled sites were rated as having a healthy tree canopy (0) or in terminal decline (4) (Table 1). DISTLM identified two parsimonious multivariate models for CD (Tables 2 and 3). In Model 1, Time Since Fire (TSF) alone explained 56% of the variation in CD (Fig. 2). TSF and exchangeable potassium (K) together explained 63.9% of the variation. In Model 2, when TSF was excluded from the analysis, Litter Depth (LD) alone explained 39% of the variation (Fig. 3) and together with exchangeable calcium (Ca), explained 44.3% of the variation in tree canopy health. Most (70%) of the power of Model 1 to 'explain' CD is associated with LD (Fig. 3). There were no visual signs of outbreak of pests or diseases in the most severely declining stands. Estimated proportions of individual leaves lost or dead were below 10%. Based on tree canopy foliage colour, there were no obvious signs of nutrient deficiency symptoms.

In the CAP analyses (Figs. 4 and 5), soil pH, K and Bray II P were correlated with the axes that best discriminated sites according to TSF. Soil pH, Bray II P and Marri BA: Total BA (hereafter Marri/Tot) were correlated with axes that best discriminated sites according to LD. When

Table 2 DISTLM showed time since fire was the dominant explanatory variable of karri crown health condition

Test procedure	Variable	*P*	Variation explained (%)
Marginal Tests (variable acting alone)	1. Time since fire	0.001	56.0
	2. Exc. Potassium	0.03	7.9
	3. Litter depth	0.001	39.4
	4. Exc. Calcium	0.08	4.9
	BIC score	R^2	Variables
Best Models (variables acting in concert)	312.4	61	Model 1: 1, 2
	336.0	43	Model 2: 3, 4

Table 3 Model 1 and 2 coefficients for multivariate model of karri canopy health condition selected by DISTLM and BIC

Model	Variables	Coefficients	Standard error	*t* Stat	*P*-value	Lower 95%	Upper 95%
1	Intercept	1.709	0.112	15.300	0.000	1.486	1.932
	Time since fire	0.017	0.002	9.151	0.000	0.013	0.021
	Exc. Potassium	0.677	0.252	2.682	0.009	0.173	1.181
2	Intercept	1.389	0.177	7.835	0.000	1.034	1.743
	Litter depth	0.015	0.002	6.554	0.000	0.011	0.020
	Exc. Calcium	0.020	0.009	2.116	0.038	0.001	0.039

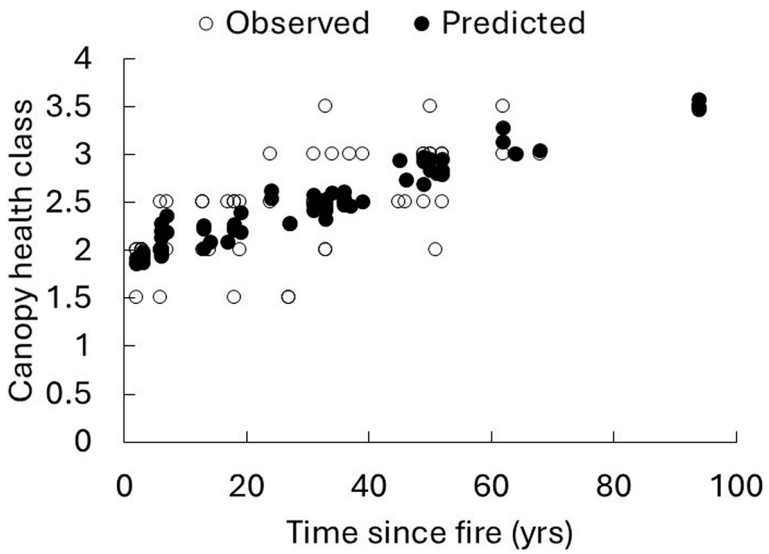


Fig. 2 Observed and Predicted karri tree canopy health condition (Table 1) using time since fire as a predictor (Model 1, Table 2)

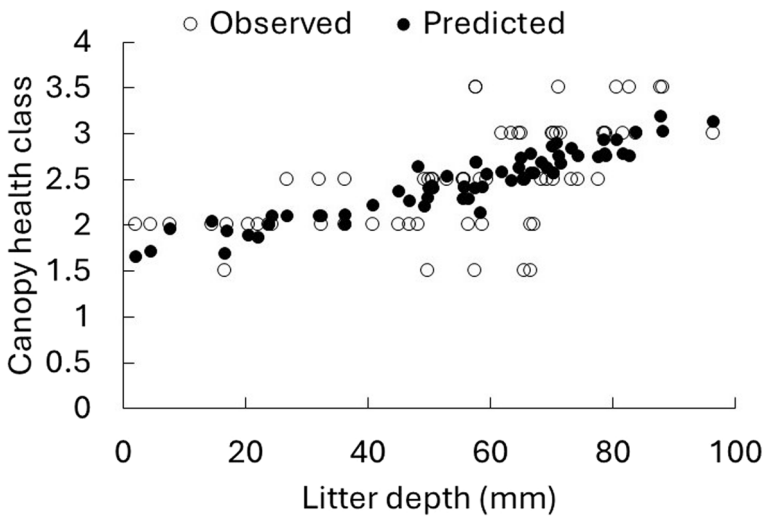


Fig. 3 Observed and predicted karri tree canopy health condition (Table 1) using litter depth as a predictor (Model 2, Table 2)

these variables were used in lieu of TSF and LD, they respectively explained only 16% and 17% of variation in canopy decline.

Soil physio-chemical attributes

Initial assessment revealed that there is considerable variability in the structure and chemistry of karri forest topsoils. For example, zero to 85% gravel; 41 to 235 mg/kg total P; 3.6 to 27 me% exchangeable Ca; 0.012–0.609 me% exchangeable Al. The levels of total N (0.09–0.49%), nitrate N (< 1 mg/kg), and Bray II P (0.2–12.8 mg/kg) were generally low. The difference between total and organic C suggests relatively high charcoal content in the topsoil. There appeared to be consistent relations between measured parameters, for example C versus N and N versus P. A rigorous examination might reveal as many as three distinct soil types, but there was no immediately obvious relationship between stand and soil parameters nor between these parameters and litter depth (LD). Based on previous studies in eucalypt forests (Turner and Lambert 2005; Turner et al. 2008) none of the measured soil parameters in the current study were indicative of potential problems for eucalypt tree health.

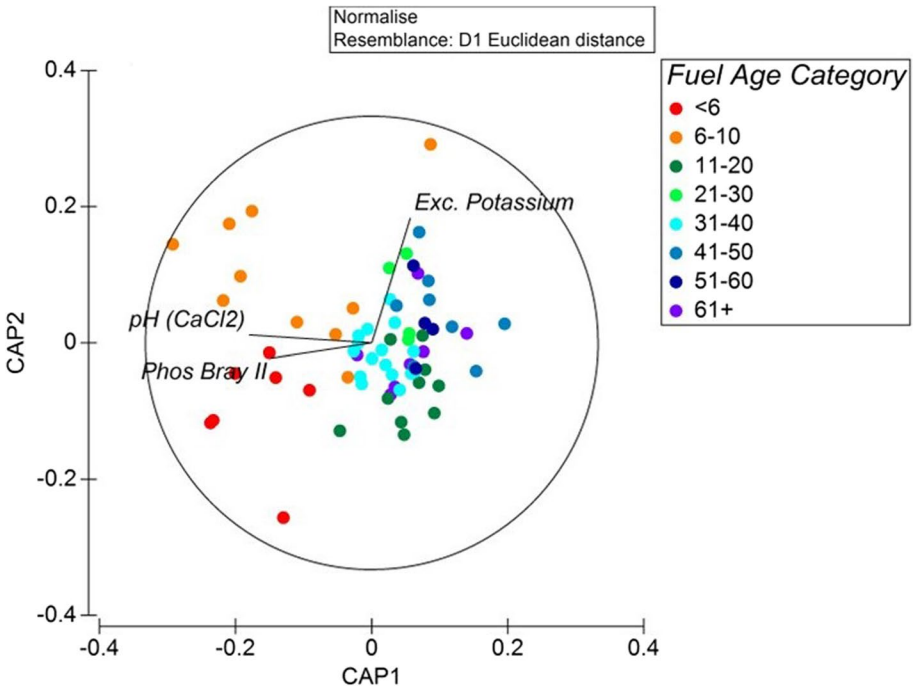


Fig. 4 Canonical analysis of principal coordinates (CAP) discriminating Time since fire categories according to soil and stand variables. Variables correlating with CAP axes with $r = 0.45$ or better are shown as vectors to indicate correlation with axes

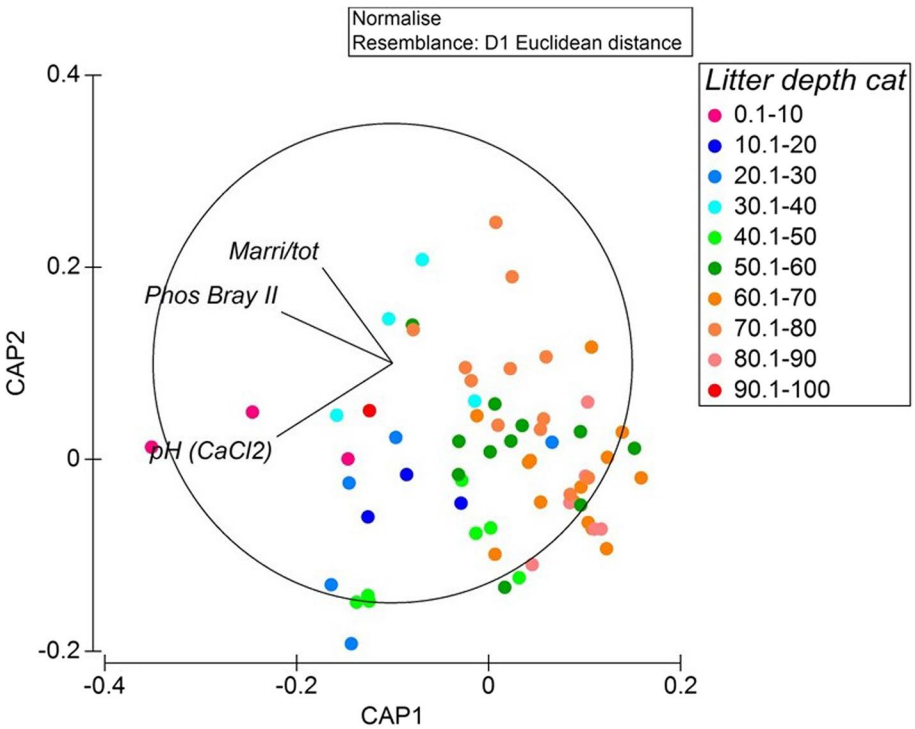


Fig. 5 Canonical analysis of principal coordinates (CAP) discriminating litter depth categories according to soil and stand variables. Variables correlating with CAP axes with $r = 0.45$ or better are shown as vectors to indicate correlation with axes

Tree canopy health and soil chemistry differences

Soils in moderate to severely declining stands (CD ≥ 2.5) tended to be slightly more acid for pH($CaCl_2$), ($P_{2\text{-tail}} = 0.007$), and have higher gravel content ($P_{2\text{-tail}} = 0.04$), exc. Magnesium ($P_{2\text{-tail}} = 0.004$), exc. Potassium ($P_{2\text{-tail}} = 0.03$), organic Carbon ($P_{2\text{-tail}} = 0.003$) and total Carbon ($P_{2\text{-tail}} = 0.02$), but lower Bray II Phosphorus ($P_{2\text{-tail}} = 0.002$) than those in early/moderately declining stands (CD < 2.5) (Fig. 6). There was no significant difference in Ca between severely declining sites (12.46 meq100g^{-1}) and other stands (11.57) (Fig. 6). It is noteworthy that canopy decline at two sites in 27 year old fuels on gravel-free soil was rated as 1.5, which is lower (healthier) than what would be expected for a long-unburnt site (Fig. 2).

Correlations between key variables

Table 4 shows correlations between measured variables and Canopy Decline. The critical value of r for $P_{(2\ \text{tail})} \leq 0.05$ is $R = 0.24$. Unsurprisingly, TSF and LD

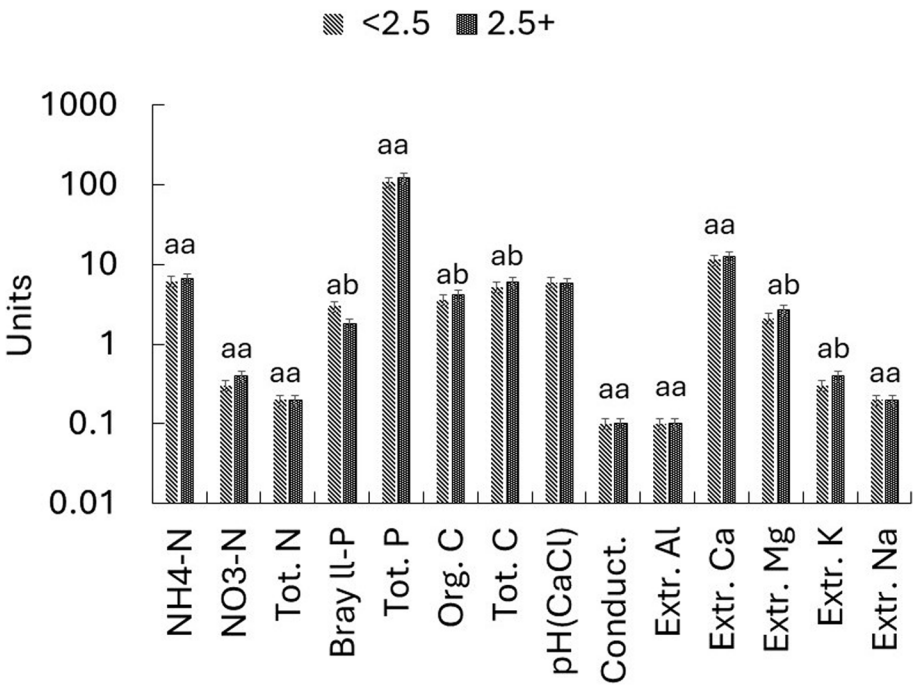


Fig. 6 Comparison of soils in early-moderately declining (CD < 2.5) and moderate-severely declining (CD ≥ 2.5) stands (gravel content not included). Bars within pairs having different letters are significantly different ($P < 0.05$, 1 tail t-test). Error bars are s.e. Note logarithmic scale of Y axis. Units vary with chemical component: Organic Carbon, total Carbon, total Nitrogen units = %; Ammonium Nitrogen, NO_3 Nitrogen, Bray II Phosphorus units = mgkg^{-1}; Exc. Al, Exc. Ca, Exc. Mg, Exc. K, Exc. Na, units = meq100g^{-1}; conductivity units = dSm.$^{-1}$

Table 4 Correlation (r) matrix. CD = canopy decline, LD = litter depth (LD) and TSF = time since fire since fire (TSF). Critical value of r for $P_{(2\ \text{tail})} \leq 0.05$ is $R = 0.24$ (bolded)

	CD	LD	TSF		CD	LD	TSF
pH ($CaCl_2$)	0.15	−0.42	−0.28	NH_4-N	0.14	0.11	0.04
pH (H_2O)	−0.08	−0.36	−0.22	Tot. N	0.18	0.12	0.10
Org. C	0.27	0.22	0.10	NO_3-N	0.08	0.06	0.15
Tot. C	0.27	0.20	0.15	P Bray II	−0.30	−0.28	−0.23
Exc. Al	−0.12	−0.02	−0.13	Tot. P	0.10	0.01	−0.02
Exc. Ca	0.18	0.00	0.09	Gravel	0.16	0.05	0.13
Exc. Mg	0.26	0.23	0.16	CD			
Exc. K	0.23	0.15	0.04	LD	0.62		
Conductivity	−0.14	−0.30	−0.21	TSF	0.74	0.78	

were closely correlated ($r=0.78$). Variables were correlated with CD in descending order of TSF (0.74), modelled LD (0.69), measured LD (0.62), Bray II P (0.30), organic C or total C (0.27) and Mg (0.26). Of the seven variables significantly different between severely and less severely declining stands, Bray II P, organic C, total C and exchangeable magnesium (Mg) were correlated with CD. pH $CaCl_2$ was not correlated with CD but was negatively correlated with both TSF and Litter Depth. Bray II Phosphorus was negatively correlated with LD but not correlated with TSF. Total C, organic C, Mg and K were not correlated with TSF or LD.

Canopy decline and rainfall

The annual and mean decadal rainfall for Pemberton for the period 1942–2024 is shown in Fig. 7. Rainfall has been trending down since the 1960s. At 1058 mm, the mean annual rainfall for the most recent period (2010–2024) is the lowest on record and is 10.3% below the long term mean (1180 mm). If moisture stress was the primary cause of canopy decline then those stands with the highest tree basal area would be expected to be most affected. However, there was no relationship between tree stocking and basal area, and canopy health (Fig. 8).

Discussion

Our results confirm that dominant and co-dominant karri trees are subject to chronic decline with time since fire. However, our findings do not support the N accumulation hypothesis for eucalypt decline reported for dry mixed forests in south-east Australia (Turner and Lambert 2005; Turner et al. 2008). There was no evidence of N accumulation with TSF in karri forest topsoil. While three sites had been burnt four times in 33 years (mean fire interval ~ 8 years), the mean fire interval at other sites ranged from 11 to 33 + years. No sites had been burnt frequently (mean fire interval ≤ 4 years) so it was not possible to investigate the effects of frequent mild fire on tree health. This requires further investigation and could be

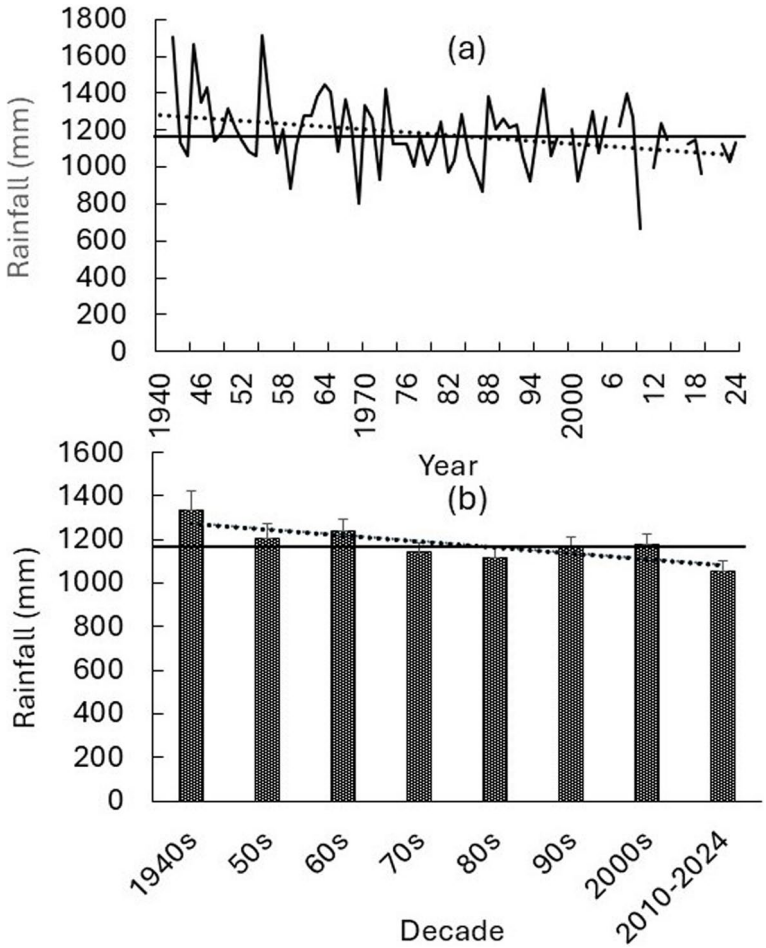


Fig. 7 **a** Annual rainfall (1942–2024) for Pemberton and **b** average decadal rainfall. Dotted line is trendline, solid line is long term mean

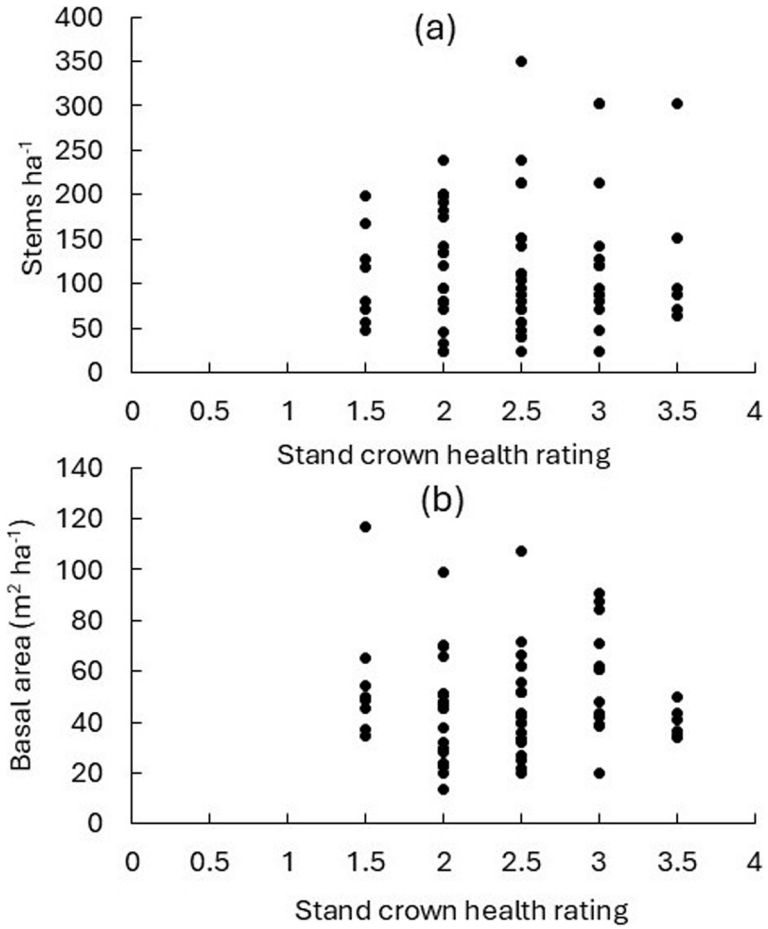


Fig. 8 Stand crown health rating for dominant and co-dominant karri trees with **a** stocking of overstorey and mid-canopy tree species and **b** basal area of overstorey tree species

implemented at an operational scale in an adaptive management framework.

Our two parsimonious multivariate models for explaining karri canopy decline indicate that soil chemistry has little explanatory power, which was an unexpected result. The best models selected according to BIC incorporate either K or Ca as the only explanatory soil variables after TSF or LD respectively, noting that LD is largely a function of TSF. K and Ca are weakly correlated with stand health (Table 4) and explain a small proportion of the variation (8% and 5% respectively). There is no apparent reason why these elements would affect tree canopy health. K is significantly higher in severely declining stands but Ca is not. These variables are correlated with a number of other variables having explanatory power, for example organic and total C (Table 4) and pH $CaCl_2$ (Fig. 4). The N accumulation hypothesis (Turner et al. 2008) is that increases in soil N, acidity and exchangeable Al with TSF impact adversely on tree health. Declining pH creates a less suitable environment for roots due to higher levels of Al. Increases in mineral N impact on the nutritional balance in trees, making them more susceptible to pests and pathogens. This was not evident in karri forests.

Fire can alter the chemical and biological properties of forest soils, especially the rhizosphere, with the extent of changes being generally proportional to fire intensity and the amount of fuel burnt (Bissett and Parkinson 1980; Tomkins et al. 1991; Sharma et al. 2017; Agbeshi et al 2022). In the current study, we observed little variation in topsoil chemical properties that could be attributed to fire history (TSF). This could be because most (at least 85%) of the fires were low intensity prescribed fires that may have had ephemeral, or no detectable effects on topsoil chemistry, and because of the low fire frequency at most sites. The only significant change was pH $CaCl_2$, which was negatively correlated with TSF (−0.28) and LD (−0.42). Apart from LD, the only variables correlated with TSF were pH $CaCl_2$ (−0.28) and Marri/Tot (−0.25). K and Ca were both correlated with pH $CaCl_2$, as is Marri/Tot. Exchangeable Aluminium was correlated with

pH $CaCl_2$ (0.61), Ca (−0.53), Mg (−0.42), K (0.30), Total N (0.29) and Marri/Tot (0.30), but not with TSF or LD. Marri/Tot was negatively correlated with gravel content (−0.27) and with TSF (−0.25) probably because sites with more marri are generally drier so are more likely to be burnt. Soils of sites with more marri may be relatively difficult for eucalypt roots by virtue of their acidity and aluminium levels, but these are not in the range that would be expected to cause tree canopy health problems.

Low gravel in topsoils could indicate that these soils have higher soil volume for roots to access water and nutrients compared to soils with high gravel contents. Gravel content and proportion of marri are environmental variables independent of fire management and which do not appear in the models of canopy decline (i.e., do not meet model entry specifications). Bray II P and pH $CaCl_2$ can be influenced by fire management and can affect canopy health (Figs. 4, 5 and 6) but do not appear in the models explaining canopy decline. Organic and Total Carbon are not influenced by TSF or LD (Table 4), but were correlated with canopy decline. They are related to environmental variation but do not appear in the models. Mg was correlated with canopy decline (0.26) and was significantly associated with severely declining sites (Fig. 5) but does not appear in the model. However, there is no reason to suspect it as a cause of decline.

Forest trees low in the landscape on infertile and poorly drained and poorly aerated soils are particularly predisposed to decline in the absence of maintenance by cool burning (Jurskis 2005). Forest tree decline has been regarded as less of an issue in eucalypt forests on better soils such as mountain ash (*Eucalyptus regnans*) in Victoria and alpine ash (*Eucalyptus delegatensis*) in New South Wales (Turner et al. 2008). Karri forests are commonly seen as ecologically similar systems, often described as wet sclerophyll forests. In dry sclerophyll forest at Eden, News South Wales, in the absence of fire, pH decreased by about 0.6 over 39 years. This was similar to the difference of 0.7 between a long unburnt and an annually burnt dry forest site in Queensland, but there were smaller differences in blackbutt (*Eucalyptus pilularis*) forest described as wet sclerophyll forest (Turner et al. 2008). In a moisture stressed river red gum (*Eucalyptus camaldulensis*) forest, tree health as expressed in growth rate, and insect damage, were both related to tree physiology, including leaf size and shape, rather than N content of leaves (Stone and Bacon 1994). In three eucalypt plantations, insect damage increased and tree resilience decreased as a result of moisture surplus or deficit (Stone 2001). Nutrient quality of foliage in declining trees is a function of leaf age and origin as well as soil nutrient status and can reinforce the process of eucalypt decline (Jurskis and Turner 2002). Studies of subtropical eucalypt forests in Queensland report that as well as being more resilient to wildfire, forests that were frequently burnt with mild fire showed less signs of tree crown decline and better tree growth than forests that were infrequently burnt (Lewis 2020; Williams et al. 2022).

A New South Wales study in blackbutt forest at Manning River reported a pH difference of 0.6 between regularly burnt and unburnt (for 12 years) dry forest and a significant increase in exchangeable aluminium. But there was little difference between burnt and long unburnt sites in wet blackbutt forest. The soils at the higher quality 'wet sclerophyll' site were well-buffered (Turner et al. 2008). In 1993, three of 68 sites on the New South Wales north coast suffering tree 'crown dieback' were blackbutt types (Stone et al. 1995). In 2001 two of 47 'dieback' sites in Bega Valley Shire on New South Wales south coast were blackbutt types (Jurskis and Turner 2002). Both sites were in swales with shallow water tables behind coastal dunes. When 'dieback' of alpine ash was first reported in 1963, its severity was described as incipient on well drained sites, moderate on a moderately well drained site and severe on an "ill-drained" site (Ellis et al. 1980).

As observations of chronic decline of eucalypt forest trees with lack of cool burning have increased since the late 20th Century, higher site quality forest types have been increasingly affected (Jurskis 2005). In New South Wales, most forest types dominated by blackbutt or spotted gum (*Corymbia maculata*) were not classified as prone to decline in 2011 (Jurskis et al. 2012) but have been widely affected since the wet period which ended the Millennium Drought in 2012 (V. Jurskis pers. obs.). Prior to the current study, there were no documented reports of tree decline in karri forests. The significant influence of litter depth, a function of time since fire, on canopy condition of karri trees, in the absence of any strong signals in soil chemistry, suggests that fire regimes may act primarily through physical changes to the rhizosphere such as moisture, temperature, aeration, and penetrability rather than chemical processes in well-buffered soils. Canopy decline was weakly (+ve) correlated with organic and total C in our data (Table 4). There is extensive literature on the effects of soil organic matter on soil physical properties as well as buffering capacity (e.g. Murphy 2015). Organic carbon is associated with many physical properties favourable for agriculture such as higher water availability and lower soil density and strength (Murphy 2015).

Proliferation of *Santalaceae* shrubs, which are root parasites, is a feature of tree decline in several dry forest types of southeastern Australia (Jurskis 2005). Nevertheless, the absence of any outbreak of arbivores, parasites or diseases in declining karri forest trees

is consistent with a general model of decline incited by physical and chemical changes in soils and affecting fine roots and mycorrhizae (Manion and Lachance 1992; Jurskis and Turner 2002; Jurskis 2005). Studies of declining *Eucalyptus delegatensis* in Tasmania suggested that impacts of changing soil chemistry on roots, mycorrhizae and soil microbial communities (Ellis and Pennington 1992; Horton et al. 2013) did not extend to increased folivory. We did not sample roots, mycorrhizae, microbial communities or soil physical factors (other than gravel content) in the current study. A long-term study in a New South Wales blackbutt forest indicated that frequent burning increased the topsoil exposure to insolation, maintaining harder and drier soil than in unburnt areas, affecting the community composition of ants in the soil (York 2000). It is likely that the soil microbial community and the relative suitability of conditions for eucalypt and understorey roots would also be affected. Foliar N levels and folivory per blackbutt leaf were unaffected by burning, but leaf turnover and therefore overall folivory were higher in the unburnt areas (Jurskis et al. 2011).

Drought and heat wave associated with climate change has been implicated in the decline of forest health (e.g.Matusick et al. 2013, 2018). While annual rainfall has been declining in the karri forest region since the 1970s (Hallett et al. 2018; Fig. 7), there is no evidence that drought is the primary cause of tree canopy decline observed in the current study. Drought-caused canopy decline will be most pronounced in denser stands, or stands with high tree basal areas on shallow soils because of the competition for soil moisture (Wardlaw 1989; Jurskis 2005; McGrath et al. 2023). For example, localised 'collapse' in jarrah forests of southwestern Australia at the height of the 'millenium drought' was confined to unnaturally dense stands (Matusick et al. 2013). We found no relationship between stand density, tree basal area and canopy decline. Drought would also be expected to be less severe in dominant trees and more severe in subdominant trees, but there was no evidence of this. Perhaps the most compelling evidence against climate change as a primary cause of decline in eucalypt forests generally, is in contrasts between the health of similar stands on adjoining properties with different land uses. There are often sharp, straight boundaries between declining stands and healthy stands, coinciding with fencelines and representing differences caused by human management rather than by climatic or other environmental factors (Jurskis 2008). Similarly, in the current study, differences in tree crown health were associated with differences in fire history. Drought is a regional-scale phenomenon, so it is unlikely that crown decline due to drought would be associated with fire history boundaries.

While there is no evidence that climate change is the primary driver of tree canopy decline in karri forests, it may be a secondary factor interacting with time since fire. Karri forests are well adapted to below average rainfall years. However, a feature of climate change in southwest Australia is occasional years of well below average rainfall, or severe drought. For example in 2010, the annual rainfall recorded at Pemberton was 669 mm (Fig. 7), about 43% below the average rainfall for the record period. If karri root systems are unhealthy due to extended periods without fire, then occasional severe drought events may place trees under stress, resulting in canopy decline. This requires further investigation.

High intensity fire can damage the crowns of overstorey trees (e.g., Etchells et al. 2020; Nolan et al. 2020). While we have fire histories for the study sites back to the 1970s, we do not have fire intensity or severity information. However, we know that most (at least 85%) of the fires were low intensity prescribed fires, which are unlikely to damage the crowns of larger overstorey tree. Also, fire-caused crown damage is most likely to be more apparent in smaller trees (Nolan et al. 2020), and not associated with the time since the last fire. However, crown decline observed in the current study was in dominant and co-dominant (larger) trees and was associated with time since last fire. Finally, past fire damage to crowns is visible in the crown architecture, and as described in the methods section, we discounted trees that displayed obvious physical damage.

It is well known that plants, including forest trees, live in association with soil microbiota, which have an important effect on plant growth and health (e.g., Turner et al. 2013; Compant et al. 2019; Terhonen et al. 2019). The composition of the soil microbiota is largely dependent on soil chemical and physical properties, especially soil moisture (Bissett and Parkinson 1980; Brockett et al. 2012; Lladó et al. 2018; Ni et al. 2022). Karri forests grow in a Mediterranean-type climate, with cool wet winters and warm dry summers and soil moisture content fluctuates accordingly. A longitudinal study of the soil profile moisture content of the top 30 cm in a regularly burnt karri forest showed that soil moisture content was mostly 12–15% (of oven dry weight) during summer and 40–45% during winter (Burrows 1987). Higher soil moisture for longer periods, and reduced fluctuations in soil moisture as a result of accumulating mulch (deep surface litter) with TSF, may especially favour competitive and antagonistic soil biota and disadvantage beneficial organisms such as mycorrhizae on karri roots that persist in 'better' soil conditions. The density of relatively short-lived karri forest understorey plants naturally declines with time since fire (Burrows et al. 2023) but there was no visual indication that persistent plants were unhealthy.

It is well established that the severity of soil-borne root pathogens mainly depends on soil moisture, temperature and pH (e.g. Christensen 1975; Shearer and Tippett 1989; Termorshuizen 2014; Stewart et al. 2021). The observed association of karri crown decline with accumulation of shade and mulch on the ground is consistent with general observations of eucalypt decline in forests, parks and gardens. In a guide to Australian arboriculture, Hadlington and Johnston (1983) stated that fungal pathogens of roots become a serious problem when soil conditions become too moist for too long for the tree species. They emphasized that each species is adapted to a particular water balance and range of natural fluctuations such as drying and/or waterlogging. 'Phytophthora dieback' has been associated with raised water tables consequent to reduction of transpiration by high intensity fire in Victorian forests and other causes in Western Australia (Jurskis 2005).

Substantial resources continue to be devoted to research of arbivores, diseases and parasites responding and contributing to forest decline, rather than towards research of primary causes (Jurskis 2005). Our study in karri forests supports the importance of fire regimes in chronic decline of eucalypt forests but it reveals that the effects of fire regimes are not limited to N cycling processes. The lack of arbivory across the range of karri forests sampled in the current study supports observations that increased arbivory can be a consequence rather than a cause of forest declines (Manion and Lachance 1992; Jurskis and Turner 2002; Jurskis 2005). Our results are not consistent with the findings of a report commissioned by the New South Wales Government (Matusick and Fontaine 2020), which emphasizes the importance of folivory by insects, and climate change in 'eucalypt dieback'. Matusick and Fontaine (2020) concluded that there are few unifying factors in eucalypt dieback. They stated that a link between fire frequency, nutrient dynamics and eucalypt dieback remains unresolved.

Our study confirms a link between time since fire and eucalypt decline independent of soil nutrient dynamics. We propose that mulch that accumulates on the soil surface in the absence of fire modifies topsoil properties including moisture and temperature regimes. Such changes can in turn alter the composition of soil microflora and soil microbiology, which could adversely impact on the functioning of the tree's fine root system, leading to decline in tree health, exacerbated by a drying climate. This supports an earlier reported concept that fire mediated changes in soil moisture regimes are a factor in chronic decline of eucalypt forests (Jurskis and Turner 2002; Jurskis 2005). Importantly, the evidence challenges a proposal (Jurskis and Turner 2002) that tall moist eucalypt forests on well-buffered soils are not susceptible to chronic decline in the absence of frequent mild fire.

Our model of tree canopy decline incorporating TSF only explains 56% of the variability in canopy decline, suggesting a more complex process associated with decline. It is possible that there is an interaction between declining tree root system health, time since fire and declining rainfall. It is reasonable to assume that unhealthy tree roots will be less capable of extracting sufficient moisture and nutrients to maintain tree health in severe drought periods. This needs further investigation.

Ecologists have argued that persistence of allegedly fire sensitive wet eucalypt forests of obligate seeders are threatened by increasingly frequent fires consequent to climate change (Fairman et al. 2015). Others have suggested that 'giant eucalypts' including karri, mountain ash, alpine ash and blackbutt are rainforest trees unusually lacking the ability to regenerate in the absence of fire (Tng et al. 2012). On the contrary, our data support observations (e.g., Jurskis 2015) that these eucalypts are not sensitive to damage by mild fires but likely depend on them to maintain healthy soil conditions for their roots. This could be increasingly important for karri forest health in a drying climate.

Conclusion

Overstorey trees in mature karri forests are in varying stages of canopy decline, in large part caused by long absence of fire. While this is consistent with declines reported in eucalypt forests in southeast Australia, we found no evidence that it is due to changed soil chemistry. We did not measure soil physical properties (other than gravel content), nor did we examine the soil microflora, but a plausible explanation is that the buildup of deep litter (mulch) in long unburnt forests is altering soil moisture and temperature regimes, and possibly other physical factors of the soil environment, disfavouring soil microorganisms that are beneficial to karri and favouring those that are harmful. Understanding forest tree canopy health and decline is obviously complex. Our modelling with TSF and exchangeable potassium content as predictor variables explained about 64% of the variability in CD so clearly, there are other factors involved.

While an understanding of the process of canopy decline in karri forests requires further investigation, our study supports the proposition that frequent mild burning can help to maintain forest health and therefore, resilience to climate change. Traditional Aboriginal burning expert Victor Steffensen said that lack of maintenance by mild burning results in "*upside-down country – thin on top and thick underneath – and sick trees with lazy roots in damp soils*". He stated that "*the Western vision of fire is all about life, property, fear and fighting fire*" (Steffensen

2020). This study of tree canopy decline with time since fire and associated accumulation of fuel in karri forests confirms "upside-down country" and "sick" trees in the absence of mild burning. Further research of physical soil conditions and the health of tree roots and mycorrhizae under contrasting fire regimes might help to confirm "lazy roots in damp soils" and reconcile "Western science" (Steffensen 2020) with traditional Aboriginal knowledge.

Recommendations

We encourage further research to better understand the relationship between fire regime, soil microbiology in the rhizosphere, climate change and karri forest tree health. There have been many reports of increasing forest decline, insect outbreaks and wildfires with droughts consequent to anthropogenic climate change (e.g. Allen et al. 2010). Observations of contrasting forest health and bushfire safety outcomes across management boundaries at a point in time, or under changing management over time (e.g. Hessburg et al. 2005; Jurskis 2005), indicate that adaptive management, especially restoration of frequent mild burning, can restore resilience of forests to climate extremes. About 70% of the mature karri forest exists in a relatively long unburnt (12+year old fuels) condition. In an adaptive management framework, we urge forest managers to increase the reintroduction of mild fires to karri forest to improve forest health and resilience in the face of a changing climate, and to help protect forests and communities from damaging bushfires.

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Authors' contributions
NB assisted with field work, assisted with data analysis and contributed to writing the paper. VJ conceptualised the study, assisted with field work and data analysis, and contributed to writing the paper. AW carried out data analysis and assisted with the interpreting and writing the results section. VD assisted with field work and with data analysis and interpretation.

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Data availability
The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare they have no competing interests.

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