

Plant and environmental factors associated with drought-induced mortality in two facultative phreatophytic trees

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Abstract

Background and Aims Drought-induced mortality of tree species is increasing globally. We aimed to investigate spatial patterns and size dependence of mortality of two dominant tree species (*Banksia menziesii* R. Br and *B. attenuata* R. Br) capable of accessing shallow watertables in a *Banksia-Allocasuarina-Eucalyptus* woodland.

Methods Living and dead trees were mapped within two plots: a high site (55 m to watertable) and a low site (9–20 m to watertable). Diameter at breast height (DBH) (cm) was measured and year of death estimated for deceased trees.

Results Tree mortality was higher for most species in the high site. Across sites mortality was greatest during 2011 for most species including *Banksia* trees following the 2010 drought. Species differences in mortality were observed between *B. attenuata* and *B. menziesii* in the high site only. A greater number of large dead *Banksias*

was observed in the high site. Spatial analysis indicated that local scale competition did not contribute to the death of these *Banksias*, however stand-level competition may have occurred.

Conclusions We conclude that drought-induced mortality of *Banksia* trees is more prevalent in landscape regions where trees cannot access the watertable and due to greater water demands of larger trees, mortality is more frequent in these individuals.

Keywords *Banksia* · Competition-induced mortality · Ecosystem change · Soil moisture · Size-dependent mortality

Introduction

Episodic, drought-associated tree mortality events have increased throughout the world in recent decades (Allen et al. 2010; Matusick et al. 2013). While the mechanisms behind this phenomenon may not always be well understood, some general causes are postulated relating to the interaction of drought, elevated temperature and evaporative demands (McDowell et al. 2011; Breshears et al. 2013; Eamus et al. 2013). Regional tree mortality events are increasingly being related to a combination of drought and heatwave conditions and referred to as ‘global-change-type drought’ (Clifford et al. 2013). These widespread mortality events have been observed to occur following drought periods and are not annual occurrences (e.g., Guarín and Taylor

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2005). With projections of further warming and drying and the likelihood of increased frequencies of heat wave conditions throughout many regions around the world, this will likely lead to more frequent mortality events in forests and woodlands (Allen et al. 2010; IPCC 2013). These tree declines will put in motion further declines in the function, resilience, provision of services (timber, carbon storage), microclimate, and non-tree biodiversity (Anderegg et al. 2013).

At the regional or local scale, tree mortality and associated shifts in community structure are mediated by tree and environment attributes. Environmental attributes such as soil hydraulic properties, soil depth, soil moisture and watertable depth can vary spatially or temporally. Tree attributes include water demand that may vary with tree size and condition, water use strategies that varies by species or tree age and the susceptibility of species to water and heat stress (Brouwers et al. 2013; Poot and Veneklaas 2013). Where water fluxes are predominantly vertical, the degree to which competition for water is expressed locally should depend upon the combination of local environmental factors and local community structure.

Extraction of water by trees can influence local soil water availability and watertable depth and may compromise subsequent tree functioning (Zencich et al. 2002; Canham et al. 2009). Competition for water depends upon tree size, as large trees often have a greater evapotranspirative demand and more extensive (lateral and/or vertical) rooting structure compared to smaller trees. However, smaller trees may have less expansive rooting structures and therefore explore a smaller volume of soil. Therefore, the spatial arrangement of trees of different sizes could influence competitive interactions and survival (Stoll et al. 2002; Moore et al. 2004; Nepstad et al. 2007). Diffuse stand-level competition for soil water may occur, however, local scale competition-induced mortality related to local tree density can be inferred from spatial patterns of living and dead trees, such as the aggregation of dead trees or spatial associations between dead and living trees (Boyden et al. 2005; Hurst et al. 2012).

Individual trees occupying a similar rooting zone may compete for vadose zone water (the unsaturated upper regions of the profile resulting from precipitation) exacerbating tree stress during periods of water deficit, and this is likely more pronounced in regions where the

watertable is not accessible (Martens et al. 1997). Data demonstrating differentiation of rooting strategies, or lack thereof, may provide some clues as to below ground competition and thus mortality. However, such data is largely destructive, and much more expensive to collect than spatial patterns of trees on the surface.

Facultative phreatophytes, plants relying on the watertable where accessible or vadose zone water (Zencich et al. 2002), are sensitive to climate change and variability as soil water recharge is reliant on rainfall (Froend and Sommer 2010; Kløve et al. 2011). Facultative phreatophytic species may utilise the watertable in periods of the year or locations where they have access to it, but can also persist in locations where they cannot access the watertable (Zencich et al. 2002). Trees positioned at different distances from the watertable in a landscape will exhibit variable drought sensitivity and this may result in heterogeneous patterns of mortality. Phreatophytic vegetation found in biodiverse Mediterranean ecosystems are most reliant on soil water during summer months when rainfall is lowest and temperatures highest (Eamus and Froend 2006). During these drought periods, soil water in the unsaturated zone may be depleted and, in turn, may lead to hydraulic failure and mortality of trees not accessing the watertable (Zencich et al. 2002). The sensitivity of facultative phreatophytic species to watertable draw down has previously been highlighted (Groom et al. 2000; Cooper et al. 2006).

In southwestern Australia, significant rainfall decline has been recorded since the mid-1970s (Bates et al. 2008). Widespread tree decline during the same period has been attributed to this climate variation and is well documented, especially for eucalypt forest and woodland species (Brouwers et al. 2013; Evans et al. 2013; Poot and Veneklaas 2013). This study focuses on mortality of the two dominant *Banksia* tree species, *B. attenuata* and *B. menziesii* in the Kings Park bushland within the biodiversity hotspot of southwestern Australia (Myers et al. 2000). These species possess structural and physiological adaptations to overcome summer periods of water deficit and poor water holding soils of the Swan Coastal Plain (Dodd and Bell 1993; Zencich et al. 2002; Hopper and Gioia 2004). Despite this, *Banksia* population decline (with ~30 % decreased density) has been observed in this bushland since the 1960's (Beard 1967; Crosti et al. 2007; Wychelerey PR, research notes, Kings Park, Western Australia, unpublished), likely in response to declining rainfall. Both of these species are facultative

phreatophytes, relying on vadose soil water and the watertable where accessible (Zencich et al. 2002). They possess a dimorphic rooting structure with surface roots and a deep tap root extending 8–9 m below ground surface (BGS) accessing soil water (Farrington et al. 1989; Zencich et al. 2002). We investigate the fine scale spatial patterns of facultative phreatophytic tree mortality within two Mediterranean woodland sites with contrasting depths to the watertable as well as temporal patterns of mortality over 3 years, 2011 to 2013 in the Kings Park bushland, Western Australia.

- Firstly, we assessed the extent that tree mortality across all tree species and specifically in the two dominant facultative phreatophytic canopy species, *Banksia menziesii* R. Br and *Banksia attenuata* R. Br was associated with a specific, extreme drought event.
- Secondly, we hypothesised that mortality, of all tree species, and of *B. menziesii* and *B. attenuata*, would be greater at the site further from the watertable than at the site closer to the watertable and that there would be no interspecific differences in mortality between *B. menziesii* and *B. attenuata* within sites as these congeners possess similar rooting structures and a previous study in this bushland found no differences in mortality rates (Crosti et al. 2007).
- Thirdly, we hypothesised that mortality of the declining canopy species would be size-dependent, either with greater mortality amongst larger trees due to their relatively higher water use per unit time or greater mortality in smaller trees due to shallower rooting depths, and this would differ among sites with varying depth to watertable.
- Lastly, we hypothesised that mortality would be due to spatial interactions (i.e., localised competition) between these species and other dominant canopy species.

Materials and methods

Study site and species

Kings Park is located close to the centre of the city of Perth, Western Australia (31.96°S, 115.83°E) and includes a large (for its urban location: 267 ha) area of native vegetation that has been reserved for ‘public

purposes’ since the first years of the city’s existence. The contemporary urbanised fragment has been subject to the effects of a long history of disturbance and management: selective tree removal (large jarrah – *Eucalyptus marginata* Sm. – individuals in the late 19th century and *Banksia* species for firewood and fencing to the early 20th century), continuous mild disturbance of many kinds, including weed invasion and suppression, and loss of ecological function through local extinction of many vertebrates. Despite these impacts, the vegetation retains a structure, function and composition similar to less disturbed analogues.

The vegetation of the Kings Park bushland is a low (5–8 m tall) mixed *Banksia* – *Allocasuarina* woodland dominated by *Allocasuarina fraseriana* Miq., *B. attenuata* and *B. menziesii* with scattered emergent *E. marginata*, *E. gomphocephala* DC. and *Corymbia calophylla* Lindl. over relatively species-rich midstorey and understoreys (Baird 1977; Mattiske and Associates 1987). A comparison of surveys from a 15.5 ha area in the west of the park between 1939 and 1999 indicated a major change in composition and density over this time (Crosti et al. 2007). Total tree density increased by 160 % over that 60-year period, with eucalypt (including *Corymbia*) numbers doubling (their dominance among trees changing from 13 to 20 %) and *A. fraseriana* doubling also (from 28 to 54 %), offset by a decline in *Banksia* tree species of one third (from 59 to 26 %) during this period (Crosti et al. 2007).

Depth to the permanent watertable varies from approximately 10 m BGS in the west of Kings Park to 60 m BGS on Mt Eliza in the east (Bessell-Browne 1990; Department of Water 2014). Data from the 1980s to the present show remarkably stable watertable depths across all groundwater bores within the park, with an average drop of 0.8 m in spring over 30 years between 1986 and 2005–2010, and scarce seasonal data suggesting fluctuations of <1 m (Kings Park bore data, West Perth, Western Australia, unpublished). Kings Park is located on Tamala limestone that has been leached significantly such that its upper surface comprises as much as 100 m of unconsolidated sand, low in nutrients and with infrequent clay lenses (Beard 1967; Bessell-Browne 1990; Davidson 1995). Limestone outcrops are present throughout the eastern margins of Kings Park.

Two sites were chosen for this study in the Kings Park bushland containing high numbers of both *Banksia* species and with contrasting depths to the watertable: a

high regional relief site remote from the watertable 'High site' situated on Mt Eliza in the east of the bushland, with a depth to the watertable of approximately 55 m (31°57'48.22"S, 115°50'6.87"E) and a low regional relief site 'Low site' in the west side (31°57'50.45"S, 115°49'27.69"E) with a depth to the watertable ranging from 9 to 20 m (Fig. 2; Department of Water 2014). A fire during the summer of 1988 and 1989 burnt 45 % of the bushland including all of the High and Low sites (BGPA GIS database 2014).

Climate

Kings Park has a Mediterranean-type climate with hot-dry summers and cool-wet winters with 80 % of rainfall occurring between May and October. Across southwestern Australia, rainfall has declined 15–25 % since the late 1960s with the strongest declines observed in autumn and winter (Hope et al. 2010; Nicholls et al. 2011). Perth's 30-year average annual rainfall is currently 750 mm. Temperatures have also been increasing in terms of both mean and extreme values and of frequency of heatwaves (three or more consecutive days with maximum temperatures over 35 °C). Perth's 30-year average maximum temperature is currently 24.5 °C (Bureau of Meteorology 2014; interpolated from nearby stations), but has been increasing by an average of 0.1 °C per decade over the century to 2010. Since 2010, mean annual maximum and minimum temperatures have also been above average (Fig. 1). With a total of 395 mm for the year, 2010 was the driest year on record (since 1876) for the Perth Metropolitan region. With three heat waves and a mean temperature 0.56 °C above average, it was also among the hottest. The Perth Metropolitan region received near average rainfall during 2011 and 2013 (Fig. 1), but temperatures continued to increase with six and seven heat waves recorded during 2011 and 2012, respectively. (Bureau of Meteorology 2014)

Soil moisture spatial variability

To confirm expectations about differences in groundwater availability between sites and to understand the spatial distribution of soil moisture within sites, one electrical resistivity tomography (ERT) (Super Sting, Advanced Geosciences, Inc, Austin, Texas) transect was measured in each site. ERT provides information on the spatial variability in resistivity of a soil profile to

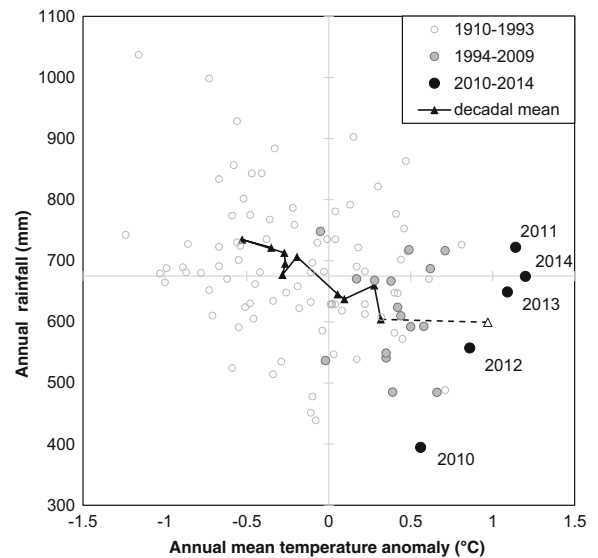


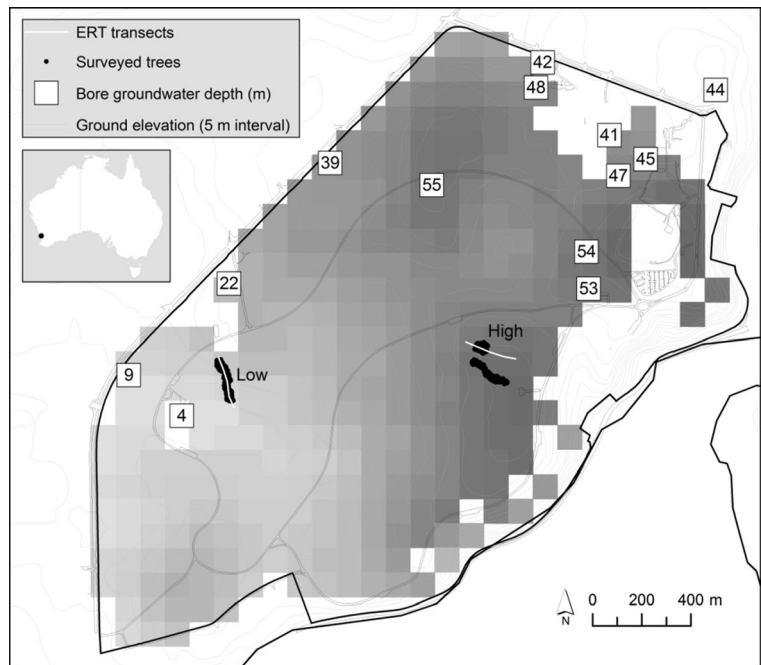
Fig. 1 Annual mean temperature anomaly and annual rainfall over the period from 1910 to 2014 with decadal mean for Perth, Western Australia (Perth Metro Station, Bureau of Meteorology 2014)

depths of 10s of meters, from which the distribution of subsurface resistivity, soil moisture and watertables can be inferred. In soils resistivity is particularly affected by variation in clay content, known to be typically less than 1 % at the sites, salinity and water. The depth of the ERT survey depends on the configuration and spacing of the electrodes at the surface (Loke and Barker 1996). A 216 m long ERT transect was established in each of the High and Low sites on 28-Aug and 11-Sept 2013, respectively. Repeat measurements were made in March 2015, providing a contrast between end-of-winter and end-of-summer soil moisture patterns typical of a Mediterranean climate. Electrodes were positioned 4 m apart and a dipole-dipole configuration was used to switch the electrodes and measure subsurface resistivity patterns.

Tree mapping and characterisation

To assess tree density and spatial patterns of mortality, mapping of all trees, living and dead, was conducted in the two sites in the Kings Park bushland with a Differential GPS (DGPS, Yuma, Trimble, USA) during Nov-2013 to Jan-2014 (Fig. 2). Sites were selected in relation to the expected distance to the watertable based on bore data and the Perth Groundwater Atlas (Kings Park bore data, West Perth, Western Australia, unpublished; Department of Water 2014). A further

Fig. 2 Study sites located within the Kings Park bushland (6, 360 m² High site, 5, 400 m² Low site), Western Australia showing mapped trees, electrical resistivity tomography (ERT) transects, ground surface elevation (grey 5 m contours) and interpolated (grey shade 9 to 65 m) and measured (bore locations) watertable depth (m below ground surface) (Kings Park bore data, West Perth, Western Australia, unpublished). Location of Perth within Australia shown in inset



factor in site selection was the presence of the study species, *B. menziesii*, which has a patchy distribution through the park. The High site was mapped in two sections with an intervening elevated walkway. These were 1, 680 and 4, 680 m² in area, totalling 6, 360 m². A single area of 5, 400 m² was mapped in the Low site. Within these areas, all trees with a diameter at breast height (DBH) \geq 4 cm were mapped. Diameter at breast height of each stem/trunk was measured using a DBH tape (Yamayo, Associated Instrumentation Pty. Ltd, Japan). For all living individuals, two perpendicular canopy widths were measured, species identified and if dead, estimated year of death was recorded. The year of death between 2013 and 2011 was determined from visual observations of appearance which included the presence of leaves, appearance of remaining bark and general decomposition. Differentiation between years of death of trees prior to 2011 was not possible and instead one class was used for deaths estimated to occur before 2011 (Table 1).

Data analysis

Analysis of geophysical data

Inversions of the resistivity data was conducted using the Earth Imager 2D (Advanced Geosciences, Inc,

Austin, Texas) software. A conjugate gradient solution technique was used in a robust inversion method to produce images of the spatial distribution of subsurface resistivity. A robust inversion assumes an exponential distribution of data errors and minimizes an L1-norm of combined data misfit and a model stabilizing functional (Claerbout and Muir 1973). Ratios of apparent resistivity from successive time periods at the same electrode pairs were calculated and used to conduct time-lapse inversion to assess spatial patterns of changes. This method effectively filters out the effect of the lithology leaving the contribution of changes in moisture content in the resulting image (Descloitres et al. 2008).

Table 1 Tree characteristics used to estimate year of death in the Kings Park bushland

Year of death	Characteristics used to differentiate between years of death of trees
2013	Leaves present, bark intact
2012	No leaves present, decomposition commencing
2011	No leaves present, high level of decomposition, bark may be falling away
Prior to 2011	No leaves present, high level of decomposition, bark absent, tree may have fallen

Analysis of stand characteristics

Banksia menziesii and *B. attenuata* trees were pooled for all spatial analysis conducted given both species are facultative phreatophytes that exhibit similar resistance to xylem cavitation (Canham et al. 2009), have similar water relations (Dodd and Bell 1993), similar mortality patterns from 1939 to 1999 in the Kings Park bushland (Crosti et al. 2007) and similar mortality within size classes in our study (no significant interspecific differences within large and small size classes within High and Low sites ($P > 0.05$)).

Two-sample proportions tests were conducted to test for differences between sites for dead and living trees (Newcombe 1998). The test was used to compare interspecific differences in mortality proportions between *B. menziesii* and *B. attenuata* and intraspecific proportions of dead trees between sites for the species: *B. menziesii*, *B. attenuata*, *E. marginata*, *C. calophylla* and *A. fraseriana*. The same test was also used to compare the overall proportions of dead trees present between sites by pooling all years of death for each species.

A generalised linear model was used to test intraspecific differences in proportions of mortality between different years within sites (Venables and Ripley 2002). Pearson's moment correlation was used to test for correlation between the position of dead *Banksia* trees along the Low site transect (along the groundwater depth gradient) and approximate depth to the watertable BGS (Newcombe 1998).

Size-dependent mortality

To determine whether tree mortality was size-dependent, comparisons of proportions of dead *B. menziesii* and *B. attenuata* trees (pooled) of different size classes were conducted across both sites and between sites with all years of death pooled. Dead *B. menziesii* and *B. attenuata* trees were allocated to two size classes of 'large' (summed DBH of all stems ≥ 7 cm) and 'small' (summed DBH of all stems < 7 cm). *Banksia menziesii* and *B. attenuata* trees with a DBH of 7 cm are considered to be approximately 7–10 years old, based on tree monitoring following restoration planting (Kings Park, West Perth, Western Australia, unpublished data), and to have a less extensive rooting structure compared to larger trees. Two sample proportions tests for analysing equality of variance were conducted on large and small

B. menziesii and *B. attenuata* trees to compare size-related mortality within and between sites.

To test significant differences between canopy areas of small and large *Banksias* the Kruskal - Wallis rank sum test was used as the data was not normally distributed, revealed by the Shapiro - Wilk normality test.

Spatial analysis of tree mortality

The univariate pair correlation function (PCF, $g(r)$) was used to describe the spatial pattern of live and dead trees (Stoyan and Stoyan 1994). The PCF determines the expected density of points in a point pattern within annuli of increasing distance (r) from arbitrary target points in the data set (see diagram) compared to a null model of the same number of points randomly placed with a Poisson null model (Stoyan and Stoyan 1994; Law et al. 2009). Values of $g(r) > 1$ indicate spatial aggregation of trees, $g(r) = 1$ indicate spatial randomness and $g(r) < 1$ indicate regularity of tree distribution (Stoyan and Stoyan 1994). Confidence envelopes indicating the range of the expected density based on the function and intensity of the point pattern were constructed via a Monte Carlo technique involving 999 simulations of the null model.

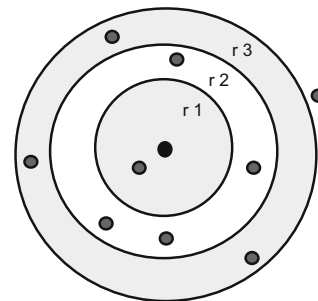


Diagram illustrating the analysis of the pair correlation function with the target point (black circle) in the centre of annuli of increasing distances (r) from this point and neighbouring points (dark grey circles) distributed throughout these rings.

Unlike other functions, the PCF is analysed in rings of increasing distances from the target point which enables simultaneous detection of spatial patterns at different scales. The PCF can assess pattern at all distances rather than the 'myopic' nearest neighbour functions which only analyses distances up to that of between nearest neighbours (Perry et al. 2006).

Univariate tests assess whether individuals had fewer or more neighbours than would be expected by chance (based on simulations of the null model). Observed values that fell above the confidence envelope indicate clustering of trees and observed values that fall below the envelope indicate fewer trees than expected at the corresponding distance. This function was used to assess clustering of all trees within sites, clustering of all dead trees and clustering of dead *B. menziesii* and *B. attenuata* trees within sites.

The aggregation analysis assesses the general spatial structure of trees. To assess whether mortality events were associated differentially with different parts of this structure (i.e., more mortality in denser patches, which strongly implies competition-induced mortality; Hurst et al. 2012), we tested for spatial association between dead and living trees. To test for this association we conducted bivariate cross PCF tests (Stoyan and Stoyan 1994), denoted $g_{12}(r)$, with a random labelling null model, keeping the initial distribution of all trees constant. Qualitative marks of ‘living,’ ‘dead’ and ‘living *Banksia*’ or ‘dead *Banksia*’ were employed and confidence envelopes developed from 999 simulations of the null model. This test was used to determine if all dead trees were spatially attracted to living trees and whether dead *B. menziesii* and *B. attenuata* trees (pooled) were spatially attracted to living *B. attenuata* and *B. menziesii* trees within each site.

The Diggle Cressie Loosemore and Ford (dclf) test (Diggle 1986; Cressie 1991; Loosemore and Ford 2006; Baddeley et al. 2014) was used to test for the goodness of fit of each observed statistic within each test. The dclf statistic was used with 999 Monte Carlo simulations of the model run at an alpha level of 0.05. The software, R version 3.0.3 (R Development Core Team 2014; www.r-project.org) was used to carry out all statistical analysis. The R package ‘spatstat’ (Baddeley and Turner 2005) was used to conduct all spatial statistical analysis.

Results

Spatial variability of soil moisture

Depth to groundwater differed significantly between High and Low sites. This was confirmed through ERT which found the watertable was greater than 40 m from the surface at the High site and between 9 m and 20 m BGS at the Low site (the site has a shallow slope) (Fig. 3). The imaged watertable, as evident from the strong linear feature

of contrasting low resistivity was consistent with depths estimated from bore data (Fig. 3b; Department of Water 2014). Depth to the watertable in the High site was expected to be approximately 55 m and the resistivity survey confirmed unsaturated conditions occurred throughout this depth (Fig. 3a; Department of Water 2014).

Variability in resistivity in the unsaturated zone was also evident in both sites (Fig. 3). The greater resistivity throughout the unsaturated zone at the High site in comparison to the majority of the unsaturated zone at the Low site suggests lower soil moisture at the High site (Fig. 3). Soil sampling to 3 m depth at both sites showed no significant differences in particle size distributions, clay contents and water retention between sites, indicating that differences in ERT profiles likely do reflect soil moisture patterns (Adekoya 2014). The Low site also displayed high variability in resistivity near the surface and shows significant drying between the surface and a depth of 5 m below the surface (Fig. 3b). A wet surface region was present extending 35 m from the lower slope end of the Low site ERT transect (Fig. 3b).

There did appear to be differences in subsurface lithology between sites. A high resistivity feature rising from approximately 30 m BGS to 15 m BGS between 50 and 130 m along the High site transect could possibly indicate the presence of a subsurface feature such as limestone (Fig. 3a). In addition, low resistivity features at 5 and 15 m BGS located between 24–100 m and 160–200 m along the transect reoccurred in data collected in 2015 suggesting potentially finer textured materials and/or zones of salt accumulation rather than higher water contents (Fig. 3a).

Considering the changes in subsurface resistivity between the end of the winter of 2013 and the end of the 2014/2015 summer (Fig. 4) it is apparent there were significant changes in subsurface soil moisture. At both sites the time-lapse ERT shows the unsaturated zone dried in the top 5 m of the soil profile at both sites (Fig. 4). At the High site soil moisture in the remainder of the subsurface scarcely changed (Fig. 4a). At the Low site however, locations which show decreases in resistivity deeper in the profile are consistent with a region at or just above the 2013 watertable elevation (Fig. 4b), which suggests the possibility of slightly higher groundwater levels at the later time.

Stand characteristics

In the High and Low sites 328 and 470 individual trees were mapped respectively including seven tree species:

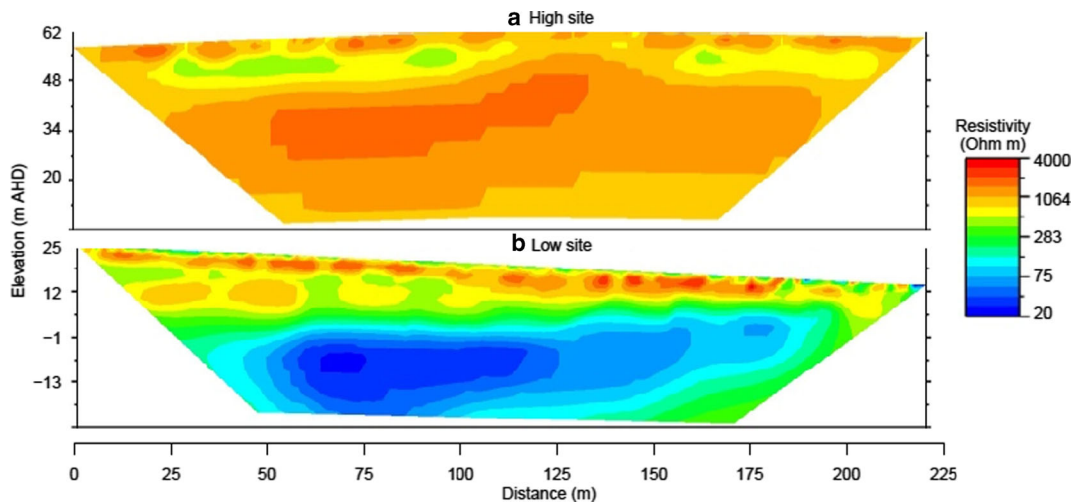


Fig. 3 Spatial variability of subsurface electrical resistivity in the High (a) and Low (b) sites in the Kings Park bushland conducted on 28th August (High site) and 11th September (Low site) 2013. Regions of high resistivity indicate low water content, high

porosity, low clay content and regions of low resistivity indicate the presence of a watertable. Elevation indicates height above sea level (m). Diagram interpretation reliability declines significantly at transect ends and with depth

B. menziesii, *B. attenuata*, *E. marginata*, *C. calophylla*, *Hakea prostrata* R. Br, *E. gomphocephala* and *A. fraseriana*. With the exception of *E. gomphocephala* and *H. prostrata*, which were only observed in the High site, all tree species were present in both sites. The density of trees of all species in the Low site (870 trees/ha) was approximately twice that of the High site (516 trees/ha; Table 2). The average nearest neighbour distance was correspondingly greater in the High site (2.1 m) compared to the Low site (1.5 m; Table 2). *Allocasuarina fraseriana*

trees dominated both sites making up 40–54 % of all trees (based on individual tree numbers) (Table 2). *Banksia menziesii* contributed 11–14 % of all trees and *B. attenuata* contributed 15–32 % of all trees present in sites (Table 2).

Mortality across sites and years and interspecific differences

A significantly higher proportion of mortality was observed in *B. menziesii* trees in the High site compared

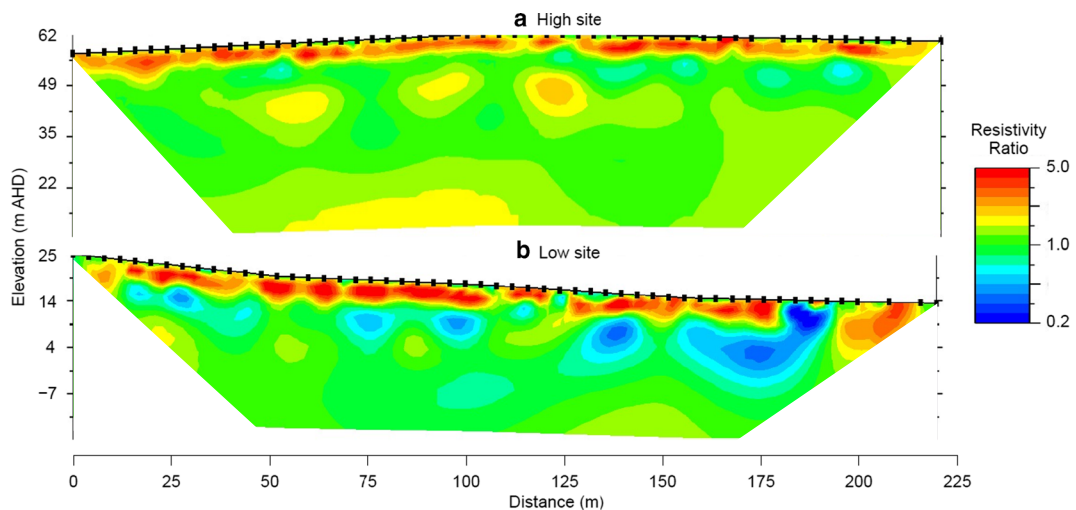


Fig. 4 Relative changes in subsurface electrical resistivity in the High (a) and Low (b) sites between August/September 2013 and March 2015. Units are the ratio of resistivities. High resistivity

ratio values indicate regions where resistivity increased between 2013 and 2015, low ratio values indicate regions which decreased and ratio values around 1.0 indicate little change in resistivity

Table 2 Stand characteristics for low elevation and high elevation sites in the Kings Park bushland: total number of trees and percentages (of total tree number) for each species, number of species, nearest neighbour distance (nnd) between all trees within sites (m), tree density, percentage of dead trees (on the basis of previous year's live stock), percentage mortality between consecutive years, total basal area (m²/ha) and frequencies (F) of summed diameter (incorporating multiple stems if present) at breast height (dbh) for trees in large and small size classes (cut-off = 7 cm) for living and dead trees (at time of survey)

Site	All tree species		<i>B. menziesii</i>		<i>B. attenuata</i>		<i>A. fraseriana</i>		<i>E. marginata</i>		<i>C. calophylla</i>		Other species	
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low
N individuals (n %)	328	470	42 (14)	52 (11)	44 (15)	144 (32)	187 (54)	214 (40)	42 (13)	41 (9)	3 (1)	52 (10)	13 (4)	–
N species	7	5	66	96	69	766	294	396	66	76	5	96	20	–
Mean nnd (m)	2.08	1.54	67	29	30	19	18	15	7	5	33	4	62	–
Density (individuals/ha)	516	870	0	3	0	1*	1	1	0	0	0	0	0	–
% dead trees (all years)	1**	1**	7*	7	6	6	8	2	0	0	0	0	38	–
% mortality 2013	7	3	58*	13**	11**	8**	3**	4**	3**	0	33	0	39	–
% mortality 2012	12**	5**	14**	10	16	6	7	9*	5	5	0	4	0	0
% trees died prior to 2011	9	8	45.44	40.81	37.32	98.97	467.75	374.78	73.37	107.28	1.19	114.56	17.58	–
Basal area (m ² /ha)	642.66	736.40	0.13	0.34	0.30	0.62	0.06	0.13	0.05	0.16	0.00	0.15	0.00	–
F dbh small living trees	0.10	0.30	0.87	0.66	0.70	0.38	0.96	0.87	0.95	0.84	0.00	0.85	0.00	–
F dbh large living trees	0.90	0.70	0.04	0.47	0.08	0.41	0.00	0.06	0.00	0.00	0.00	0.00	0.00	–
F dbh small dead trees	0.03	0.26	0.96	0.53	0.92	0.59	1.00	0.94	1.00	1.00	0.00	1.00	0.00	–
F dbh large dead trees	0.97	0.74	0.04	0.04	0.08	0.41	0.00	0.06	0.00	0.00	0.00	0.00	0.00	–

Significance levels: 0.001 *** 0.01 ** indicate significant differences between proportions of dead trees between years of death within all tree species or individual species within site

with *B. attenuata* ($P < 0.05$) while there were no differences in proportions between the two species in the Low site ($P > 0.05$). The highest mortality was interpreted as occurring in 2011 for the majority of tree species, including *B. menziesii* and *B. attenuata* trees in both sites (excluding trees that died prior to 2011) (Table 2). Tree mortality of all species differed significantly between the High (26 %) and Low sites (17 %; $P < 0.01$) with all years of death pooled. Mortality of *B. menziesii* in the High site (67 %) was more than double that of the Low site (29 %; $P < 0.001$). There was no significant difference in mortality between sites for *B. attenuata* trees (High site 30 %, Low site 19 %; $P > 0.05$). Within species, mortality did not differ between sites for either *A. fraseriana* or *E. marginata* trees ($P > 0.05$). Other species were too infrequent to test.

In the sloping Low site, the position of dead *Banksia* trees along the transect and the approximate depth to the watertable at their location was strongly, positively correlated ($r = 0.946$) with a greater proportion of dead *Banksia* trees present in regions further upslope where the trees are less likely to be accessing the watertable. Despite this, there were no dead *Banksia* trees present within the upper 30 m of the transect where the depth to the watertable was greatest.

Size-dependent mortality

Large living *Banksia* trees had a significantly greater canopy extent (mean = 8.8 m²) than small *Banksia* trees (mean = 2.7 m²; $P < 0.001$). Across both sites, mortality of large *Banksia* trees was more than three times higher than small *Banksia* trees ($P < 0.001$). Mortality of large *Banksia* trees was higher than small *Banksia* trees in the High site ($P < 0.001$), however in the Low site there was no significant difference in mortality between size classes ($P > 0.05$).

Spatial patterns of tree mortality

All trees (living and dead) were spatially aggregated at distances of up to 8 and 10 m in the High and Low sites, respectively ($P = 0.002$ High site, $P = 0.001$ Low site; Fig. 5a–b). Aggregation of dead trees of all species occurred at both sites at similar or shorter distances (<8 m High site, $P = 0.017$, <4 m Low site, $P = 0.004$; Fig. 5c–d). Dead *Banksia* trees were not aggregated at short distances in the High site ($P = 0.021$; Fig. 5g) while in the Low site, there was evidence of some clustering of

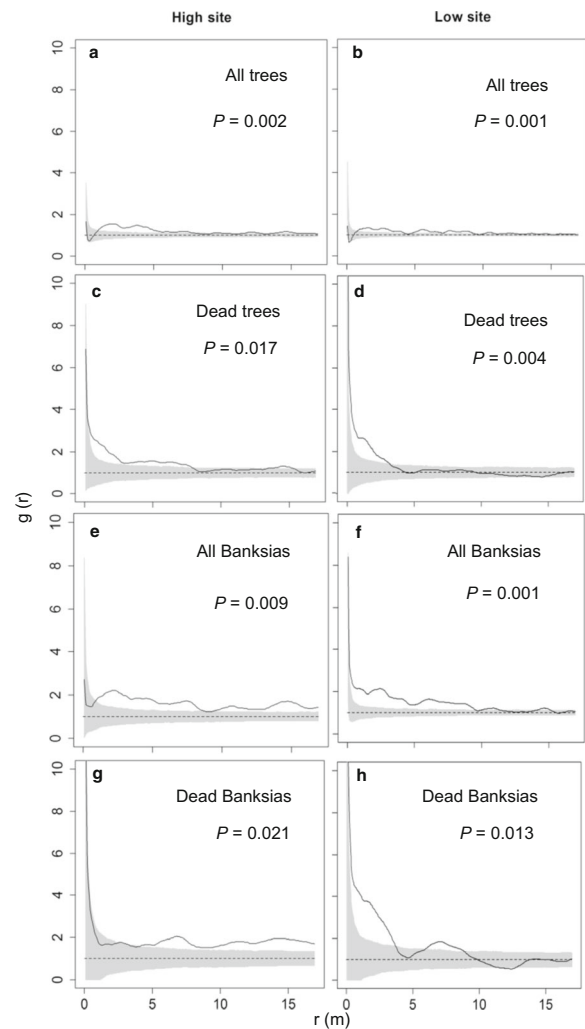


Fig. 5 Univariate pair correlation functions, $g(r)$ as a function of radial distance r (m), for spatial patterns of living trees of all species in the High (a) and Low (b) sites, dead trees of all species in the High (c) and Low (d) sites, all *Banksia* trees (pooled) in the High (e) and Low (f) sites and dead *Banksia* trees (pooled) in the High (g) and Low (h) sites in the Kings Park bushland. The observed pattern is indicated by the solid line at increasing distances (r (m)). Confidence envelopes are indicated in grey with observed values that lie above the confidence envelope indicating spatial clustering at the corresponding distance. The dotted line at $g(r) = 1$ is the theoretical value of (random) Poisson distributed points. Dclf P values indicate the significance of the deviation between the observed point pattern values and the modelled point process

dead *Banksia* trees at short distances (<4 m) as well as spatial structure at greater distances (clustering at 7–8 m; $P = 0.013$; Fig. 5h).

Evidence for spatial structure in mortality beyond that of the initial pattern of trees was not revealed by cross PCF analysis. This analysis found no attraction

between dead and living trees with all species pooled at any distance (Fig. 6a and b). The distribution of dead and living trees in relation to each other was approximately random in both sites (Fig. 6a and b). Significant, spatially-structured attraction between dead and living *Banksia* trees was also not observed in either the High or Low site (Fig. 6c and d).

Discussion

Temporal patterns of tree mortality

Our study found that the magnitude of tree mortality was not consistent each year during the study period, with mortality being greatest for most species in 2011. In the Perth region, the calendar year of 2010 was the driest since records began over a century ago, and it included three heat waves

(Fig. 1; Bureau of Meteorology 2014). The year of 2010 was cooler in comparison with the years 2011–2014 and therefore the low rainfall during 2010 is more likely the driver of decline than high temperatures (Fig. 1). There has been no evidence to suggest that factors other than low rainfall would have resulted in the large scale tree mortality observed in this bushland. Some foliar insect damage was observed on *Banksia* trees at the time mapping was carried out, which may be a secondary factor leading to decreased tree vigour, however is unlikely the primary cause of death (Bigler et al. 2006). We believe that this record drought in 2010 coupled with the record hot year of 2011 (Fig. 1) was the ultimate cause of high tree mortality observed in 2011. Another study conducted on the same region documented sudden, widespread canopy dieback in *Eucalyptus* species following the same drought in 2010/2011 (Brouwers et al. 2013).

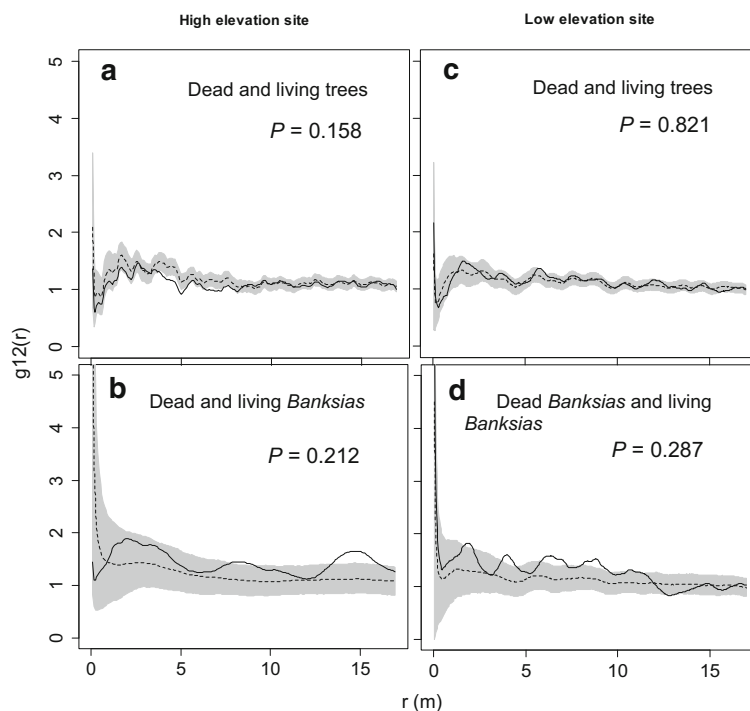


Fig. 6 Bivariate cross pair correlation, $g_{12}(r)$, as a function of radial distance r (m), for spatial association between dead and living trees of all species in the High (a) and Low (b) site and living and dead *B. attenuata* and *B. menziesii* trees (pooled) in the High (c) and Low (d) site in the Kings Park bushland. Observed values (solid line) indicate variation in the proportion of dead trees found within increasing distance of live trees. Grey confidence envelopes were derived from simulations of the null model. The null model employed random assignment of ‘dead’ and ‘living’

labels (in the observed proportions) among the observed pattern of all trees. Observed values that fall above the confidence envelope indicate spatial attraction between dead and living trees of all species or dead and living *Banksia* trees and observed values that fall below the confidence envelope indicate spatial repulsion at the corresponding distance. Dclif P values indicate whether there is a significant deviation between the observed point pattern values and the point process model

General models of tree physiological response to heat and drought suggest that either hydraulic failure or carbon starvation lead to tree death (McDowell et al. 2008). Given that *Banksia* trees continue to open their stomatas during periods of water deficit (Veneklaas and Poot 2003), the proximate cause of tree mortality is more likely to be hydraulic failure rather than carbon starvation.

Stand patterns of tree mortality

Consistent with our second hypothesis, and the distance to the watertable, mortality of all tree species was greater in the High site than in the Low site. However, this result varied between species. *Banksia menziesii* mortality was twice as high in the High site (67 %) compared with the Low site (29 %). While in *B. attenuata*, there was no significant difference in mortality between sites, despite one and a half times more mortality in the High site (19 % Low site, 30 % High site). Unexpectedly, in the High site there was a greater proportion of mortality in *B. menziesii* trees compared to *B. attenuata* trees ($P < 0.05$). In the Low site there was no difference in proportions between these species ($P > 0.05$).

Patterns of subsurface soil water, revealed by ERT reflects tree mortality patterns between sites. ERT results confirmed that the High site was remote from the watertable and found that the watertable at the Low site (9–20 m BGS) was potentially within access of roots of the more down-slope positioned *Banksia* trees (Farrington et al. 1989; Zencich et al. 2002). ERT results indicate that trees at the High site are unlikely to be accessing the watertable which is approximately 55 m BGS, and they therefore must rely exclusively on vadose zone water. Time-lapse ERT results showed similar depths of drying, to 5 m BGS, between a winter and a summer period at both sites suggesting this is a dominant region of competition for water. At the High site the remainder of the unsaturated zone remained unchanged in resistivity and the higher resistivity there as compared with the Low site suggests the potential for greater water stress. Trees in the down-slope region of the Low site have a greater potential to access the watertable and may be more likely to maintain physiological functioning through drought periods. Vadose-dependent *Banksia* trees positioned further upslope in the Low site with a depth to the watertable > 9 m may not have access to sufficient soil water during drought periods to survive and this is supported by the greater number of dead

Banksia trees present upslope. It is likely that tree available soil water decreases as depth to the watertable increases along the transect.

Despite similarities in rooting structures, water relations and resistance to xylem cavitation, differences in mortality were observed between *B. menziesii* and *B. attenuata* in the less drought-buffered High site. The lower proportion of mortality in *B. attenuata* in this site suggests that it is more drought tolerant than *B. menziesii*. In the Low site, trees may have access to more water than those in the High site and therefore this interspecific difference in drought tolerance is not observed.

Previous studies in a similar system found physiological differences in trees at different landscape positions. Canham et al. (2009) showed that *B. attenuata* and *B. menziesii* trees growing on a dune crest (> 30 m from watertable) had a greater resistance to xylem cavitation compared to those growing lower in the landscape (< 8 m from watertable). Despite this potential for physiological adjustment we observed differences in mortality between sites that suggest that site differences in water availability are significant enough that more trees at the High site are pushed beyond those physiological adjustment limits in extreme drought years. In the Low site, this physiological adjustment in response to water availability would be more gradual along the transect as depth to the watertable increases.

Size-dependent mortality

Supporting our third hypothesis, mortality was observed to be size-dependent in one site, the High site. Mortality was more than three times higher in large than small *Banksia* trees in this site. This may be due to a greater average canopy size of large *Banksia* trees in the High site compared to those in the Low site ($P < 0.05$) and therefore trees in the High site require absolutely more water to maintain functioning. Larger trees have been found to have a greater water use per unit time compared with smaller trees (Meinzer 2003) and during periods of drought this may result in greater vulnerability of larger trees to xylem cavitation. Driven by their larger canopy leaf area, larger trees have greater evapotranspirative demands, and large *Banksia* trees (defined by stem diameter) do indeed have greater canopy areas than small *Banksias* (mean canopy extent 8.8 versus 2.7 m²). During the most extreme dry summers, large trees in the High site may not have the capacity to access sufficient water to

survive while smaller *Banksias* may have an expansive rooting structure enabling access to sufficient water.

Previous studies (Mueller et al. 2005; van Nieuwstadt and Sheil 2005; Nepstad et al. 2007) have found greater mortality in larger trees than in smaller trees following drought events in semiarid and tropical ecosystems. Mortality in *Banksia* trees of different size classes has not been previously reported. In this study we do not incorporate seedlings, which are often considered to be the most vulnerable life stage of trees to disturbance. Tap root growth rates of *B. menziesii* and *B. attenuata* trees are rapid during early stages with seedling tap roots found to penetrate to depths of 1.5 m (Rokich et al. 2001) therefore rooting depths may not differ considerably between trees that are a century old and those that are several decades old. The small size class in this study is made up of trees approximately 4–10 years of age likely with expansive rooting systems exploring a large volume of soil (estimated from a small sample of bushland planted trees of known age). Trees of different sizes in the Low site may be able to access the watertable and this may explain why there was no size-dependent mortality observed in this site. Greater size-dependent mortality observed in the High site while not observed in the Low site may support this concept in that large trees require more water to maintain physiological functioning and are more susceptible to catastrophic xylem cavitation.

Spatial patterns of mortality

Contrary to our fourth hypothesis, evidence of competition-induced mortality contributing to the death of *Banksia* trees was not found in either the High or Low sites from bivariate spatial analyses. All trees were aggregated at short distances in both the High and Low sites and some aggregation of dead trees was observed, however this does not suggest that competition is a driving factor of mortality, but likely reflects the spatial structure of populations. Mortality from hydraulic failure in this system appears to be a rapid occurrence with trees showing no visible signs of stress prior to death. The process of competition for water is likely an occurrence over a longer period and therefore death of *Banksia* trees in this system is likely to be more an individual scale phenomenon.

Interpretations of processes from snapshots of spatial pattern are often not straightforward (Perry et al. 2008). The spatial aggregation of stems observed within sites results from processes which we cannot definitively

identify, but likely includes localised dispersal potentially interacting with heterogeneity in resources such as soil moisture and water availability. The fact that the sites differ in stem density in a way that reflects their hydrological differences does imply a long-term role of water availability in structuring the system. Nonetheless, the random labelling test employed here for pattern in mortality of *Banksia* trees takes into account the initial structure and therefore is more powerful than most other spatial tests as an indicator of competition driven mortality. It found no evidence that trees growing nearer to other trees had higher mortality than trees growing further away from neighbours. Intriguingly, ERT results in the Low site did reveal patchy spatial distribution of surface soil water that might indicate competition amongst trees for unsaturated zone water due to the high density of trees compared to the High site. ERT measurements also confirmed seasonal patterns in water change and site differences that informed the spatial density and mortality data.

While this lack of a spatial signature for competition is analytically powerful, our other results do point to varying resource (water) availability as a driver of mortality and system change. These include, the presence of spatial structure at the tree (aggregation within plots) and landscape (density variation within landscape position) scales, between-site differences in mortality, and between-site, size-dependent mortality observed in the less drought-buffered High site. The solution to this apparent contradiction may lie in a combination of factors. Firstly, competition amongst *Banksia* trees may occur but be spatially diffuse as their shallow rooting systems can extend laterally as far as 10 m (Lamont and Bergl 1991), such that individual trees may overlap foraging zones with many more trees than simply their near neighbours. Secondly, the coarse soil texture and associated rapid decrease in water potentials with declining soil moisture, may minimise spatial consequences of local water use under extreme drought conditions. Thirdly, patchy spatial distributions of surface soil water, revealed by ERT results may lead to greater vulnerability of trees located in drier patches to water deficits compared to those in wetter patches.

Variability in rooting structures may result in the High and Low sites in response to water availability. *Banksia* trees in the High site in which the watertable is not accessible may invest more in dynamic surface roots in order to take up water following rain events. The distribution of water here is likely to be patchy due to uptake by

individuals and clusters of trees. In contrast, *Banksia* trees positioned closer to the watertable may be advantaged from producing deep penetrating roots which can access the watertable where accessible and capillary fringe.

Species-specific susceptibility to drought events, as documented here, may result in structural shifts to vegetation composition over time. These vegetation shifts may lead to a change from one or several dominant species to a new species that is better adapted to survive periods of water deficit (e.g., Mueller et al. 2005; Sommer and Froend 2014). In the Kings Park bushland *A. fraseriana* is increasing in abundance (Beard 1967; Crosti et al. 2007). This species made up 54 % of all trees present in the High site and the relatively low mortality observed in this study (18 %) suggests that it may have a greater tolerance to drought in comparison with *Banksia* trees (*B. menziesii* 67 % mortality, *B. attenuata* 30 %). In a previous study conducted by Crosti et al. (2007) in the Kings Park bushland, a doubling of *A. fraseriana* density was observed from 1939 to 1999. Dominance of *A. fraseriana* trees in the bushland may result with continued shifts in these species abundances (Crosti et al. 2007). Elsewhere, widespread species-specific mortality has been observed in southwestern US following a drought event during 2002–2003 resulting in widespread mortality in the more drought sensitive dominant tree species, *Pinus edulis*, while the drought tolerant co-occurring species, *Juniperus monosperma* largely persisted (Breshears et al. 2005, 2009).

In conclusion, widespread tree mortality of the dominant *B. attenuata* and *B. menziesii* trees observed in the Kings Park bushland is likely related to catastrophic hydraulic failure resulting from extreme drought events, perhaps including diffuse competition leading to depleted vadose water rather than localised (nearest-neighbour) below-ground competition amongst trees for water. Trees growing at landscape positions further from watertables are more vulnerable to drought periods, particularly large trees which require greater water contents to maintain functioning. Mortality of vadose-dependent trees may occur during drought periods if vadose water available to trees is depleted and not replenished in time by autumn and winter rainfall (Zencich et al. 2002). Geophysical methods can be applied to aid in characterising the subsurface environment of trees and to relate to surface patterns of mortality. Widespread tree mortality may be most abundant during extreme hot, dry years and therefore may not occur annually. With predictions of further rises in mean

and maximum temperatures, even further rainfall declines and increased frequencies of heat waves in southwestern Australia and other Mediterranean ecosystems (IPCC 2013), drought related tree mortality will likely increase in the future resulting in further losses of trees and shifts in vegetation structures in these ecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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