



Season of fire influences seed dispersal by wind in a serotinous obligate seeding tree

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Abstract In temperate ecosystems, fire management involving prescribed burning and wildfire suppression often causes a shift in fire season from hot and dry summer conditions to cooler, moister conditions in spring or autumn. The effects of this change on seed dispersal by wind after fire are unknown. However, calmer wind conditions and increased standing vegetation after fires in cooler seasons may reduce seed dispersal following fire. We studied seed dispersal in different seasons for a serotinous obligate-seeder, *Callitris verrucosa*, growing in a semi-arid environment in South Australia. We measured primary (wind-borne) and secondary (on-ground) seed dispersal during spring, summer and autumn, using empirical

observations and modelling based on detailed measurement of wind characteristics. At comparable horizontal wind speeds, primary dispersal was greater in summer compared to spring and autumn. Secondary dispersal was similarly short in all three seasons when vegetation cover was high, but when cover was low, seeds travelled much further in summer than in the other two seasons. A shift in the seasonal timing of seed release can decrease dispersal distances of serotinous obligate seeders, which is likely to reduce gene flow and the ability to colonise new sites. This can lead to changes in population and community structures which may further affect fire patterns. These findings could be applicable to other serotinous obligate seeding plant species found in other families such as Proteaceae, Myrtaceae, Pinaceae and Cupressaceae.

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Introduction

Understanding how anthropogenic changes to fire regimes affect species' persistence is central to maintaining biodiversity in fire-prone ecosystems (Johnson and Miyanishi 1995; Keith et al. 2002; Allen 2008; Bennett et al. 2010; Penman et al. 2011). Some effects of changed fire regimes on plants, such as recovery from disturbance and seedling establishment, are relatively well understood (Knox and Clarke 2006; Sheuyange et al. 2005; Bradstock et al. 1996; Howe 1994). In contrast, understanding the impacts of changed fire regimes on dispersal of plant propagules remains poor yet the influence that changes in fire regimes have on the dispersal of propagules may be strong (Banks et al. 2013).

One component of how humans influence fire regimes is through modification of ignition patterns (Bradstock 2010; Bowman et al. 2009, 2012; Pyne 2010). In temperate ecosystems around the world, most wildfires occur during the drier and hotter summer months. These fires achieve high temperatures and often burn large areas (Pausas 2004; Pausas et al. 2009; Meyn et al. 2007; Keeley and Zedler 2009). However, most managed burning is carried out during cooler and wetter times of the year when fires are easier to control (Slijepcevic et al. 2007; Van Wilgen et al. 2010). As a result, these fires generally burn with lower intensity (Gill et al. 2001; Van Wilgen et al. 2010).

Some impacts of changes in fire season on plants have been previously studied, most notably: The temperatures generated by fire that are required to stimulate the release of seeds from their woody fruits (Lamont et al. 1993; Nathan et al. 1999; Knox and Clarke 2006), the success of seedling recruitment linked to the weather conditions in the post-fire environment (Enright and Lamont 1989; Hodgkinson 1991; Bond and van Wilgen 1996; Thomas et al. 2010), and more recently through seasonal effects on seed dormancy (Mackenzie et al. 2016). In contrast, the effect of changed fire season on seed dispersal has not been explored. Seed dispersal contributes to gene flow between existing populations and to demographic

rescue and recolonisation, and consequently influences the persistence of plant populations over time (Nathan and Muller-Landau 2000; Keith 2012).

For serotinous plant species (species that release seeds in response to an environmental trigger such as fire) with wind-dispersed seeds, post-fire seed dispersal depends on the prevailing wind conditions after a fire, which could vary among seasons for two reasons. First, local turbulences can be caused by solar heating of the ground surface; hence, it is likely that the wind after fire will be less turbulent on cooler days in spring and autumn than during hotter days in summer (Sullivan et al. 2012; Kuparinen et al. 2009). Updrafts associated with turbulence may be more important for causing long-distance seed dispersal than horizontal wind speed (Tackenberg et al. 2003a, b; Tackenberg 2003). A study in boreal forests showed that there was a positive correlation between air temperature and wind-driven dispersal distances (Kuparinen et al. 2009). Thus, for serotinous species with wind-driven dispersal, cooler season burns may cause seeds to travel shorter distances. Second, less-intense fires usually leave more intact and taller vegetation that will act as a wind break, reducing wind speed, and obstructing seed movement (Schurr et al. 2005; Soons et al. 2004). Together these factors might reduce dispersal of seeds that are released by cool season management fires, relative to those released by natural summer wild-fires.

In this study, we asked whether the season of seed-releasing fires could affect seed-dispersal distances in *Callitris verrucosa*, a serotinous gymnosperm. In this species, adult plants are killed by high intensity fires, and population persistence relies on dispersal of seeds released from their serotinous fruits into the post-fire environment (Bradstock et al. 2006). To determine whether seed dispersal of *C. verrucosa* is affected by fire season, we measured primary seed dispersal in the wind conditions experienced during spring, summer and autumn, using both empirical observations and modelling. In addition, we assessed the effect of vegetation cover on the secondary dispersal of seeds along the ground.

The findings of this study help to provide guidance on appropriate seasonal timing for burning practices to sustain gene flow amongst populations and colonisation potential of wind-dispersed serotinous obligate seeding plant species.

Material and methods

Study region

The study was conducted in Hincks Wilderness Protection Area (33°45'S, 136°03'E) a 67,000 ha reserve on the Eyre Peninsula, South Australia. The region is semi-arid, with an average annual rainfall of 340 mm. The main topographic features are white sand dunes interspersed by hard, reddish-brown swales. The dominant vegetation type in the reserve is mallee with hummock grass and mallee heath and shrublands ("NatureMaps" 2017), characterised by multi-stemmed eucalypts. Common trees are *Eucalyptus costata*, *E. socialis* and *Callitris verrucosa*. Common understory species include the shrub *Melaleuca uncinata* (Smith 2012), and the hummock grass *Triodia irritans* (Driscoll and Henderson 2008).

Study of species, *Callitris verrucosa*

Callitris verrucosa (A.Cunn. Ex Endl.) F.Muell., the native mallee-pine, from the family Cupressaceae, is a canopy dominant of mallee vegetation and a serotinous obligate seeder (Bond and van Wilgen 1996; Bradstock and Cohn 2002). It grows as a small stunted tree often with several trunks, usually up to 3 m, and rarely up to 6 m high. Cones occur solitarily or clustered on short lateral branches and increase in number with tree age (Bradstock and Cohn 2002).

An individual cone can contain up to 30 seeds (Bonney and Miles 1994; pers. obs.). Each seed has two wings which generally make up more than 70% of the total width with the actual seed located in the middle (Bradstock and Cohn 2002). Diaspore width which includes seed and wings, ranges from 2 to 6 mm, and weigh between 2 and 30 mg. (Bradstock and Cohn 2002; pers. obs.). Trees produce their first fruits at an age of 10–15 years and can live for 250 years (Bradstock and Cohn 2002; Zimmer et al. 2011).

Canopy seed banks of *C. verrucosa* are usually exhausted following a crown fire (Pausas et al. 2004; Lamont et al. 1991). We have also observed spontaneous release of seed without fire, both when branches bearing cones have died and also when they remain alive. Other studies also assume that a small number of seeds can be released independently of fire events (Bradstock et al. 2006; Bonney and Miles 1994).

Fire usually initiates the release of seeds, as cones open after exposure to high temperatures. Seed release and dispersal are promoted when there are strong turbulent winds and little or no rain (pers. obs.).

Callitris verrucosa relies on dispersal of seeds from its canopy seed banks as this species does not develop appreciable soil seed banks due to lack of seed dormancy. The germination of seeds on the soil surface can increase through the exposure of seeds to variable weather conditions, such as high temperatures and low water potential over an extended period of time (Adams 1999).

In Hincks Wilderness Protection Area, *C. verrucosa* occurs in clusters of various sized individuals as well as scattered and isolated individual trees. In the older burns, *C. verrucosa* was found to be a canopy-dominant species. Within the reserve, *C. verrucosa* only grows in areas with white sandy soils often associated with elevated dune topography (Harden 1990; Zimmer et al. 2011; pers. obs.).

Empirical observations of seed dispersal

In 2011–2012, we measured seed dispersal using daylight visual tracking during three different seasons; spring, summer and autumn. We conducted seed experiments at three sites in each of two burns about 6 km apart that had both recently undergone a planned burn, one in spring 2009 and the other in autumn 2011. Within those two burns, the three release sites were positioned 800 m apart from each other along a transect that was placed parallel to and 100 m from the burn edge within the burn.

Seed release experiments were conducted in October (spring) 2011, January/February (summer) 2012 and April (autumn) 2012. Although the release locations varied in post-fire age from 0.5 to 2.5 years during the experiment, regrowth of vegetation was limited in all sites over the duration of the experiment. We tested the effects of post-fire age by including it as a factor in the analysis.

Seeds were collected from other populations of *C. verrucosa* within the reserve. At each release site and in each season, 20 randomly chosen seeds were released from each of three different heights (1 m, 2 m and 3 m) giving a total of 360 seeds released per season. The seeds were given a dot of fluorescent coloured dye to make relocation easier. We tested one hundred of the seeds with dye (8.3 ± 4.3 mg;

3.0 ± 0.05 m/s) and found no significant difference in the falling time ($t_{198} = 0.943$; $P = 0.346$) compared to 100 seeds without dye (9.8 ± 4.9 mg; 3.1 ± 0.07 m/s). In the field trials, the 20 seeds were released at each height individually during daylight by placing them on a small platform on a mast, and allowing them to be carried away by the wind. The different heights represented the natural height of cones carried by young trees soon after they reach maturity (1 m), the height of cones at the top of the canopy of fully grown mature trees (3 m), and a common height (2 m) at which many cones were found on plants in the reserve (Table 1). The released seeds were followed by eye and the linear distance from the release point to where the seed first landed was measured to the nearest cm. We also measured wind speed (Model Kestrel 3000 Pocket Weather Meter, Nielsen-Kellerman, USA) at the release platform, at the moment of take-off for each seed. Seed release experiments across all sites and burns were conducted over a 10 day period in each season spending approximately 1–2 days per site depending on wind conditions. Seeds were only released within a horizontal wind speed range of 8–25 km/h. At lower wind speeds, seeds would not take-off, and at higher wind speeds, seeds could not be relocated. While this limited our ability to detect long-distance seed dispersal that might be associated with higher wind speeds, we could still address our main question about dispersal differences among seasons. Using a similar range of horizontal wind speeds in each season allowed us to identify any seasonal effect associated with seasonal differences in turbulence.

To understand the effect of standing vegetation on the on-ground seed dispersal, we established groups of 10 seeds on the ground within 10 m of each of the six previous release sites. The ground surface was naturally bare in all sites. If leaf litter was present, it was mostly accumulated around existing plants. The location within sites was randomly chosen. No site

preparations were applied except for marking the starting point with a small flag stuck into the ground. The seeds were treated with fluorescent coloured dye and placed on the bare ground next to the flag. After four days, a UV light was used to search for the seeds at night within a 5 m radius, and to record the distance moved since release. This was repeated at each site in spring, summer, and autumn. To quantify the potential obstruction to movement from standing vegetation, we visually estimated the percentage of vegetation cover up to 1 m height within a 5 m radius around each release point using a tape measure to keep track of distances and height.

Using analysis of variance, we tested the influence of wind speed (m/s), height of seed release (three heights), season (spring, summer, and autumn), and their interactions on the distances that seeds were predicted to travel. We log-transformed distance which gave more even spread of residuals when plotted against fitted values. We also fitted as fixed effects, representing blocking factors: burn (a factor identifying the two burns, 2009 and 2011) and site nested in burn (where site is a factor identifying the six sites). Due to the low number of levels in site and burn, it was inappropriate to fit these as random effects in a generalised linear mixed model (Lin 1997). Since seeds dispersed further with higher wind speed, we adjusted dispersal distances for wind speed at the time of release (distance dispersed/wind speed) and repeated the analysis with the additional difference that wind and all interactions involving wind were omitted.

We also used analysis of variance to examine the relationship between distance seeds moved across the ground with season, vegetation cover and their interaction. Vegetation cover was measured at each site, so we could not also fit site to the models as a fixed effect as we did in the previous analysis. We fitted burn as a fixed effect to account for multiple measures

Table 1 Distribution of seed cones and plant heights of *Callitris verrucosa* observed in the study area ($N = 98$ trees)

Percentile	Lowest cone (m)	Highest cone (m)	Plant height (m)
25th	0.26	0.57	0.50
50th	0.35	0.88	0.87
75th	0.50	1.39	1.33
Max.	1.03	3.40	3.49

within the two burns. Distance was log + 1 transformed, which improved model fit. Analyses were completed in R (R Development Core Team 2011).

Modelling seed dispersal

Seed dispersal of *C. verrucosa* was modelled using the programme PAPPUS (Tackenberg 2003), a trajectory model that simulates seed dispersal by wind. The modelling study complemented our empirical observations independently because PAPPUS uses wind speeds measured over a longer period of time and therefore incorporates more of the variation in wind speeds that can occur within and among seasons. It produces predictions of seed-dispersal distance based on high-precision wind profiles, measured in the field at a frequency of 10 Hz. PAPPUS has performed well in predicting seed dispersal of other species over longer distances (Tackenberg 2003).

Wind measurements were taken on a sand dune crest close to one release site located in the 2011 burn. Measurements continued for two weeks in each season (spring, summer, autumn) including the time during which seed release experiments were conducted. An ultrasonic anemometer (Model WindMaster (Part 1590-PK-020), Gill Instruments Ltd, Lymington, UK) measured horizontal wind speed, horizontal wind direction, and vertical wind speed every 0.1 s, producing a dynamic, three dimensional wind speed vector. The measured values were used later to simulate the course of the wind vector in PAPPUS. The anemometer measured wind at a height of 2 m, and PAPPUS then generated wind profiles for 1 m and 3 m by extrapolation. Generated values for all three heights were used in the model and included in the analysis.

PAPPUS derives predictions for seed-dispersal distances taking into account wind profile, landscape slope (hilly, sloping upwards/downwards, even), surface roughness (influenced by vegetation height and density), and terminal falling velocity of the seeds. We used the pre-set landscape feature “rolling hills” in PAPPUS that we considered was comparable to the sand dunes found in the study area. To determine the terminal falling velocity, we dropped 100 randomly chosen seeds from 10 m height under calm conditions inside a building. Falling duration was timed with an electronic watch [compare Hammill et al. (1998)]. The overall average seed falling rate (3.0 ± 0.6 m/s) was

then used as the falling velocity in PAPPUS (Tackenberg 2003).

PAPPUS simulated 1000 random seed releases and related dispersal distances based on the wind profiles generated over the two weeks anemometer recording period. This was repeated for each season and at each release height (1, 2 and 3 m).

Wind turbulences for each season

To identify the strengths of turbulences during each season, we used the vertical wind speeds measured by the anemometer. To simplify the large amount of data generated by the anemometer, we chose to use a range of vertical wind speeds within 60 s periods. Those periods were evenly distributed over the day using three hourly intervals starting from 0600 to 1800 h. We used the difference between the lowest and the highest values among the 1800 measurements of vertical wind speed from the 5×60 s periods and interpreted higher variability to indicate greater turbulence.

Results

Wind conditions each season

The mean horizontal wind speed at the time when seeds were released (Table 2) increased significantly with height ($p < 0.001$) but there was no significant difference among seasons ($p = 0.808$; Kruskal–Wallis 1-way ANOVA). However, the means of the continuous anemometer readings of the horizontal wind speed at 2 m height over the 2-week period were significantly different among seasons ($p = 0.017$; Kruskal–Wallis 1-way ANOVA) with the highest wind speeds in summer (Table 2). A similar, and marginally significant trend was observed for anemometer readings of mean vertical wind speeds (spring 0.22 m/s \pm 0.01; summer 0.30 m/s \pm 0.03, autumn 0.21 m/s \pm 0.03) ($p = 0.08$; Kruskal–Wallis 1-way ANOVA) (Fig. 1a). Turbulence increased as the day progressed and was consistently as high or higher, at each time of day, in summer than in the other two seasons (Fig. 1b). An overall frequency distribution of vertical wind speeds showed that extreme values were more frequent in summer although the mean values were not significantly different among

Table 2 Mean horizontal wind speed (m/s) (SE) at the moment of each seed release, at each release height and season ($N = 360/\text{season}$); and mean horizontal wind speed (m/s) (SE)

Season	1 m	2 m	2 m PAPPUS	3 m
Spring	1.7 ± 0.76	2.1 ± 0.89	2.1 ± 0.15	2.8 ± 0.94
Summer	2.0 ± 1.03	2.1 ± 1.03	3.0 ± 0.36	3.4 ± 1.37
Autumn	1.9 ± 0.94	2.4 ± 0.95	1.6 ± 0.23	2.9 ± 1.21

measured at 2 m height (2m PAPPUS) with the anemometer over a timeframe of 7 days

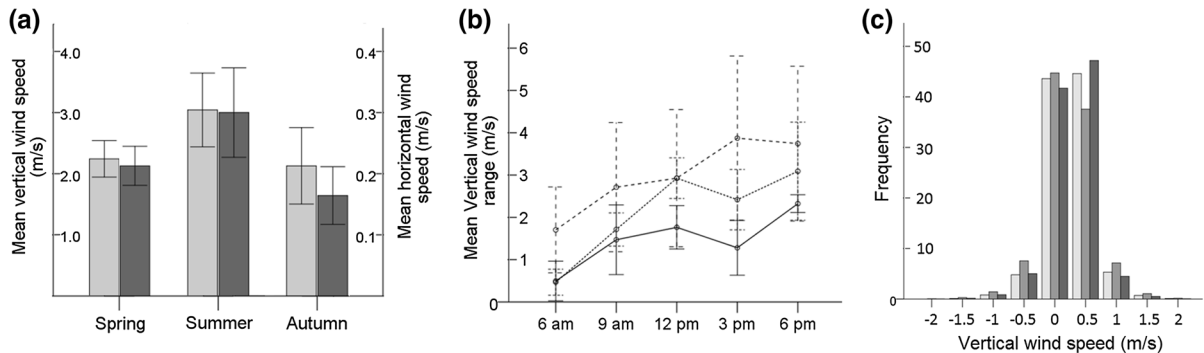


Fig. 1 Wind profiles for the different seasons **a** mean vertical and horizontal wind speeds for spring summer and autumn. The dark grey bars present horizontal wind speed, and light grey bars the vertical wind speed. **b** Range of vertical wind speeds over the period of a day based on wind data measured over three days. Error bars display the standard error. (Spring = dotted line;

Summer = dashed line; Autumn = solid line) **c** Frequencies of vertical wind speeds measured over the period of one week. On the x-axis, the positive values represent upwards movement, and negative values represent downwards movement of vertical winds (Spring = light grey bars; Summer = medium grey bars; Autumn = dark grey bars)

seasons ($p = 0.78$; Kruskal–Wallis 1-way ANOVA) (Fig. 1c).

Empirical observations of seed dispersal

Most released seeds landed close to the release point. In spring and autumn, 90% of the seeds were wind dispersed less than 3 m, and in summer less than 4 m. The maximum observed dispersal distances were from seeds released at 3 m height (7.5 m in spring; 10.6 m in summer; 6.6 m in autumn) (Fig. 2).

The ANOVA showed that dispersal distance was significantly affected by site, season, release height and wind speed, and the two-way interaction of season and height (Table 3). Dispersal distance increased with wind speed at each release height, the increase was consistently greater in summer than in the other two seasons, and the increase with wind speed was lowest in spring for seeds released at 1 m, while it was lowest in autumn for seeds released at 3 m (Fig. 3).

When we adjusted dispersal distances for wind speed at the time of release (distance dispersed/wind speed), there was still a significant interaction effect between season and height on the adjusted dispersal distance (Table 3). Adjusted dispersal distance increased with release height in each season except in summer which had equally long dispersal (and the longest mean values in the data set) at both 2 m and 3 m release heights (Fig. 4).

The PAPPUS model also showed maximum dispersal in summer, but the estimates were always higher than the empirical observations (Table 4).

On-ground dispersal

Out of the 180 seeds released we considered dispersal distances of the 161 (89%) that could be relocated. Most seeds (90%) were found within 0.5 m from their release point, and the furthest dispersal was 1.4 m (Fig. 5a). GLM analyses, identified % vegetation cover as a significant factor (Table 5) with seeds

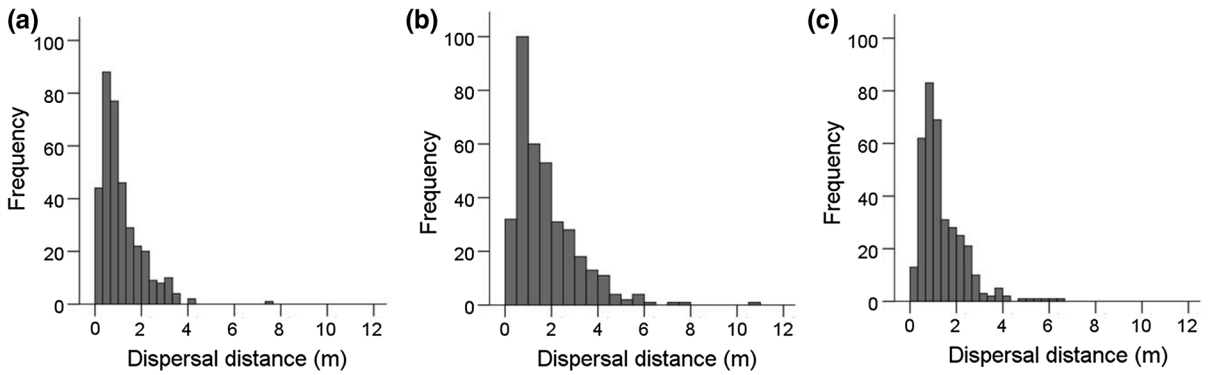


Fig. 2 Distribution of accumulated seed-dispersal distances for seeds released from 1 m, 2 m and 3 m heights (total of 360 seeds) in spring (a), summer (b) and autumn (c)

Table 3 Results of Analysis of variance for influence on (a) absolute seed-dispersal distance of season, release height and wind speed; and (b) seed-dispersal distance relative to wind speed of season, and release height

Factor	a		b	
	<i>F</i> -value	<i>P</i> -value	<i>F</i> -value	<i>P</i> -value
Burn	0.49	0.48	0.60	0.44
Burn/site	6.93	< 0.001	3.97	0.003
Season	73.03	< 0.001	41.04	< 0.001
Height	751.11	< 0.001	180.02	< 0.001
Wind speed	291.33	< 0.001		
Season: height	6.12	< 0.001	3.98	0.019
Height: wind	0.78	1		
Season: wind	2.99	0.05		
Season: height: wind	0.481	0.62		

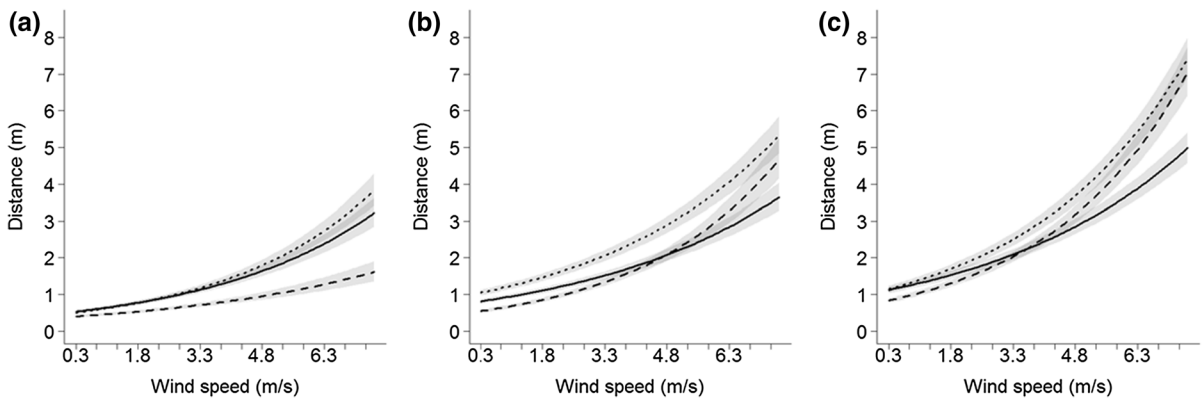


Fig. 3 Dispersal distance of seeds released over a range of wind speeds from heights of a 1 m; b 2 m; and c 3 m. Grey area = 95% confidence limits. (Spring = dashed line; Summer = dotted line; Autumn = solid line)

travelling similar short distances in all three seasons when cover was high. A statistically non-significant trend indicated seeds may travel further in summer

than in the other two seasons when cover was low (Fig. 5b).

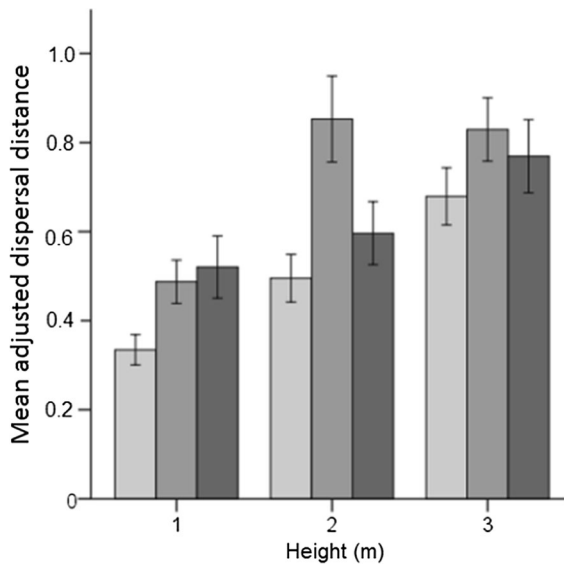


Fig. 4 Mean adjusted dispersal distance for wind speed [distance (m)/ wind speed (m/s)] in each season and at each release height. Error bars display the standard error. (Spring = light grey, Summer = medium grey, Autumn = dark grey)

Discussion

Wind-borne dispersal distance of seeds was mainly influenced by an interaction between season, height and wind speed. Seeds released from greater heights or in stronger winds tended to disperse further in all seasons but there was an additional significant impact of season. The dispersal distances for the same wind speeds and same release heights were higher in summer. Since seed release of *C. verrucosa* primarily occurs after fire, this finding suggests seeds will disperse further after fires in summer than after fires in other seasons.

Longer dispersal in summer is likely to be driven by wind turbulences caused by hot soil surfaces. Earlier

studies that have shown that seeds disperse further during stronger winds included autocorrelated turbulent fluctuations within the vertical wind velocity (Soons et al. 2004; Tackenberg et al. 2003a, b; Bullock and Clarke 2000; Nathan et al. 2001). Even in low wind velocity, seeds dispersed further in turbulent air (Soons et al. 2004; Tackenberg 2003). Tackenberg (2003) reported that for variations in seed-dispersal distance, horizontal wind speeds were less important than thermal updrafts and turbulent air conditions. In summer, solar heating of the ground creates instability in the atmosphere and causes thermal updrafts favouring seed uplift and long-distance dispersal (Sullivan et al. 2012; Kuparinen et al. 2009; Nathan 2005; Wright et al. 2008). In our measured wind profiles, the range of vertical wind speeds over the duration of a day was highest during summer. The heat absorption by the blackened ground surface associated with the post-fire environment exacerbates these effects, increasing the occurrence of “willie-willies” or “dust devils”, local convective circulations, and similar turbulences (Oke et al. 2007). In addition, during dry thunderstorms in summer, gusty and erratic winds potentially enhance seed dispersal (Sullivan et al. 2012; Heidorn 2005). Our data are consistent with these generalisations, even though the time since fire at our experimental sites may have dampened solar heating. Nevertheless, wind dynamics found during summer are more favourable for promoting seed dispersal compared to spring and autumn.

Our study also suggested that the secondary dispersal of seeds on the ground will be reduced after non-summer burns if reduced fire intensities have led to higher densities of vegetation cover. We found that, in each season, seeds deposited in sites with higher vegetation density had lower secondary dispersal, probably because the vegetation acted as a wind break

Table 4 Proportion of seeds in the dispersal distance spectra for daylight visual tracking and for the trajectory Model PAPPUS accumulated from all distributions for 1 m, 2 m and 3 m heights

Method	Season	0–5 m	> 5–10 m	> 10–15 m	> 15–20 m	> 20–25 m
Daylight visual tracking						
	Spring	99.7	0.3	0	0	0
	Summer	97.2	2.5	0.3	0	0
	Autumn	98.6	1.4	0	0	0
Trajectory model PAPPUS						
	Spring	79.1	20.3	0.6	0	0
	Summer	58.7	29.9	11.4	0.8	8.57E-03
	Autumn	87.2	10.8	1.9	0.1	0

Fig. 5 **a** Distribution of on-ground seed-dispersal distances for *Callitris verrucosa* combining data from all three seasons ($n = 161$). **b** Relationship between on-ground dispersal distance and percent vegetation cover up to 1 m height for each season. Grey area = 95% confidence limits. (Spring = dashed line; Summer = dotted line; Autumn = solid line)

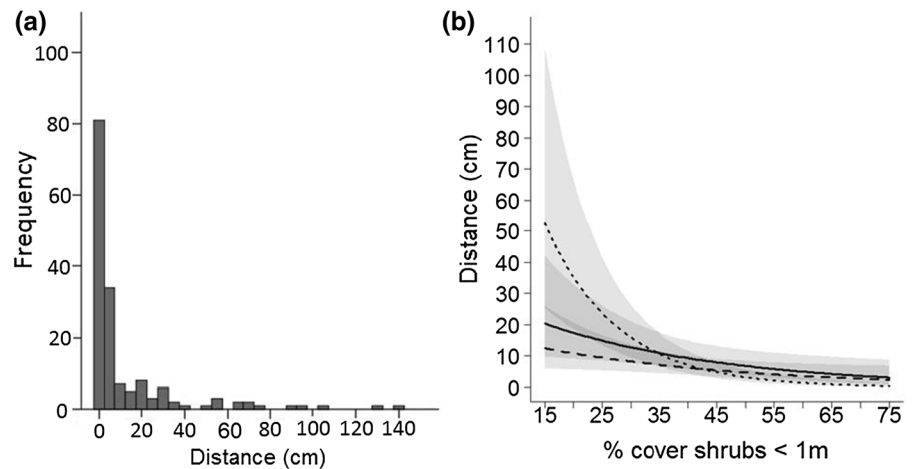


Table 5 Results of Analysis of variance for influence on seed-dispersal distances on the ground of percent vegetation cover at < 1 m height and season

Factor	<i>F</i> value	<i>P</i> -value
Burn	3.719	0.1
Season	0.431	1
Vegetation cover (%)	8.839	0.01
Season: vegetation cover (%)	1.725	1

or as an obstruction to seed movement. Height and density of the surrounding vegetation greatly influences wind velocity on the ground and hence seed-dispersal potential and distances (Schurr et al. 2005; Soons et al. 2004). Prescribed burns in autumn or spring are characteristically low severity fires (Bradstock and Auld 1995) and are likely to leave more vegetation and more obstructions to seed movement than summer wildfires (Gavazzi and McNulty 2014; Prosser and Williams 1998). Secondary wind dispersal can markedly alter the seed-dispersal shadow, and may have an important influence on the long-distance movement of seeds and spatial patterning of plant populations (Schurr et al. 2005). Thus, both the primary wind-borne dispersal following seed release from the tree, and the secondary dispersal along the ground can be synergistically affected by an anthropogenic shift in fire season from summer to either autumn or spring, resulting in an overall reduction in the seed-dispersal capability of *C. verrucosa* and other species with similar dispersal mechanisms.

Although we primarily examined the proximal portion of the dispersal kernel, we expect the seasonal relationship to hold true under stronger turbulent wind conditions, and hence the tail of the dispersal kernel. The PAPPUS modelling method addressed some of the limitations in estimating initial wind-borne dispersal, but again extreme wind conditions or other meteorological events that could be particularly important for long-distance seed dispersal may have been missed during the sampling period of two weeks. Nevertheless, we suggest that the relationships revealed from the inner portion of the kernel, and specifically the longer-distance dispersals in summer, are likely to be maintained across the entire kernel because convection and updraft are likely to be promoted by surface heating, which is greater in summer than at other times of year (Sullivan et al. 2012; Kuparinen et al. 2009). Therefore, our results suggest that fire season is important in generating long-distance dispersal of fire-released seeds, and hence for promoting gene flow (Cain et al. 2000; Loveless and Hamrick 1984; Levin and Kerster 1974), recolonisation (He et al. 2004; Cain et al. 2000), rescue effects (Bohrer et al. 2005) and colonisation of new sites (Trakhtenbrot et al. 2005; Nathan and Muller-Landau 2000; Clark et al. 1998) in populations of *C. verrucosa* and other serotinous trees.

The general findings of this study are expected to be applicable to other serotinous obligate seeders in fire-prone ecosystems that rely on seed dispersal by wind for their population persistence and re-establishment. More wind-dispersed serotinous obligate seeding tree species may be found within the families of

Proteaceae, Myrtaceae, Pinaceae and Cupressaceae which grow in the fire-prone, nutrient-poor and seasonally dry sclerophyll vegetation of Australia, South Africa, North America and Mediterranean Europe (Lamont et al. 1993). The potential reduction in seed-dispersal distances of these plant species if fire is constrained to cooler seasons could cause changes in population and community structure (Foster and Tilman 2003). Changes in structure can affect future fire patterns (Wilson et al. 1992) and animal species that depend on those species for habitat.

We conclude that the application of prescribed burning as a fire management tool, when carried out during cooler seasons compared to natural wildfires, reduces dispersal distances of wind-borne seeds. To improve our understanding of this topic, further work is needed to explore and quantify differences in fire seasonal effects between species and over the tail of the dispersal kernel. Effects of fire season on seed dispersal must be viewed in the context of other plant population processes (such as germination, survival and reproduction) that may be influenced by fire season, as well as its interactions with fire severity. These in combination may profoundly affect gene flow and population persistence.

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