Implications of terminal velocity and wing loading on *Hakea* (Proteaceae) seed dispersal

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Abstract

Hakea (Proteaceae) has winged seeds that rely on wind movement for dispersal, with seed dispersal being most effective in a post-fire environment. Seeds from 14 southwestern Australian species (8 fire-killed, 6 resprouters) had their seed mass, wing loading, and terminal falling velocity recorded to determine if a) overall relationships existed between seed properties and seed aerodynamics, and b) if seed dispersal was inherently different between the two post-fire persistence strategies. An increase in seed wing loading, calculated as the mass divided by area of the winged seed, resulted in an increase in seed terminal velocity. Using terminal velocity data to estimated initial seed dispersal distance, *Hakea* seeds have the potential to be dispersed up to 5 m from a parent plant, assuming seeds dispersed from less than 1.5 m above ground, and prevailing wind speeds of no more than 5 m s^{-1}. However, under field conditions *Hakea* seeds are dispersed up to 20 m from the nearest adult. Secondary dispersal, the movement of seeds across the ground, is therefore more important in explaining *Hakea* post-fire dispersal patterns, and is a function of seed mass, prevailing surface wind conditions and the occurrence of litter microsites. Despite detecting no significant difference in wing loading or terminal velocity between fire-killed and resprouting in this study, field observations suggest that seeds of resprouter *Hakea* species tend to disperse their seeds further away from the parent plants.

Keywords: winged seeds, wind dispersal, falling speed, primary and secondary dispersal, seed movement

Introduction

Within the family Proteaceae, wind dispersed seeds mostly occur within genera that possess woody fruit (*i.e. Banksia, Hakea, Xylomelum* from Australia) or woody cones (*e.g. Petrophile* (Australia); *Protea, Leucadendron* (South Africa)). The former producing seeds that possess papery broad wings. The wing provides airborne seeds with greater lift by decreasing the seeds' terminal velocity, defined as the speed at which a seed ceases to accelerate because the downward force of gravity equals the upward force of air drag. For winged objects the terminal velocity is proportional to the square root of the object wing loading, defined as its total mass divided by area (Norberg 1973). A decrease in terminal velocity has implications for longer dispersal distances (Green 1980), potentially kilometres away from the parent plant, when conditions are favourable (He *et al.* 2004, 2009; Schurr *et al.* 2005). However long distance dispersal only accounts for approximately 1–3% of wind-dispersed seeds (Nathan *et al.* 2002; Soons & Ozinga 2005).

Within the genus *Hakea* seed size varies from 2 – 500 mg (mean of 32 mg) (Groom & Lamont 1996) with the wing accounting for at least a quarter of the winged seed area. Seed release can occur within hours of the fruit opening, often in response to the passage of fire or other types of stem damage (McCaw & Smith 1992). Once dispersed the seeds tend to accumulate in litter microsites or become trapped within the existing vegetation (Lamont *et al.* 1993). Most *Hakea* species release their seeds into a post-fire environment (Groom *et al.* 2001) which provides a suitable barren landscape for effective dispersal of wind dispersed seed (Manders 1986; Bond 1988; Yeaton & Bond 1991; Lamont *et al.* 1993; Hammill *et al.* 1998; Schurr *et al.* 2005).

This paper investigates the relationships between seed mass, wing loading and terminal velocity of 14 southwestern Australian *Hakea* species and the implications of these traits on seed dispersal following fire. Fire-killed and resprouter species were selected to investigate whether there is any functional significance in dispersal traits that relates to differences in post-fire persistence strategies.

Methods

Seed collection

Approximately 20 fruits per species were harvested from natural populations of 14 *Hakea* species from locations near Eneabba (*H. circumalata, H. incrassata, H. smilacifolia*), Kalamunda (*H. amplexicaulis, H. erinacea, H. cyclocarpa, H. lissocarpa, H. undulata*), the Stirling Ranges (*H. lehmanniana, H. pandanicarpa* subsp. *crassifolia, H.*

prostrata, H. trifurcata) and Watheroo (*H. psilorrhyncha, H. cygna* subsp. *cygna*), Western Australia. Location details are provided in Groom & Lamont (1995). Species were co-occurring at each location, and were selected to ensure that a range of fire-killed and resprouting species were represented. The woody fruit were allowed to air dry for two weeks in a glasshouse to enable the fruit to naturally dehisce. Once open, seeds were carefully extracted using forceps to ensure the removal of entire diaspores (seed plus wing). Enough fruit opened to obtain 20 intact seeds per species.

Seed properties

For each species the fresh mass and projected area of 20 winged seeds, and the fresh mass of the seed only were measured. Mass was measured using a 4 decimal place balance. Projected areas (*i.e.* silhouette of each winged seed) were measured using a digital imaging system (DIAS-II, Delta T Devices, UK) that utilised a digital video connected to a computer to capture, and calculate the area of seed images. The loading on the winged seed (known as 'wing loading') is calculated as the mass divided by area of the winged seed (Matlack 1987).

Falling speed and terminal velocity

Winged seeds for each species were dropped one at a time from a windless indoor height of 4.5 m onto white sheeting. Two observers recorded the time taken for each winged seed to reach the floor using digital stop watches, and the mean fall time calculated. Seeds were retimed if the two values differed by more than 0.1 s. A tenth of a second represents an error in terminal velocity of 5% or less (Marchetto *et al.* 2010). Falling speed was measured as the drop height (*h*) divided by the fall time (*t*), and is also known as initial terminal velocity (Greene & Quesada 2005). True terminal velocity (*v_f*) needs to take into account that a falling seed has an initial period of acceleration, and was calculated according to Greene & Quesada (2005) as:

$$v_f = \frac{gt - \sqrt{g^2t^2 - 2.773gh}}{1.386} \quad \ldots\ldots\ldots\ldots \text{ eqn 1}$$

where *g* is acceleration due to gravity (9.81 m s⁻¹), *t* is elapsed time (s), and *h* is release height (m)

Estimation of dispersal distance

Predicted dispersal distances of seeds (*d*) for each species was calculated as follows (after Cremer 1977):

$$d = \frac{w.z}{v_f} \quad \ldots\ldots\ldots\ldots \text{ eqn 2}$$

where *w* = wind speed (m s⁻¹) and *z* = height within the canopy (m). A release height of 1 m and a wind speed of 5 m s⁻¹ were used to allow for comparisons with other data sets (*e.g.* Hammil *et al.* 1998). The latter is comparable with wind speeds recorded at the closest meteorological stations to the collection sites (Bureau of Meteorology, Western Australia). Distances were also calculated using a release height of 1.5 m, reflecting the mean canopy height of the study species.

Results

Correcting for gravitation acceleration (as per Eqn 1) resulted in 3–26% increase in terminal velocity from the original falling speeds (Table 1). Winged-seed area was linearly correlated with mass for winged seeds (*r* = 0.89, *P* < 0.0001; Figure 1a) with seed terminal velocity increased linearly with square root of the resultant wing loading (*r* = 0.65, *P* = 0.012; Figure 1c). There was no relationship between winged-seed mass and terminal velocity (*r* = 0.12, *P* = 0.689; Figure 1b) or winged-seed mass and wing loading (*r* = -0.13, *P* = 0.965). The wing increased the weight of the diaspore by 0.1 g (*H. smilacifolia*) to 15.7 g (*H. pandanicarpa*), representing 0.7% (*H. smilacifolia*) to 14% (*H. trifurcata*) of the entire diaspore.

Seeds released 1 m above the ground have the capacity to be dispersed 1.2–3.2 m at a wind speed of 5 m s⁻¹, with an average of 2.4 m (Table 1). Releasing seeds at 1.5 m extends the average distance to 3.6 m. Calculated dispersal distance decreased linearly with the square root of wing loading (*r* = -0.644, *P* = 0.013; Figure 1d) and hence with terminal velocity (*r* = -0.962, *P* < 0.001). There was no significant difference in seed dispersal properties or calculated dispersal distances between fire-killed and resprouter species (Table 1).

Discussion

Seed wind dispersal comprises of two phases. Primary dispersal involves the movement of seed through the air, with the end result that the winged seed is deposited on the ground. For *Hakea* species, this requires the seeds to be blown out of the open woody fruit. Seeds may then be blown across the ground until they are permanently trapped by leaf litter, organic debris and existing or dead vegetation, or until the membranous wing is damaged. This is known as secondary dispersal, and has more direct implications on post-dispersal seedling recruitment patterns (Bond 1988; Chambers & MacMahon 1994; Hammill *et al.* 1998; Schurr *et al.* 2005) as it is affected by seed traits, prevailing ground wind conditions and barriers to seed movement (Johnson & Fryer 1992; Schurr *et al.* 2005). The duration of wind assisted seed movement is dependent on when a seed becomes entrapped by surface obstacles or covered by soil, or when the first heavy rains occur.

Primary dispersal is directly linked to the winged seed's terminal velocity and is a linear function of seed wing loading, providing the winged seed acts as a drag device (Greene & Quesada 2005). Previously published terminal velocity values for *Hakea* seeds range from approximately 1 m s⁻¹ (Richardson *et al.* 1987, Hammill *et al.* 1998) to a maximum of 2.1 m s⁻¹ (Lamont *et al.* 1993), the latter being within the range of speeds presented in this paper (Table 1). Differences between datasets (*i.e.* lower values for eastern Australian hakeas (Hammill *et al.* 1998) and higher values western Australian hakeas (Lamont *et al.* 1993; this paper)) may imply that eastern Australian hakeas are more likely to disperse over greater distances. Experimental data collected by Hammill *et al.* (1998) suggests that *Hakea* seeds with an average wing loading of 220 g m⁻² will have a primary dispersal distance between 5–6 m, almost twice that predicted from this study at
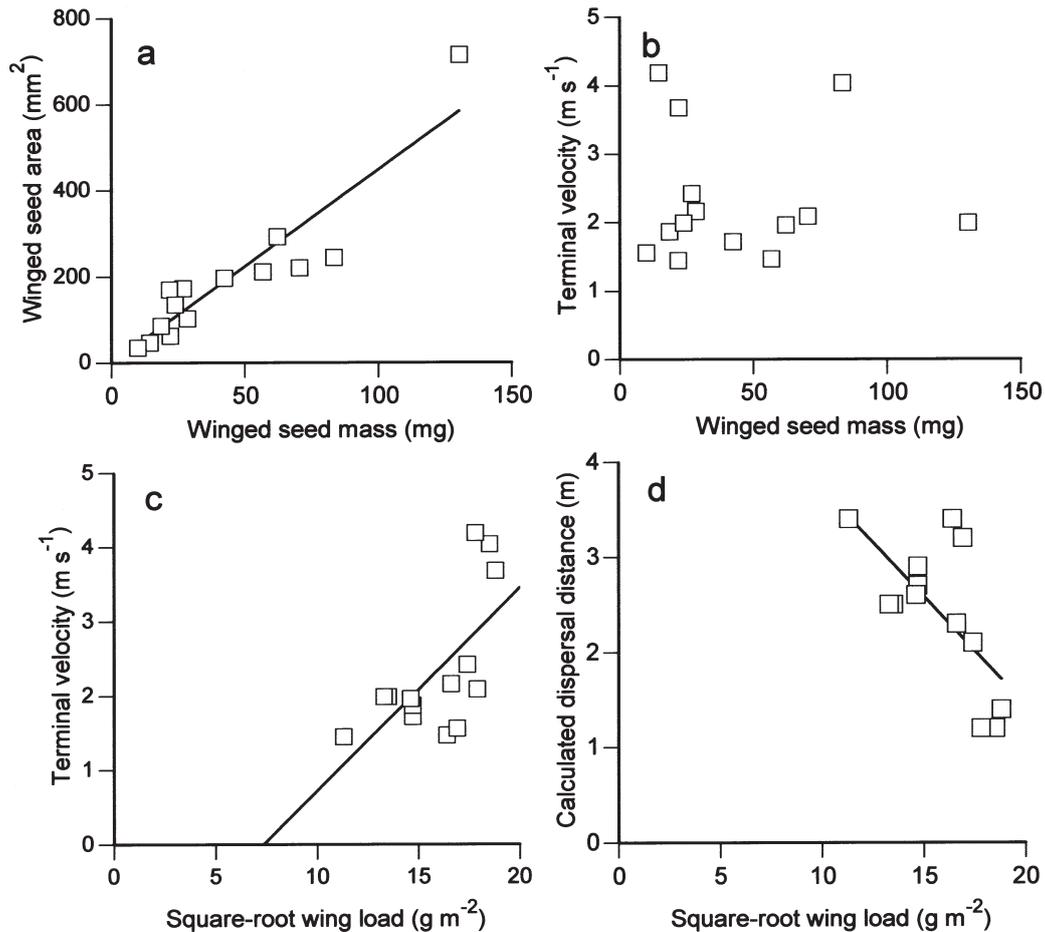
Figure 1. Relationships between winged seed morphology, terminal velocity and calculated primary dispersal distances (from 1 m release height) for 14 *Hakea* species. Trend lines are provided for significantly correlated data. See Table 1 to identify data for individual species, and hence species' contribution to overall trends.

Table 1

Seed traits and seed dispersal properties of 14 *Hakea* species. Dispersal distance calculated for all species assuming a release height of either 1 or 1. 5 m and a wind speed of 5 m s⁻¹. Data mean ± SE. Trait comparison between fire-killed and resprouter conducted using *t*-tests.

Species	Seed mass (no wing) (mg)	Winged Seed Area (cm²)	Wing loading (g m⁻²)	Fall speed (m s⁻¹)	Terminal Velocity (m s⁻¹)	Dispersal distance (m) 1 m	1.5 m
Fire-killed							
H. circumalata	26.5 ± 1.8	1.35 ± 0.07	176.5	1.88 ± 0.04	1.99 ± 0.05	2.5	3.8
H. cygna subsp. *cygna*	25.3 ± 1.2	1.03 ± 0.02	276.7	2.01 ± 0.08	2.16 ± 0.11	2.3	3.5
H. erinacea	21.7 ± 0.7	0.46 ± 0.01	315.2	3.28 ± 0.03	4.19 ± 0.07	1.2	1.8
H. pandanicarpa subsp, *crassifolia*	114.7 ± 6.7	7.15 ± 0.53	182.4	1.87 ± 0.05	1.99 ± 0.07	2.5	3.8
H. psilorrhyncha	65.8 ± 7.5	2.20 ± 0.10	320.2	1.95 ± 0.05	2.09 ± 0.07	2.4	3.6
H. smilacifolia	9.8 ± 0.6	0.34 ± 0.01	287.0	1.50 ± 0.04	1.56 ± 0.05	3.2	4.0
H. trifurcata	15.9 ± 1.3	0.85 ± 0.03	217.5	1.77 ± 0.11	1.87 ± 0.13	2.7	4.0
H. undulata	18.9 ± 0.4	0.62 ± 0.01	353.6	3.02 ± 0.08	3.68 ± 0.19	1.4	2.0
Mean	37.3 ± 12.5	1.75 ± 0.80	266.1 ± 23.5	2.16 ± 0.32	2.44 ± 0.34	2.3 ± 0.2	3.3 ± 0.3
Resprouters							
H. amplexicaulis	31.1 ± 0.9	1.97 ± 0.13	215.3	1.67 ± 0.04	1.72 ± 0.04	2.9	4.4
H. cyclocarpa	80.5 ± 2.3	2.44 ± 0.11	341.2	3.21 ± 0.04	4.04 ± 0.08	1.2	1.8
H. incrassata	49.2 ± 3.3	2.92 ± 0.17	212.8	1.85 ± 0.05	1.96 ± 0.07	2.6	3.8
H. lehmanniana	17.5 ± 0.6	1.70 ± 0.08	127.9	1.40 ± 0.07	1.45 ± 0.07	3.4	5.2
H. lissocarpha	32.3 ± 0.6	1.13 ± 0.04	303.8	2.19 ± 0.24	2.42 ± 0.29	2.1	3.1
H. prostrata	34.9 ± 1.0	2.11 ± 0.06	268.6	1.42 ± 0.10	1.47 ± 0.11	3.4	5.1
Mean	40.9 ± 8.9	2.04 ± 0.25	244.9 ± 31.0	1.96 ± 0.28	2.18 ± 0.40	2.6 ± 0.3	3.9 ± 0.5
Fire-Killed vs Resprout (*P* values)	0.314	0.164	0.830	0.998	0.884	0.553	0.553

similar release height and wind speed. These values will underestimate the maximum possible primary dispersal distance under field conditions, as primary dispersal distance increases as a function of air turbulence (Greene & Johnson 1992; Nathan *et al.* 2002) and release height. Terminal velocity thus has limited explanatory value in predicting the final dispersal distance within the genus, as wind exposure, microsite availability and soil texture of the surface on first landing are all important external factors influencing secondary dispersal distances of *Hakea* seeds (Lamont *et al.* 1993).

Winged *Hakea* seed can travel up to 8 m at a constant wind tunnel speed of 6.5 m s^{-1} with the potential to travel more than 12 m in a post-fire environment depending on post-fire wind conditions (Hammill *et al.* 1998). This is similar to the seedling recruitment pattern observed in the field for southwestern Australian hakeas (P. Groom, *pers. observ.*) with seedlings tending to occur within a 5–20 m radius of a parent plant. Seedlings of fire-killed *Hakea* species are more likely to occur closer to an adult, as they recruit more seedlings post-fire than expected by chance alone (Groom *et al.* 2001), resulting in a relatively large number of seedlings recruiting per pre-fire adult. This complements the findings of studies on wind dispersed South African *Protea* species where most seedlings are found in greatest abundance directly underneath the parent plants and lowest in the open, with 95% of seedlings occurring within 15 m of the parents following fire (Manders 1986; Yeaton & Bond 1991). A maximum distance of 26 m from the parents (Manders 1986) implies that the movement of seeds rolling over the soil surface is an important determiner of their final resting distance (Bond 1988).

Fire has a direct impact on secondary seed dispersal, creating the litter (burnt leaves, stems, fruit parts) and burnt vegetation that become the traps for tumbling seeds, with the rate of post-fire litter accumulation and litter microsite formation increasing with time since fire (Lamont *et al.* 1993; Denham *et al.* 2009). In a fire-prone landscape, seeds are often initially dispersed into a barren environment, where litter is relatively scarce (Denham *et al.* 2009). With wind assistance winged seeds can travel up to 4 m in 1 hour (Hammill *et al.* 1998). Secondary dispersal thus is an important consideration when investigating post-fire dispersal patterns of wind-dispersed seed (Schurr *et al.* 2005), with winged seed density in these litter microsites being 18–39 times greater than adjacent bare patches (Lamont *et al.* 1993). Hammill *et al.* (1998) found that *Hakea* seeds moved smaller distances along the ground than *Banksia* seeds (due to their larger seed wing loading) increasing their resistance to movement by wind, and differences in seed morphology. The proportion of the winged seed that is seed (embryo plus testa) is important in understanding the secondary surface dispersal of hakeas.

Wind dispersed seeds of serotinous South African Proteaceae do not disperse as far as their Australian counterparts (Manders 1986; Bond 1988; Hammill *et al.* 1998; Yeaton & Bond 1991), despite plumed and parachute seeds (mostly South African Proteaceae) being more mobile than winged seeds (mostly Australian Proteaceae) (Schurr *et al.* 2005). Recent demographic studies have demonstrated the potential for winged *Banksia* seeds to travel up to 2.6 km from the parent

population in the Eneabba sandplains (He *et al.* 2004; 2009). Similar distances have been noted for invasive *Pinus* (pine) species, all of which have winged seeds (van Wilgen & Siegfried 1986). To be transported such long distances, wind updrafts and vortices come into play, as long-distance dispersal is directly related to seed uplifting (Nathan *et al.* 2002). Lamont and colleagues (Lamont *et al.* 1993; He *et al.* 2004; 2009) have suggested that willy-willies (also known as 'dust devils') and prevailing winds play an important role in long-distance dispersal in a post-fire landscape, having the ability to transport soil and surface debris to heights of hundreds of metres (Oke *et al.* 2007). It would be expected that *Hakea* species with smaller wing loads, and hence lower terminal velocities (*e.g. H. circumalata*), would remain within the convective vortex for longer time periods. Thus having greater potential for long-distance dispersal. Although this is dependent on the assumption that the papery wing of *Hakea* seeds does not sustain any significant damage during the process. Removing the wing causes a 12–17% increase in terminal velocity (Lamont *et al.* 1993).

There was no difference in any of the dispersal-related seed properties measured in relation to post-fire survival strategies. It might be expected that seeds of fire-killed hakeas would not disperse as far as resprouter species because of the lack of seedling competition with adults. Although the current study showed no significant difference in seed mass between the two strategies, Groom & Lamont (1996) found that resprouting hakeas tend to produce heavier seeds without increasing wing loading. Experimental work suggests that in terms of secondary wind dispersal, large seeds require higher wind speeds to move across a surface (Johnson & Fryer 1992), and hence one might expect seeds of fire-killed hakeas to quickly move across the ground after their initial dispersal from the parent plant. Field observations suggest that obstacles (*i.e.* accumulated litter) and localised air turbulence just above the ground surface play an important role in seed dispersal patterns within *Hakea* populations, as has been modelled for wind dispersed South African Proteaceae (Schurr *et al.* 2005). The ability to protect and retain viable quantity of canopy stored seeds between fires is more important in explaining differences in post-fire recruitment patterns of co-occurring fire-killed and resprouting *Hakea* species (Groom *et al.* 2001).

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