

SHORT COMMUNICATION

Positive effect of seed size on seedling survival in fire-prone savannas of Australia, Brazil and West Africa

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All plant species face a fundamental reproductive trade-off: for a given investment in seed mass, they can produce either many small seeds or few large seeds. Whereas small seeds favour the germination of numerous seedlings, large seeds favour the survival of seedlings in the face of common stresses such as herbivory, drought or shade (Leishman *et al.* 2000). One mechanism explaining the better survival of large-seeded species is the seedling size effect (SSE) (Westoby *et al.* 1996): because seeds with large reserves result in bigger seedlings, seedlings from large-seeded species would have better access to light and/or to reliable water supply than seedlings from small-seeded species.

However, the relationship between seedling size and seed mass usually weakens through time, as seedling relative growth rate tends to be negatively correlated with seed mass (Leishman *et al.* 2000). Therefore, the advantage of large-seeded species is expected to be greatest during early seedling establishment and to diminish until seed reserves have been fully exhausted (Leishman *et al.* 2000, Moles & Westoby 2004). In accordance with this expectation, Dalling & Hubbell (2002) and Walters & Reich (2000) found no relationship between the survival probability of well-established seedlings and seed size in a species comparison experiment. In contrast, Baraloto *et al.* (2005), Hoffmann (2000) and Moles & Westoby (2004) found a positive relationship. With the exception of Hoffmann (2000), all these studies were on forest tree species.

As in forests, seedling survival is a critical process in savannas that influences both the abundance and species diversity of trees. But in contrast to forests, the factors affecting seedling survival, and potentially selecting for seed size, are expected to be different in savannas.

In contrast to forests, seedlings in savannas are strongly competing with grass for access to light, water and nutrients (Kanegae *et al.* 2000, Nardoto *et al.* 1998). Consequences of competition are more severe for small seedlings than for tall seedlings due to the higher grass biomass encountered. The smaller seedling size of small-seeded species is thus likely to persist, as they are continually unfavoured. We therefore expected the SSE to last in savannas even after exhaustion of the seed reserves.

Fire is also a major constraint on seedling survival in moist savannas, which commonly burn at intervals of 1–3 y. Grass fire almost invariably destroys the entire shoot of seedlings so that seedlings must be able to resprout to survive (Bond & Midgley 2001). Resprouting requires sufficient root reserves of total non-structural carbohydrates (TNC) and nutrients to regenerate shoots and leaves, which depend both on the root biomass and on the resource allocation strategy of the species (Bond & Midgley 2001, Canadell & Lopez-Soria 1998). Tree species with high root:shoot ratio are indeed likely to accumulate more TNC in roots than tree species with low root:shoot ratio (Chapin *et al.* 1990).

Although differences in resource allocation among tree species may weaken the relationship, we expected an overall positive effect of seed size on seedling survival due to the SSE in savannas. To test this hypothesis, we re-analysed data on savanna tree species available in

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Table 1. Dry seed mass and seedling survival of tree species in fire-prone savannas of Australia, Brazil and West Africa (Abb. = abbreviation). Dry seed masses are means with standard errors, if available.

Abb.	Species	Family	Study site	Dry seed mass (mg)	Seedling survival
Cf	<i>Crossopteryx febrifuga</i> Benth.	Rubiaceae	Côte d'Ivoire	0.3 ± 0.03	0.11 ¹
Ma	<i>Miconia albicans</i> (Sw.) Steud.	Melastomataceae	Brazil	2.4 ²	0 ²
Cc	<i>Corymbia clarksoniana</i> (D. J. Carr & S. G. M. Carr) K. D. Hill & L. A. S. Johnson	Myrtaceae	Australia	6.9	0.07 ⁷
Pf	<i>Psorospermum febrifugum</i> Spach	Hypericaceae	Côte d'Ivoire	11.5 ± 0.7	0.44 ¹
Ao	<i>Acacia oncinocarpa</i> Benth.	Mimosaceae	Australia	12.8 ± 0.4	0.21 ⁸
Bs	<i>Blepharocalyx salicifolius</i> (H.B.K.) Berg.	Myrtaceae	Brazil	13.5	0.1 ⁵
Rm	<i>Roupala montana</i> Aubl.	Proteaceae	Brazil	19.9 ± 1.1 ²	0.37 ²
Mg	<i>Myrsine guianensis</i> (Aubl.) Kuntze	Myrsinaceae	Brazil	24.1 ± 1.5 ²	0.14 ²
Zm	<i>Zeyheria montana</i> Mart.	Bignoniaceae	Brazil	29.8 ± 3.0 ²	0.62 ²
Em	<i>Eucalyptus miniata</i> A. Cunn. ex Schauer	Myrtaceae	Australia	32.2 ± 0.6	0 ⁸
Pm	<i>Periandra mediterranea</i> (Vell.) Taub.	Fabaceae	Brazil	32.4 ± 1.4 ²	0.48 ²
Kc	<i>Kielmeyera coriacea</i> Mart.	Clusiaceae	Brazil	37.5 ± 0.4 ²	0.66 ²
Bf	<i>Bridelia ferruginea</i> Benth.	Euphorbiaceae	Côte d'Ivoire	47.8 ± 4.9	0.10 ¹
Gn	<i>Guapira noxia</i> (Netto) Lundell	Nyctaginaceae	Brazil	63.7 ± 4.1 ²	0.42 ²
Pe	<i>Pterocarpus erinaceus</i> Poir.	Fabaceae	Côte d'Ivoire	71.3 ± 12.8	0.63 ¹
As	<i>Annona senegalensis</i> Pers.	Annonaceae	Côte d'Ivoire	91.1 ± 10.2	0.39 ¹
Dm1	<i>Dalbergia miscolobium</i> Benth.	Fabaceae	Brazil	90.5	0.50 ⁴
Pt	<i>Ptilostigma thonningii</i> (Schumach.) Milne-Redh.	Caesalpiniaceae	Côte d'Ivoire	95.9 ± 2.4	0.56 ¹
Ri	<i>Rourea induta</i> Planch.	Connaraceae	Brazil	135 ²	0.67 ²
Ts	<i>Terminalia schimperiana</i> Planch. ex Benth.	Combretaceae	Côte d'Ivoire	136.3 ± 22.7	0.50 ¹
Dm2	<i>Dimorphandra mollis</i> Benth.	Caesalpiniaceae	Brazil	243	0.54 ³
Bg	<i>Brosimum gaudichaudii</i> Trecul.	Moraceae	Brazil	772 ± 43.4 ²	0.72 ²
Ba	<i>Borassus aethiopum</i> Mart.	Arecaceae	Côte d'Ivoire	119025 ± 4019	0.73 ⁶

¹Lahoreau *et al.* (2004, unpubl. data); ²Hoffmann (2000); ³Andrade *et al.* (2001); ⁴Franco *et al.* (1996); ⁵Matos (1994); ⁶Barot (unpubl. data); ⁷Williams (2004); ⁸Setterfield (2002).

the literature throughout the tropics. To get comparable data, we restricted our comparison to observations for which survival probabilities over 1 y have been assessed for seedlings around 4 mo old and burned during their first dry season.

Data were compiled for a total of 23 savanna tree and shrub species, including three species from Australia (Setterfield 2002, Williams 2004), 12 species from Brazil (Andrade *et al.* 2001, Franco *et al.* 1996, Hoffmann 2000, Matos 1994) and eight species from West Africa (Barot, unpubl. data, Lahoreau *et al.* (2004, unpubl. data) (Table 1). Seedling survival for *Borassus aethiopum* might be underestimated as it integrated the probability that seeds germinated and that seedlings survived over 18 mo (Barot, unpubl. data). Seedling survival for *Corymbia clarksoniana* might be overestimated, as it was determined over a period of only 3 mo (Williams 2004).

Except for *Corymbia clarksoniana*, seed masses were measured individually on a number of seeds between 3 and 535. For *Corymbia clarksoniana*, seed mass was weighed on five batches of 25 seeds. Seeds of 6 out of the 8 West African tree species came from herbarium specimens of the French National Museum of Natural History (P). Seed water content for seeds weighted dry was estimated as 10% based on data from *Bridelia ferruginea* (7.9%, Lahoreau, unpubl. data) and on the fact that most savanna tree species have relatively dry seeds when

dispersed. This rough estimation had virtually no effect on our results, primarily because we were comparing species with seed masses ranging over seven orders of magnitude, from 0.3 to 119 025 mg (Table 1). Seed mass of 14 out of 23 species lay between 10 to 100 mg (Table 1). Except for the two species with the largest seed sizes, the seed reserves were likely to be exhausted when seedlings were 4 mo old, as typical for tree seedlings (Ichie *et al.* 2001, Kitajima 2002).

We found that survival probability (logit transformed with $\text{logit}(S + 0.1) = \ln\left(\frac{S+0.1}{1-(S+0.1)}\right)$) was positively related to seed mass (log-transformed) (Figure 1; $n = 23$, $r^2 = 0.45$, $P = 0.0006$). This result is robust: when the two or the four species, with the lowest and the highest seed masses were discarded, the relationship still remained significant with $P = 0.0004$ and $P = 0.0088$ respectively. The effect of the continent was almost significant ($P = 0.0593$).

As expected, we thus found that the advantage of large seeds persisted in savannas even after exhaustion of the seed reserves. The similar relationship found across three continents suggests that seed size has evolved under similar selective pressures, related to fire and drought constraints. The positive effect of seed size on seedling survival probably results from the SSE. However, seed size might also indirectly influence the ability of seedlings to resprout after fire.

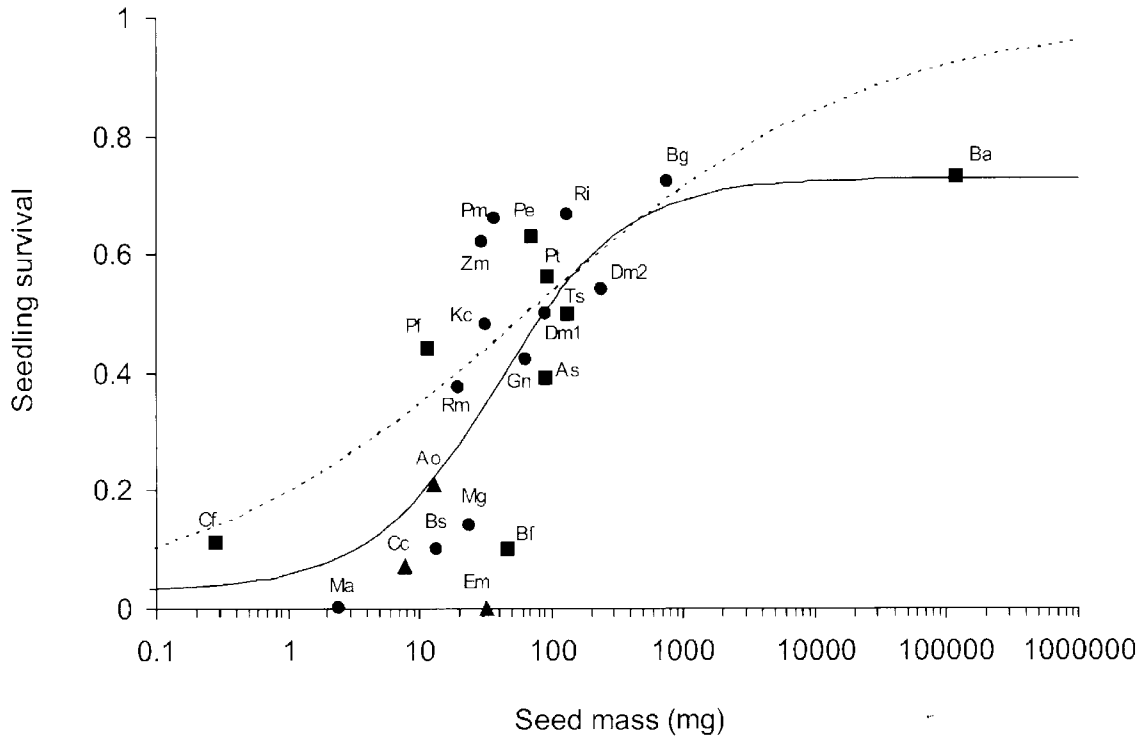


Figure 1. Survival of savanna seedlings in function of seed mass for Australian species (triangles), Brazilian species (dots) and West African species (squares). The dashed line represents the linear relation between logit survival and log seed mass ($P = 0.0006$). We also fitted a logistic curve through non-linear regression as a visual indicator of the shape of the relation (PROC NLIN in SAS[®]) ($y = 0.729 \frac{0.697}{1 + 0.0382x^{0.891}}$, $P = 0.0013$). Each point represents a tree species. See Table 1 for species abbreviation.

Resprouting ability requires reserves to support growth but also the presence of viable buds (Bond & Midgley 2001). As cotyledonary nodes are privileged sites for bud development in seedlings (Del Tredici 1992, Pascual *et al.* 2002), only cotyledonary buds located below the soil surface will be protected from fire (Jackson 1974, Verdaguer *et al.* 2000). Different studies have shown that seed size correlates with germination type of tree species (Hladik & Miquel 1990, Ibarra-Manríquez *et al.* 2001); whereas small seeds are often associated with epigeal and photosynthetic-type cotyledons, large seeds are more frequently associated with hypogeal and storage-type cotyledons. The positive effect of seed size on seedling survival might thus also result from the correlation between seed size and germination type.

It is not possible without specially designed experiments to test whether SSE or germination type is responsible for the positive effect of seed size on seedling survival of savanna tree species. Moreover, strategy of resource allocation might also influence the ability of seedlings to resprout after fire. To address thoroughly the issue of the determinants of resprouting ability of savanna tree species, more studies investigating both plant allocation strategy (root:shoot ratio, TNC, root biomass) and plant

bud bank (cotyledonary buds but also buds located on roots) should be conducted.

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