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Seed size and seedling emergence: an allometric relationship and some ecological implications

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Abstract We develop a geometric model predicting that maximum seedling emergence depth should scale as the cube root of seed weight. We tested the prediction by planting seeds from 17 species ranging in weight from 0.1 to 100 mg at a variety of depths in a sand medium. The species were spread across 16 genera and 13 families, all occurring in fire-prone fynbos shrublands of South Africa. Maximum emergence depth was found to scale allometrically with seed weight with an exponent of 0.334, close to the predicted value. We used the allometry to predict recruitment response to experimentally simulated variation in fire intensity. Five species with small (<2 mg) seeds and five with large (>10 mg) seeds were planted at ≤20-mm and 40-mm depths and exposed to low and high heat treatments and a control. The allometric equation predicted that species with large seeds would be able to emerge from a depth of 40 mm but those with small seeds would not. Only 1% of 481 seedlings from small-seeded species emerged from the 40-mm planting compared with 40% of 626 seedlings from the large-seeded group. The simulated fire treatments killed seeds in shallow, but not deeper, soil layers. At simulated high fire intensities, seedling emergence was poor in small-seeded species but good in large-seeded species, with most seedlings emerging from the 40-mm planting depth. Seed size could be a useful general predictor of recruitment success under different fire intensities in this system. We suggest that allometric relationships in plants deserve wider attention as predictive tools.

Key words Seed size · Allometry · Mediterranean-type shrublands · Fire response

Introduction

There is a large, and sometimes contentious literature on seed size and its significance (Westoby et al. 1992). Much of this concerns analyses of correlative patterns of seed size with other plant attributes or the habitats in which plants grow (e.g. Salisbury 1942; Mazer 1989; Michaels et al. 1988) and attempts to separate direct effects of seed size from its correlates, including phylogenetic relatedness (e.g. Kelly 1995; Leishman et al. 1995). As a helpful signpost to studies in the field, Leishman et al. (1995) identified four independent though complementary questions. We studied the relationship between seed size and maximum seedling emergence depth and its ecological implications, addressing the first of their questions. We do not consider correlates of seed size with environmental conditions for recruitment, correlates of seed size with other plant attributes or patterns within phylogenetic lineages. However, we do suggest that a simple general allometric relationship may underlie patterns of seed size and emergence for a large number of unrelated taxa.

Allometric relationships are powerful predictive tools in ecology. Body size in animals, for example, is a useful predictor of a wide range of ecological traits, including lifespan, litter size, food requirements and home range (Peters 1983). Seed size is the closest plant analogy to body size in animals. It has been shown to predict the ability of plants to establish from seeds in the face of a variety of hazards including competition (Black 1958; Rees 1995), shading (Grime and Jeffrey 1965), drought (Leishman and Westoby 1994), nutrient limitation (Lee and Fenner 1989; Jurado and Westoby 1992) and depth of seedling emergence (Gulmon 1992; Peterson and Facelli 1992; Vasquez-Yanes and Orozco-Segovia 1992). We first develop a theoretical argument for the relationship between seed size and emergence depth. We then report on an experi-

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mental study to test the predicted relationship. Finally we describe an application of the scaling relationship for ecological prediction. We show that seed size can be useful in predicting recruitment response to variation in fire intensity in fire-prone shrublands.

A model of seed size and seedling emergence

We wish to establish a relationship between seed size (volume or weight) and the maximum depth at which a seed can be buried below the soil, germinate and emerge as a seedling. We start by assuming a spherical seed with diameter r and weight w buried at a depth d below the soil surface. To reach the soil surface, it has to produce a column of tissue of length d to emerge as a seedling. Assuming that a column requires maximum radius, r , to push through the soil, then the maximum depth from which seedlings may emerge, d_{\max} , is given by rearranging the volume, V , of a sphere into a column.

Thus:

$$r^3 \propto r^2 d_{\max}$$

and

$$d_{\max} \propto r$$

so maximum emergence depth is proportional to the radius of an idealised spherical seed.

This radius can be estimated from seed weight, w , since:

$$w \propto Vc$$

$$w \propto r^3 c$$

and

$$r \propto w^{0.33} c$$

Since d_{\max} is proportional to r ,

$$d_{\max} \propto w^{0.33} c$$

Thus maximum seedling emergence depth should scale as the cube root of seed weight. The constant, c , may differ among sites (e.g. with different soil textures) or species (e.g. with different seed contents).

Materials and methods

An experimental study of the allometric relationship

We explored the relationship between seed weight and maximum emergence depth by planting seeds of different sizes at different depths in a sandy soil. We wished to determine whether there was any allometric relationship for a range of species with diverse taxonomies. We obtained seeds from 17 species from the seed collection at Kirstenbosch National Botanical Garden. Seed weight covered more than three orders of magnitude from 0.07 to 105 mg (Table 1). All the species occur in fire-prone fynbos shrublands of the Cape flora of South Africa and included 16 genera and 13 families. Seeds were subjected to various treatments according to available literature and horticultural practices to promote germination (Jeffery et al. 1988; Brown 1993; Keeley and Bond 1997). Larger seeds were germinated in Petri dishes and, when the radicles

Table 1 Species used in this study. All species occur in fynbos shrublands of the Cape Floristic Region of South Africa. Names follow Bond and Goldblatt (1984). Species marked with an asterisk were also used in the fire simulation experiment

Species	Family	Seed weight (mg)
<i>Albica canadensis</i>	Hyacinthaceae	0.80
<i>Chondropetalum tectorum</i>	Restionaceae	0.11
* <i>Coleonema pulchellum</i>	Rutaceae	1.80
* <i>Dorotheanthus bellidiformis</i>	Mesembryanthemaceae	0.32
* <i>Erica mammosa</i>	Ericaceae	0.09
<i>Heliophila</i> sp.	Brassicaceae	0.68
* <i>Helipterum</i> sp.	Asteraceae	0.33
<i>Indigofera filicaulis</i>	Fabaceae	8.10
* <i>Leucospermum glabrum</i>	Proteaceae	105.00
* <i>Lobelia valida</i>	Campanulaceae	0.07
* <i>Phylica pubescens</i>	Rhamnaceae	22.00
* <i>Podalyria calyptrata</i>	Fabaceae	23.50
<i>Podalyria sericea</i>	Fabaceae	29.50
<i>Restio brachiatus</i>	Restionaceae	0.44
<i>Virgilia oroboides</i>	Fabaceae	86.50
* <i>Wachendorfia thyrsiflora</i>	Haemodoraceae	14.70
* <i>Watsonia tabularis</i>	Iridaceae	10.50

emerged, were planted in pots at depths of 10, 20, 30, 50, 75 and 100 mm below the soil surface. Three replicates of ten seeds each were used for each soil depth except for *Leucospermum glabrum* where we used five seeds per replicate. *Wachendorfia thyrsiflora* has seeds ranging from 2 to 22 mg. Seeds were sorted into two batches: “big” (mean seed weight 18.8 mg) and “small” (mean seed weight 2.9 mg). These were germinated in Petri dishes and treated in the same manner as other species.

Species which require a special smoke treatment (*Phylica pubescens*, *Coleonema pulchellum*), or have very fine seeds which are too small to handle individually (e.g. *Erica mammosa*, *Lobelia valida*, *Dorotheanthus bellidiformis*) were planted in glass boxes. In this way, we could ensure that seeds had germinated and grown successfully. A spatula tip full of these fine seeds was planted against the side of the glass at the desired depth. The sides of the boxes were covered with black plastic to ensure that seeds germinated in darkness. Those species requiring a smoke treatment were covered with only 10 mm of sand during smoking (so that all seeds received the same amount of smoke residue) before the boxes were filled to the required depth. Four species were planted in each box (one species per side) at two depths. The depths were separated by at least 40 mm. Seeds of all species were planted in the same batch of pure sand to ensure uniform soil compaction. Pots were placed in a growth chamber and watered three times weekly. Pots were checked four times a week for 12 weeks to record seedling emergence.

Seedling emergence under simulated fire

Seed size, if it affects maximum seedling emergence, could be a useful predictor of how fire intensity affects seedling recruitment of species occurring in fire-prone shrublands. High fire intensities, which kill seeds in the surface soil layers, would favour those plants capable of emerging from deeper soil layers. We conducted an experiment to simulate the effects of low- and high-intensity fires on seedling emergence from different-sized seeds. We used seeds from 10 of the 17 species used in the first experiment (Table 1). These were planted in rows separated by 20 mm in 230-mm-diameter pots filled with acid-washed sand. We planted seeds at two levels, either 10 mm or 40 mm, or 5 mm and 20 mm in each pot. Pots were subjected to either of two heating treatments or a control of no heating. There were five replicate pots in each treatment.

We simulated the effects of fire on soil-stored seeds by heating soil with a heating element placed at two heights above the soil.

Before applying the heat treatment, we determined soil temperature profiles for different durations and heights of the heating elements using thermocouples situated at various soil depths. For the high-intensity treatment, the heating element was placed 30 mm above the soil for 16 min. This generated, at 20 mm depth, a peak temperature of 150°C and temperatures >120°C for 10 min. For the low-intensity treatment, the element was held at 100 mm above the soil for 15 min which produced, at 20 mm depth, an estimated peak temperature of 95°C and temperatures >75°C for 10 min.

We could not subject seeds to germination-promoting treatments, as in the first experiment, since heating to simulate fire might kill pregerminated seeds. However, to help promote germination of smoke-stimulated species, we supplied each pot with 100 ml of smoke water with a fine spray within 2 h of the heat treatment. The smoke water was made by bubbling smoke from burning fynbos material through a litre of distilled water for an hour, after which the water turned brown/ yellow in colour (Brown 1993). The pots were then placed in a greenhouse, watered regularly and seedling emergence monitored over 20 weeks. As seedlings emerged they were removed from the pots and depth of planting noted.

The significance of the effects of heat treatment, planting depth and seed size (small or large) on seedling emergence was tested by log-linear analysis of a three-way contingency table using the software programme Statistica.

Results

Allometric relationships

Maximum depths from which seedlings emerged in the first experiment are plotted against seed weight in Fig. 1. Maximum emergence depth had an allometric relationship with seed size with a slope of 0.334 (Fig. 1; $df = 15$, $R^2 = 0.85$, $P < 0.01$) compared with the predicted value of 0.333. The allometric relationship for maximum emergence depth is $27.3 \times \text{seed weight}^{0.334}$. Maximum emergence depth of the small-seeded *Wachendorfia* (mean seed weight 2.9 mg) was 20 mm which was less than the predicted value of 39 mm from the regression equation. The large seeds (mean seed weight 18.8 mg) emerged from a maximum depth of 75 mm compared to the predicted value of 73 mm.

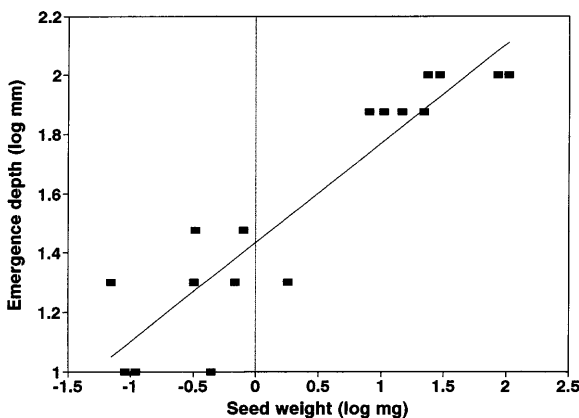


Fig. 1 Relationship between mean seed weight (log mg) and maximum depth of seedling emergence (log mm). The regression line was fitted by least squares: $\log \text{ emergence depth} = 1.436 + 0.334 \log \text{ seed weight}$, $R^2 = 0.85$, $P < 0.01$, $df = 15$. Alternatively, maximum emergence depth = $27 \text{ seed weight}^{0.334}$

Simulated fire response

We used the allometric equation to predict species response to simulated variation in fire intensity. Five of the experimental species are “small seeded” (seeds <2 mg) and five are “large seeded” (seeds >10 mg). Maximum emergence depth of a 2-mg seed is <40 mm according to the allometric equation and of a 10-mg seed is > 40 mm. Therefore the allometric prediction is that more seedlings of large-seeded species should emerge from simulated high fire intensities because they can emerge from greater depths than small-seeded species.

There was considerable variation in the number of seedlings emerging among species, replicates and treatments. We therefore combined all replicates and report only on total number of seedlings emerged for species and seed size classes. Small- and large-seeded species responded differently to depth of planting and the heating treatments, as predicted (Table 2, Fig. 2; the log-linear analysis showed that all three factors contributed significantly to seedling emergence at $P < 0.001$). Only 5 out of a total of 481 seedlings of the small-seeded group emerged from the 40-mm deep planting across all treatments and planting depths (Table 2). In contrast, 249 out of a total of 626 seedlings emerged from this planting level in the large-seeded group (Table 2). The ability to emerge from deeper depths influenced patterns of seedling emergence in response to heating. Very few seedlings of either the small-seeded or large-seeded group emerged from the 5-mm planting for both heat treatments. The high-heat treatment influenced small and large seeds differentially. A total of only 17 seedlings of small-seeded species emerged from simulated high fire intensities at any depth (Table 2). In contrast, 86 seedlings of large-seeded species emerged successfully in this treatment, 53 of these from the 40-mm planting depth (Table 2).

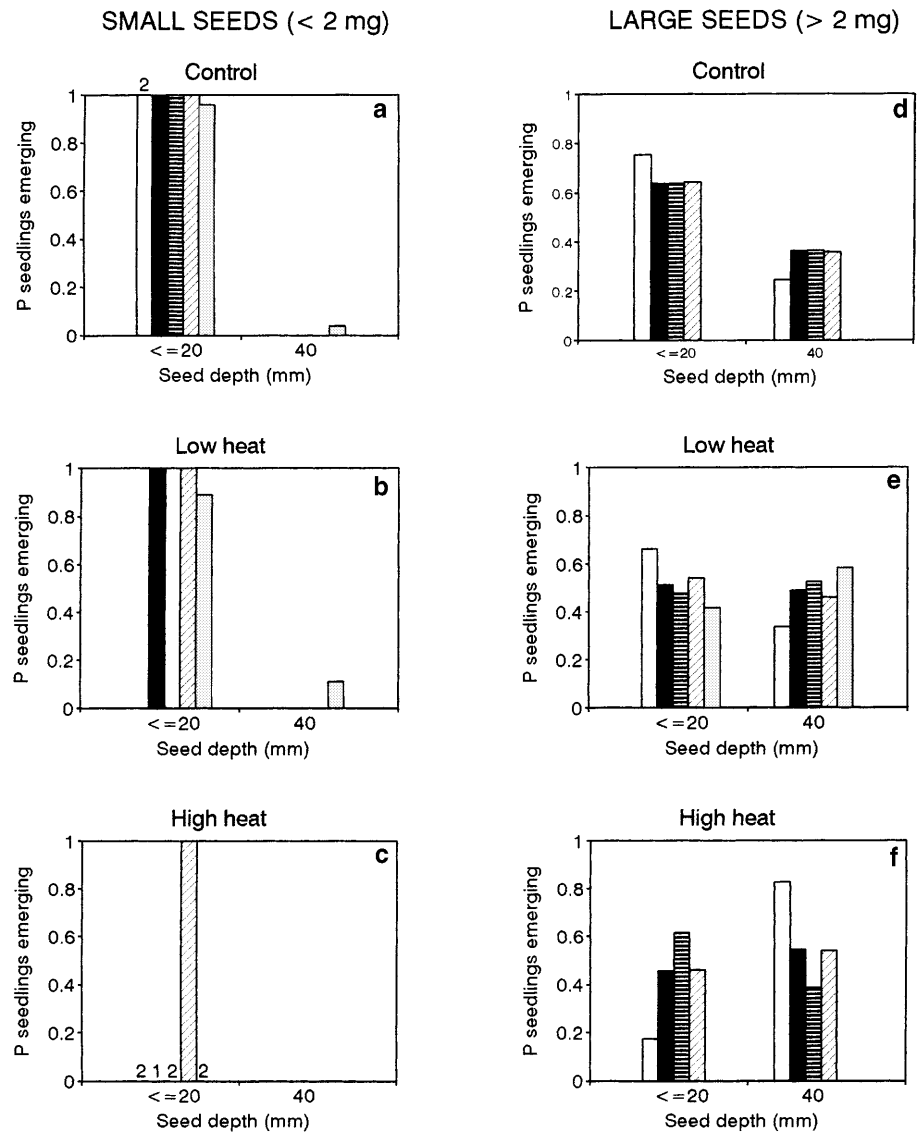
Discussion

Our results show an allometric relationship between seed size and maximum seedling emergence depth. Depth scaled to seed weight with a scaling exponent of 0.334 compared to our predicted value of 0.333. This result suggests a general scaling between seed size and seedling emergence depth that cuts across taxonomic boundaries.

Table 2 Response of small- and large-seeded fynbos species to simulated fire and depth of planting. Data are number of seedlings emerging from a total of five species in each seed size class. Small seeds were <2 mg and large seeds >10 mg. Log-linear analysis indicated that all three factors (heat treatment, planting depth, seed size) significantly influenced seedling emergence ($P < 0.001$)

Seed size	Control		Low heat		High heat	
	≤20 mm	40 mm	≤20 mm	40 mm	≤20 mm	40 mm
Small	288	1	171	4	17	0
Large	217	96	127	100	33	53

Fig. 2 The effect of heat treatments on seedling emergence in relation to seed size. Bar graphs indicate the proportion (P) of seedlings emerging above or below 20 mm planting depth for control (a,d), low (b,e) and high (c,f) heat treatments. Species are grouped into small-seeded (< 2 mg) (a–c) and large-seeded (> 10 mg) (d–f) groups on the basis of their predicted ability to emerge from 40 mm below the soil. Species are ranked from smallest to largest seed weight. Small-seeded-species are: *Lobelia valida* (open), *Erica mammosa* (solid), *Dorotheanthus bellidiformis* (horizontal lines), *Helipterum* sp. (hatched), *Coleonema pulchellum* (dotted). Large-seeded species are: *Watsonia tabularis* (open), *Wachendorfia thyrsiflora* (solid), *Phyllica pubescens* (horizontal lines), *Podalyria calyptrata* (hatched) and *Leucospermum glabrum* (dotted). When fewer than ten seedlings emerged, bars have been replaced by number of seedlings



Our assumption that a germinating seedling has to maximise tissue column width in order to push through to the soil surface seems justified, at least for this experimental set-up. If this were not so, and seedlings reached the soil by very slender columns of tissue, seed size and emergence depth would not be coupled. The fact that the scaling relationship holds across 13 families and 16 genera suggests that it is relatively insensitive to variation, phylogenetic or otherwise, in factors such as seed shape or contents. This somewhat surprising finding, implying a constant c in the allometric equation, may reflect limitations of the experimental design (limited number of planting depths) and in our ability to detect finer-scale departures from the general pattern. However, the relationship seems sufficiently robust for use as a tool in ecological prediction. The substrate is likely to have a far greater effect on seedling emergence depth than differences in seed content. The sand used in our experiments is a reasonable approximation of many fynbos soils but we expect that the scaling coefficient, c ,

but not the scaling exponent, will vary greatly for different soil types.

Our simulated fire experiment is an example of a potential application of seed size/emergence relationships to problems of ecological prediction. Like many fire-prone shrublands, fynbos recruitment varies after fires of different intensities (e.g. Bond et al. 1990). Low-intensity burns are generally favoured for prescribed burns because of their greater safety. Lightning (“natural”) burns usually occur under hot dry conditions, producing fires of higher intensity. Particularly intense fires are produced after felling of invasive pines and *Hakea* species which create unusually high fuel loads (Richardson and van Wilgen 1986). How does one predict recruitment success of the many constituent species of fynbos under varying fire intensity?

Auld (1986, 1987) analysed the effects of fire intensity on seedling recruitment in an Australian shrub. In this seminal study, he showed that recruitment varies with pattern of soil heating, lethal temperature thresholds for

seed survival, minimum temperatures required to stimulate germination in hard-seeded species, maximum emergence depth and the distribution of seeds in the soil. This is a formidable list for general ecological prediction, though progress has been made in obtaining temperature limits for some species (Jeffery et al. 1988; Auld and O'Connell 1991; Keeley 1991).

We suggest that the seed size/emergence depth relationship provides a simple general tool for predicting the limits of recruitment response to variation in fire intensity. High-intensity burns can cause deeper heat penetration into soil killing seeds to greater depths than low-intensity burns. High-intensity burns should therefore generally favour recruitment of species with large seeds relative to those with small seeds. Our simulated fire experiments support this pattern of recruitment (Table 2, Fig. 2). The utility of this prediction in nature is complicated by factors such as differential distribution of large and small seeds down the soil profile, spatial variability in fuels and fire intensity (Bradstock et al. 1992), and heterogeneity of soil conductance to heat (due, for example, to rockiness or moist patches). Many large-seeded fynbos species, including *L. glabrum* in our data set, are dispersed by ants, thereby reaching safe soil depths (Bond and Slingsby 1983). The depth distribution of smaller seeds is not known. Nevertheless it is interesting to note that intense burns in fynbos, following felling of invasive pines and *Hakea*, have caused severe reduction of plant cover and species richness with the larger-seeded species recruiting most successfully (Richardson and van Wilgen 1986; P.M. Holmes, D.M. Richardson, B.W. van Wilgen, C. Gelderblom, unpublished data).

Allometric relationships can be powerful tools for prediction in ecology. Once general patterns are identified, they are also useful for pointing to exceptions that require more detailed analysis (see Le Maitre and Midgley 1991 for a plant example). Allometric relationships imply fundamental physical constraints on plant growth (Niklas 1994). The study of physical constraints related to seed size has been comparatively neglected in recent plant literature in comparison with studies of phylogenetic constraints. Both need attention for a more complete understanding of the relationship between form and function.

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References

- Auld TD (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: fire and the transition to seedlings. *Aust J Ecol* 11:373–385
- Auld TD (1987) Population dynamics of the shrub *Acacia suaveolens* (Sm.) Willd.: survivorship throughout the life cycle, a synthesis. *Aust J Ecol* 12:139–151
- Auld TD, O'Connell MA (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Aust J Ecol* 16:53–70
- Black JN (1958) Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. *Aust J Agric Res* 9:299–318
- Bond P, Goldblatt P (1984) Plants of the Cape flora: a descriptive catalogue. *J S Afr Bot [Suppl]* 13
- Bond WJ, Slingsby P (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S Afr J Sci* 79:231–233
- Bond WJ, Le Roux D, Erntzen R (1990) Fire intensity and regeneration of myrmecochorous Proteaceae. *S Afr J Bot* 56:326–331
- Bradstock RA, Auld TD, Ellis ME, Cohn JS (1992) Soil temperatures during bushfires in semi-arid, mallee shrublands. *Aust J Ecol* 17:433–440
- Brown NAC (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytol* 122:1–9
- Grime JP, Jeffrey DW (1965) Seedling establishment in vertical gradients of sunlight. *J Ecol* 53:621–642
- Gulmon SL (1992) Patterns of seed germination in Californian serpentine grassland species. *Oecologia* 89:27–31
- Jeffery DJ, Holmes PM, Rebelo AG (1988) Effects of dry heat on seed germination in selected indigenous and alien legume species in South Africa. *S Afr J Bot* 54:28–34
- Jurado E, Westoby M (1992) Seedling growth in relation to seed size among species of arid Australia. *J Ecol* 80:407–416
- Keeley JE (1991) Seed germination and life history syndromes in the California chaparral. *Bot Rev* 57:81–116
- Keeley JE, Bond WJ (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecol* 133:153–167
- Kelly CK (1995) Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* 102:377–388
- Lee WG, Fenner M (1989) Mineral nutrition allocation in seeds and shoots of 12 *Chionochloa* species in relation to soil fertility. *J Ecol* 77:704–716
- Leishman MR, Westoby M (1994) Hypotheses on seed size: tests using the semiarid flora of western New South Wales, Australia. *Am Nat* 143:890–906
- Leishman MR, Westoby M, Jurado E (1995) Correlates of seed size variation: a comparison among five temperate floras. *J Ecol* 83:517–530
- Le Maitre DC, Midgley JM (1991) Allometric relationships between leaf and inflorescence mass in the genus *Protea* (Proteaceae): an analysis of the exceptions to the rule. *Funct Ecol* 5:476–484
- Mazer SJ (1989) Ecological, taxonomic and life history correlates of seed mass among Indiana dune angiosperms. *Ecol Monogr* 59:153–175
- Michaels HJ, Benner B, Hargerink AP, Lee TD, Rice S, Willson MF, Bertin RE (1988) Seed size variation: magnitude, distribution, and ecological correlates. *Evol Ecol* 2:157–166
- Niklas KJ (1994) *Plant allometry: the scaling of form and process*. University of Chicago Press, Chicago
- Peters RH (1983) *The ecological implications of body size*. Cambridge University Press, Cambridge
- Peterson CJ, Facelli JM (1992) Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. *Am J Bot* 79:1209–1216
- Rees M (1995) Community structure in sand dune annuals: is seed weight a key quantity? *J Ecol* 83:857–863
- Richardson DM, Wilgen BW van (1986) The effects of fire in felled *Hakea sericea* and natural fynbos and implications for weed control in mountain catchments. *S Afr For J* 139:4–14
- Salisbury EJ (1942) *The reproductive capacity of plants*. Bell, London
- Vasquez-Yanes SC, Orozco-Segovia A (1992) Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiol* 11:391–400
- Westoby M, Jurado E, Leishman M (1992) Comparative evolutionary ecology of seed size. *Trends Ecol Evol* 7:368–372