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## Comment on “A Brief History of Seed Size”

Moles *et al.* (1) showed, through a sophisticated phylogenetic analysis, that the greatest divergences in seed size among the flowering plants (the angiosperms) have been associated overwhelmingly with the differentiation between (i) shorter and taller plants and (ii) temperate and tropical plants. Although we support the general thrust of their paper, we disagree about one of the key points made in their discussion, and we draw attention to an important variable that they did not consider.

First, we reject the suggestion that the association of greater seed size with greater plant height can be understood in terms of Charnov’s life-history theory for mammals (2), according to which “offspring size is

coordinated with size at adulthood, because larger offspring offset the low survivorship to adulthood that would otherwise be a consequence of longer juvenile periods” (1). If Charnov’s idea were to be applicable to plants, we would expect to see a simple correlation between seed size and adult plant height (as is found for offspring size in mammals) rather than the “wedge-shaped relationship” commonly found in log-log plots and illustrated in Fig. 1. In this case, quantile regression reveals a slope for the upper boundary line that is about twice as steep as the slope for the lower one [i.e., slope of 95% quantile line,  $2.05 \pm 0.25$  (1 SE), versus that of 5% quantile line,  $0.97 \pm 0.50$ ]. For plants 1 to 40 m tall, maximum seed mass increases by about three orders of magnitude, whereas minimum seed mass increases by a little over one order of magnitude. One key difference between plants and higher animals in this context is that the former do not provide parental care, whereas the latter do. It is inconceivable that an elephant should produce and look after thousands of babies the size of a newborn shrew. In contrast, many hundreds of species of plant that are large at maturity produce huge numbers of tiny seeds that develop into offspring with a very low chance of survival. The enormous strangling figs of tropical rainforests provide a clear example (3, 4). A more

parsimonious basis for the overall increase in seed size with adult plant height is that the range of feasible seed sizes increases dramatically with whole-plant size.

Second, Moles *et al.* did not mention the possibility that seed size may be constrained biomechanically, following the correlations among inflorescence size, twig diameter, and leaf area reflected in “Comer’s

Rules” (5–7). Such effects may negate the usual correlation between seed size and plant height. For example, in the tribe Shoreae of the family Dipterocarpaceae (8, 9), there are strong scaling relations between nut volume and twig cross-sectional area (CSA) ( $r = 0.286$ ,  $P < 0.001$ ) (Fig. 2A), and between nut volume and individual leaf area ( $r = 0.546$ ,  $P < 0.0001$ ) (Fig. 2B). In contrast, nut volume is not significantly different between species rated as small, small-medium, medium, medium-large, large, or very large, where “size” is an amalgam of mature tree height and maximum girth (nut volume was log-transformed; analysis of variance,  $F_{5,142} = 1.55$ ,  $P = 0.18$ ). Biomechanical explanations are likely to apply only when there is one seed per fruit, as in the Dipterocarpaceae, and when there is little flexibility in number of fruits per inflorescence, but this scenario is likely to be found in a number of clades in tropical rainforests.

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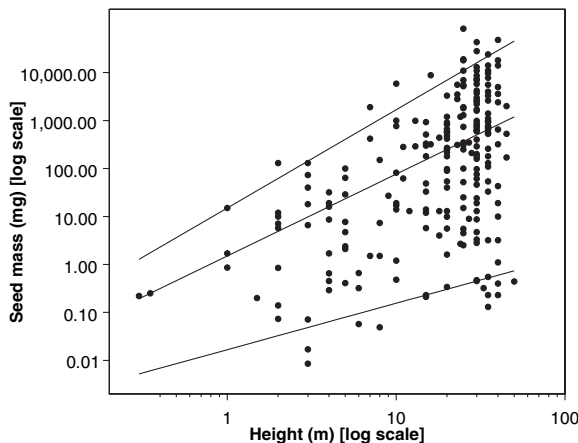


Fig. 1. The relation between mean seed dry mass (3, 4) and mature plant height (10) for 226 species in tropical lowland rainforest in Australia; the median line and 95% and 5% quantile lines were fitted by quantile regression (11) implemented in R.

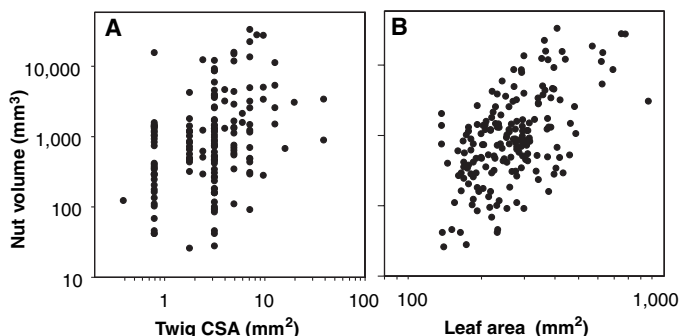


Fig. 2. The relation between nut volume and (A) twig cross-sectional area (CSA) and (B) individual leaf area in 148 species of Shoreae in rainforests between the Malay Peninsula and Papua New Guinea (9, 12). Nuts were assumed to be spheroids and leaves, ellipses; volumes and areas were estimated from mean length and width measurements.

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