Seed mass of Indiana Dune genera and families: taxonomic and ecological correlates

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Summary
Several surveys have documented an association among species between habitat type and seed mass, suggesting that habitat attributes impose a direct selective force on seed mass. Previous comparative surveys, however, have not controlled for the statistical effects of shared phylogenetic history (at the genus or family level) and life form when evaluating the relationship between habitat and seed mass. This study of the Indiana Dunes angiosperm flora provides statistical 'control' of genus and family membership by: (i) partitioning out the statistical effect of genus membership prior to measuring the effect of habitat on seed mass, and (ii) seeking an association between habitat and seed mass within eight genera (206 species) and ten families (366 species). To measure the associations between ecological factors, taxonomic membership and seed mass, I examined life form, phenological schedules and seed mass among species in 8 genera distributed among 13 habitat types (assigned to 1 of 4 categories of inferred water and light availability). One-way ANOVAs indicated that genus, life form, habitat, water/light category, the onset of flowering and the duration of flowering accounted for 71%, 51%, 10%, 4%, 14% and 14% of the variance in seed mass, respectively. However, multi-factor ANOVAs measured the variance in seed mass accounted for by each variable independently of the others: only genus explained a significant proportion (11%). Genus membership is strongly associated with the other ecological factors, accounting for the difference between one-way and multi-factor ANOVAs. Within the ecologically widespread genera and families of this study, there was no significant association between water/light category and seed mass, even though this association can be detected across taxa. Among congeners and confamilials, interspecific variation in seed mass (measured as the coefficient of variation) was as high within habitat types as among them, suggesting that habitats do not provide upper limits to the range of seed mass exhibited by the species within them. A previous study of 648 Indiana Dune species showed that species segregate among habitats on the basis of seed size; large-seeded species tend to occupy closed habitats and small-seeded species tend to inhabit open habitats. This segregation creates the ecologically meaningful observation that low-light habitats support larger-seeded species than high-light habitats, even though this pattern cannot be detected independently of taxonomic membership. Generalist taxa may occupy a wide range of habitats for reasons other than their seed size. If this is a common feature of ecological generalists, it may not be possible to detect an association between habitat and seed size independently of taxonomic membership.

Keywords: Character convergence; community ecology; comparative biology; Indiana Dunes; life history variation; phenology; phylogenetic constraints; seed mass variation; seed size

Introduction
Seed mass is a character that exhibits tremendous variation both within and among species and is associated with numerous life history characteristics and fitness components. It can influence dispersal distance, probability of predation, germination rate, growth rate and seedling survivorship (Howe and Richter, 1982; Fenner, 1983; Gross, 1984; Hendrix, 1984; Jordano,
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1984; Stanton, 1984, 1985; Weller, 1985; Mazer, 1987; for additional references see Mazer, 1989). Because of the notable phenotypic variation in seed mass, the ease with which it can be measured, and its clear ecological significance, seed mass is a character that has been the focus of numerous evolutionary studies at two levels: the population and the community. Evolutionary ecologists have evaluated the evolutionary significance of seed mass in wild and domesticated species using methods from two disciplines: population ecology and comparative biology.

The first method uses demographic and quantitative genetic techniques to estimate the direction and intensity of natural selection on seed mass (Venable, 1984). The potential for selection to cause evolutionary change in seed mass (if heritable) is deduced from the statistical effect of the mass of sown seeds on some measure of individual fitness. Most intraspecific studies, however, do not include heritability estimates of seed mass under diverse field conditions; this shortcoming limits their predictive value. In addition, most within-species studies are conducted in one population, for one or a few generations, and under a limited range of environmental conditions. This makes it difficult to observe or to predict accurately long-term evolutionary change under natural conditions or to generate results that apply to most species. Nevertheless, phenotypic correlations between seed size and performance reported for a variety of species agree: under competitive conditions, large seed mass is often associated with enhanced ability to emerge from deep burial, higher seedling survivorship and relative growth rate, or higher individual fitness (see Mazer, 1987, 1989, for references demonstrating correlations between seed mass and performance). These studies suggest that natural selection can operate to mold seed mass within wild populations. In particular, under conditions in which resources available to a germinating seed are highly limited, as in low-light or arid habitats, we expect large seed size to be favored.

Another way to examine the role of natural selection on seed mass is to seek its long-term results by using a comparative approach (Salisbury, 1942, 1974; Baker, 1972; Levin, 1974; Stebbins, 1976; Hayashi, 1977; Rockwood, 1984; Foster and Janson, 1985; Foster, 1986; Hodgson and Mackey, 1986; Bradshaw, 1987; Thompson, 1987; Michaels, et al., 1988; Mazer, 1989). Two distinct processes may result in an association between habitat type and seed mass among species: (i) in situ evolution, and (ii) segregation of species among habitats on the basis of seed size. First, if an environmental factor such as water or light availability imposes a strong selective force on seed mass, then co-occurring species would all experience this selective force. All else being equal, we would expect that co-occurring species (or species that occupy the same type of habitat) ought to converge on seed mass over evolutionary time, although such convergence among sympatric species might be opposed by selection for resource partitioning. Second, if different habitats allow the successful colonization only of species that exhibit a limited range of seed masses, then species will segregate among habitats according to seed mass, generating an association among species between habitat and seed mass. Convergence among co-occurring species due to either of these processes may not be precise, as not all co-occurring species have the same germination behavior, life history, or other attributes that may be associated with seed mass (Grubb, 1977; Silvertown, 1981; Mazer, 1989).

Previous interspecific comparisons of seed mass have established an association between habitat and seed mass; open or mesic habitats tend to support species with smaller seeds than low-light or arid habitats (Salisbury, 1942, 1974; Baker, 1972; Foster and Janson, 1985; Mazer, 1989). In his studies of coastal plant communities in Britain, Salisbury was the first to document strong associations between seed size and habitat, but he did not offer statistical tests of the significance of his observations. Baker analysed data from about 3000 species in a wide range of plant communities throughout California. He conducted one-way ANOVAS to detect significant differences among plant communities (e.g. coastal dunes, marshes, and alpine forests), and