

**Seed Size, Life Span, and Germination Date as Coadapted Features of Plant Life History**



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## SEED SIZE, LIFE SPAN, AND GERMINATION DATE AS COADAPTED FEATURES OF PLANT LIFE HISTORY

Seed weights vary between species over a range of 10 orders of magnitude, but mean seed weight within species is one of the least plastic components of plant structure (Harper et al. 1970). Seed size appears to be so finely tuned to the ecological life history of species that it is generally conserved at the expense of seed number when environmental conditions necessitate a reduction in the reproductive output of a plant (e.g., Harper and Gajic 1961). Two major studies of seed weight in relation to environmental conditions have shown shade and drought to be the most important correlates of seed size in the native floras of Britain and California, respectively (Salisbury 1942; Baker 1972). Seed size and lifespan are also correlated in the Californian flora but until now such a correlation has been reported absent from Britain (Salisbury 1942; Hart 1977). I show here that such a correlation does indeed exist when the effect of habitat on seed size is taken into account and I also report the first statistical observation of a positive correlation between seed size and germination date. All disseminules (in some cases actually fruits) are defined as "seeds," following the convention of previous authors (Salisbury 1942; Baker 1972) and to allow comparison with other studies.

By confining an analysis of seed size to the flora of a single habitat it is possible to uncover ecological correlates of this variable which would otherwise be masked by the strong effect of habitat differences on seed size. Calcareous grasslands (C. G.) offer a greater number of species for ecological comparison than any other habitat in the British Isles (Ratcliffe 1977). Mean seed weights of 75 dicot species obtained by weighing samples collected from this habitat in southern England (Silvertown 1979) and from published measurements (Salisbury 1942; Grubb 1976) show that biennials and perennials have similar ranges of seed weight while annuals have significantly lighter seeds than longer-lived herbs (Wilcoxon two-sample test,  $P < .01$ ; fig. 1).

The low seed weight of annuals, in association with their characteristically greater reproductive effort (Harper 1977) maximizes seed number and opportunities for colonizing gaps in the vegetation by dispersal (Baker 1974; Rabinowitz 1978). Small size also favors the chances of a seed being incorporated in the pool of buried seed (Grime 1979)—an important strategy for persistence in species which have a short lifespan as reproducing individuals (Cohen 1966; Roberts and Feast 1973). The importance of habitat in determining seed size within a group of species of similar life span is emphasized by a comparison of the seed weights of annual arable weeds with the annuals of calcareous grassland in figure 1. The C. G. annuals are significantly lighter than the arable weeds ( $P < .01$ ; there is no significant difference in seed weights between C. G. biennials, C. G. perennials, and arable annuals).

Germination dates for C. G. plants were obtained by direct observation of permanent quadrats during a study of this habitat, and from literature sources

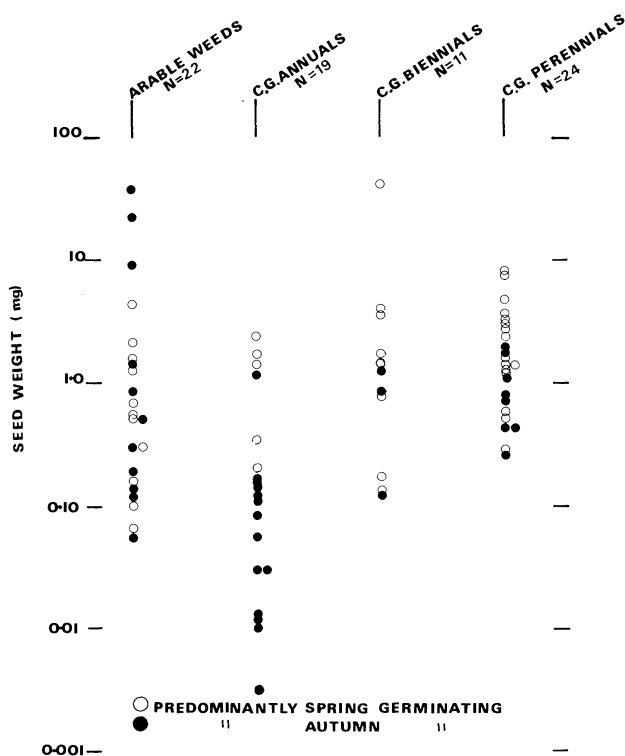


FIG. 1.—The ranked seed weights of 22 annual weeds of neutral and calcareous arable habitats and of 54 plants of calcareous grassland (C. G.) in Britain. Open circles = species which germinate predominantly in the spring; closed circles = species which germinate predominantly in the autumn (see Appendix). Data on seed weights of an additional 21 C. G. species, for which germination date is unknown, were used in a comparison of life span, habitat, and seed weight.

cited in the report of that study (Silvertown 1979). The germination dates of arable weeds are taken from the quantitative investigations of Brenchley and Warington (1930).

Within the C. G. habitat a statistically significant association between germination date (autumn/spring) and seed weight (fig. 1) occurs independently in both annual and longer-lived species groups. Small-seeded species tend to be autumn germinators ( $P < .001$  and  $P < .01$  for annuals and longer-lived species, respectively). No association between germination date and seed size is found among annual arable weeds (fig. 1). This suggests that the prevalence of autumn germination among C. G. annuals is a consequence of their characteristically small seed size rather than a unique characteristic of the annual life history.

Both the correlations between seed size and life span and between seed size and germination date are the product of two possible processes of selection: (1) evolution within habitats resulting from the selective elimination of certain seed phenotypes (e.g., Putwain et al., in press) and (2) ecological displacement of

certain species from habitats where seed size is a constraint on successful colonization or establishment. The second of these processes must have operated on the distribution of adventives of the Californian flora which show similar correlations between seed weight and habitat to those of native species (Baker 1972).

British C. G. habitats are anthropogenic, and their flora is also a relatively recent assemblage of species which were originally endemics of sand dunes and other naturally open habitats. This suggests that more weight should be given to ecological displacement than to natural selection as a possible explanation of the correlation between seed weight and germination date in the C. G. flora. In other words, ecological constraints may exclude large-seeded autumn germinators and small-seeded spring germinators from the C. G. habitat. Three seasonally important factors may account for such constraints. (1) The growth rate of established plants in British grasslands reaches a nadir in the autumn (Morris and Thomas 1972; Al-Mufti et al. 1977). (2) Winter conditions are a significant mortality factor in autumn-germinating seedling populations (e.g., Arthur et al. 1973; Silvertown 1979). (3) As a result of (1), the growth of established plants must close small vegetation gaps more rapidly, and hence must interfere with seedling survival more strongly in the spring than in the autumn.

Small seeds, with small reserves of stored food, may gain a relative release from interference by germinating in the autumn, but suffer winter mortality. Large-seeded species are more tolerant of shading and would hence benefit less from autumn germination, while suffering the same penalty of winter mortality as small-seeded species germinating at this time. The implications of this hypothesis are that small-seeded species of C. G. habitats are limited to conditions of low interference and large-seeded ones to conditions of more intense interference from neighboring plants. These predictions may be tested by demographic and experimental techniques.

The timing of interference between crops and weeds in arable habitats depends on the timing of soil disturbance and the emergence of the crop, rather than upon the seasonal changes in growth rate which occur in C. G. The correlation between seed weight and germination date found among C. G. annuals is therefore absent from the arable weed flora. Nevertheless, the process of ecological displacement operates strongly, but independent of seed weight, in arable habitats promoting those species whose germination phenology coincides with current cultivation practices at a site (Brenchley and Warington 1930; Roberts and Ricketts 1979).

Although the importance of ecological constraints is emphasized here, these same constraints, when operating in a consistent manner over a sufficiently long period of time, may also give rise to evolutionary changes in germination phenology. Seed size, life span, and germination date may therefore be regarded as coadapted features of plant life history.

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## APPENDIX

SEVENTY-SIX SPECIES FOR WHICH GERMINATION DATE IS KNOWN  
(ranked in descending order of seed weight within each classification)

Arable weeds: *Scandix pecten-veneris*, *Galium aparine*, *G. tricornis*, *Polygonum convolvulus*, *Atriplex patula*, *Aethusa cynapium*, *Torilis arvensis*, *Medicago lupulina*, *Myosotis arvensis*, *Polygonum aviculare*, *Anagalis arvensis*, *Euphorbia exigua*, *Stellaria media*, *Legousia hybrida*, *Matricaria inodora*, *Aphanes arvensis*, *Senecio vulgaris*, *Papaver rhoeas*, *Veronica arvensis*, *Odontites verna*, *Chaenorhinum minus*, *Arenaria serpyllifolia*

Calcareous grassland annuals: *Rhinanthus minor*, *Iberis amara*, *Medicago lupulina*, *Ajuga chamaepitys*, *Trifolium dubium*, *Euphrasia* sp., *Aphanes arvensis*, *Cardamine hirsuta*, *Aira carophylea*, *Veronica arvensis*, *Myosotis ramosissima*, *Erigeron acer*, *Arenaria serpyllifolia*, *Arabidopsis thaliana*, *Cerastium semidecandrum*, *Centaureum erythrea*, *Saxifraga tridactylites*, *Blackstonia perfoliata*, *Erophila verna*

C. G. biennials: *Cynoglossum officinale*, *Pastinaca sativa*, *Echium vulgare*, *Carlina vulgaris*, *Daucus carota*, *Teucrium botrys*, *Reseda lutea*, *Hyoscyamus niger*, *Linum catharticum*, *Gentianella amarella*, *G. anglica*

C. G. perennials: *Centaurea scabiosa*, *Ononis repens*, *Poterium sanguisorba*, *Centaurea nigra*, *Anthyllis vulneraria*, *Hippocrepis comosa*, *Cirsium acaulon*, *Scabiosa columbaria*, *Ranunculus bulbosus*, *Asperula cynanchica*, *Pimpinella saxifraga*, *Helianthemum chamaecistus*, *Polygala vulgaris*, *Primula veris*, *Galium mollugo*, *Astragalus danicus*, *Leontodon hispidus*, *Filipendula vulgaris*, *Plantago media*, *Silene nutans*, *Chrysanthemum leucanthemum*, *Thymus drucei*, *Phyteuma tenerum*, *Hieracium pilosella*

Orchids, whose seedlings depend crucially on a fungal symbiont for survival are not included in this analysis.

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