

## WHY ARE BIENNIALS SOMETIMES NOT SO FEW?

Hart (1977) has drawn attention to the rarity of the biennial life history among plants. In a total of 14,500 species in the North American flora a mere 200 (1.4%) are biennial while 3,155 (21.3%) are annual. These data, compiled on a continental basis, illustrate an overall trend which obscures the more complex picture of plant life history that emerges when plant families are examined individually.

To illustrate this point I have tabulated the data on lifespan for European species of Umbelliferae, Compositae, Gramineae, and Cyperaceae (table 1). Eleven percent of umbellifers and 5% of composites in the European flora are described as biennial in *Flora Europaea* (Tutin et al. 1964-1980). "Biennial" is in fact an unsatisfactory term since demographic studies have often shown that some individuals in biennial populations flower more than 2 yr after germination. Moreover, in other biennial populations, plants are facultatively annual. If all species which exhibit the monocarpic perennial life history to some degree are summed, we find that 25% of European umbellifers and 9% of composites fall into this category. Furthermore 30% of genera in the Umbelliferae and 20% of genera in the Compositae contain species with monocarpic perennial populations. Thus this type of life history, although rare in the angiosperms as a whole, has evolved many times in the European members of these particular families. The frequency of monocarpic perennials in these two families contrasts with the virtual absence of this life history in the European Gramineae and Cyperaceae (table 1). Table 1 shows that the frequency of the monocarpic perennial life history in the four families is not correlated with the frequency of (monocarpic) annuals in each family. This paper modifies the argument of Hart (1977) and advances a new hypothesis to explain why biennials are relatively common in some families and virtually absent in others.

Following Charnov and Schaffer (1973), Hart (1977) used the following model to calculate the rate of increase,  $\lambda$ , for annuals, biennials, and perennials. This model has since been modified to take account of the cost of sex (Waller and Green 1981) but the relevance of this refinement depends upon various contingencies such as breeding system which complicate the present argument unnecessarily (Charnov et al. 1981). Let  $C_1$  = fraction of plants surviving from the seed stage until the end of the first growing season (when annual plants flower and die).  $C_2$  = the fraction of plants beginning another (second or subsequent) year's growth, which survive to the end of that year.  $S_a$ ,  $S_b$ , and  $S_p$  = the number of seeds produced per plant for annuals, biennials, and perennials, respectively. Then the rates of increase for plants with the three types of life history are:

$$\lambda_a = C_1 S_a \quad (1)$$

$$\lambda_b = (C_1 C_2 S_b)^{1/2} \quad (2)$$

$$\lambda_p = C_2 + C_1 S_p \quad (3)$$

TABLE I  
LIFE HISTORY OF EUROPEAN SPECIES IN FOUR PLANT FAMILIES

Family	No. of European Genera	No. of Genera in Sample	No. of Species in Sample	1 No. An (%)	2 No. An/Bi (%)	3 No. Bi (%)	4 No. Bi/Pt (%)	5 No. Pt (%)	No. 2+3+4 (%)	No. of Genera Containing 2, 3 or 4 (%)
Umbelliferae	110	106	303	65 (21)	18 (6)	32 (11)	23 (8)	165 (54)	73 (25)	32 (30)
Compositae	181	179	1,796	219 (12)	41 (2)	87 (5)	30 (2)	1,419 (79)	158 (9)	36* (20)
Gramineae	155	151†	776	214 (28)	9 (1)	0 (0)	1 (0)	552 (71)	10 (1)	5† (3)
Cyperaceae	12	12	190	20 (10)	1 (1)	0 (0)	0 (0)	169 (89)	1 (1)	1 (8)

NOTE.—An = annual; Bi = biennial; Pt = perennial.

\* Includes the genus *Centaurea* which is omitted from the species total because of the lack of precise information on which *Centaurea* species are biennial.

† Includes the genus *Bromus* which is omitted from the species total.

‡ Three of the genera omitted from the total European sample are introduced bamboos which include long-lived monocarpic perennials. These are discussed in text.

When post first-year survivorship ( $C_2$ ) is low, annuals and perennials have similar rates of increase. When the ratio  $C_1/C_2$  is low and  $S_a = S_p$ , perennials are favored.

According to this model when  $S_b = S_p$  and either  $C_1$  or  $C_2$  is low, biennials will have a lower rate of increase than one or both of the other types of plant. Biennials may compensate for this disadvantage by increasing their seed production. Even under the optimum conditions for biennials, when values of  $C_1$  and  $C_2$  are both moderate, a biennial must produce four times the number of seeds produced by a perennial and twice those produced by an annual to gain a rate of increase which is higher than either of the other types of plant. Hart argued that the relatively low rate of increase for biennials shown in this model relative to annuals and perennials explained the paucity of biennials among angiosperms. Figures for seed production compiled from Salisbury (1942) bear out Hart's argument and show that biennials produce four to five times the number of seeds per plant produced by annuals or perennials (Hart 1977).

If the argument set out above is correct, why should monocarpic perennials have evolved in as many as 30% of umbellifer genera and 20% of composites in Europe? Hart's model takes into account changes in survivorship between the first and subsequent years of a plant's life but it does not allow for the fact that the sites of disturbance typically occupied by biennials deteriorate with time. Again drawing on Salisbury's (1942) data, Hart showed that biennials are most common in intermittent habitats such as woodland gaps. Grubb (1976) has described the close association of grassland biennials with temporary gaps.

There is good field evidence that the first-year survival ( $C_1$ ) of seedlings declines in the grassland biennial *Verbascum thapsus* because gaps where they appear are recolonized and filled in (Gross 1980). Declining seedling survivorship and recruitment in successive cohorts of the colonizing grasses *Poa annua* and *Corynephoros canescens* have also been observed as fresh areas of disturbance are progressively occupied (Law 1981; Symonides 1979).

Hart's original model may be modified to take account of the temporary nature of biennial colonization sites. For the simplest case, but one which is quite realistic, envisage a gap which is completely closed to successful colonization by new seedlings after 1 yr. If new gaps appear on average at intervals of  $x$  years and seeds remain dormant in the soil with zero mortality during these intervals, then the rate of increase for annuals and biennials is:

$$\lambda_a = (C_1 S_a)^{1/x} \quad (4)$$

$$\lambda_b = (C_1 C_2 S_b)^{1/x+1}. \quad (5)$$

The advantage of annuals over biennials when  $S_a = S_b$  can now be offset by relatively smaller increases in  $S_b$  than was the case in the original model. Perennials do not generally require gaps in order to produce seeds (although they may require gaps for successful seedling survival) and in this type of model their rate of increase will remain as in equation (3), though the realism of this type of model for calculating rates of increase in perennials is questionable.

According to this modification of Hart's model, annuals and biennials colonizing temporary gaps in vegetation share more similar rates of increase than in sites

where recruitment is possible every year. Annuals will still be favored over biennials and perennials in permanently open habitats where  $C_2$  is likely to be high and perennials will still be favored in closed habitats where annuals and biennials are unable to persist as reproducing individuals. This "site-deterioration model" potentially explains the relative abundance of monocarpic perennials in the European Umbelliferae and Compositae.

Three other factors may reinforce the evolution of the monocarpic perennial life history. (1) Delayed flowering allows a plant to accumulate the resources necessary for a single very large reproductive event. This concentration of reproductive effort may have advantages in attracting pollinators (Schaffer and Schaffer 1979) or in swamping seed predators (Silvertown 1980). The importance of these two phenomena among herbs is not known at present.

2) If the survival of nonflowering rosettes is higher than that of dormant seeds in the soil, a monocarpic plant which delays flowering and then synchronizes reproduction with the appearance of new gaps may leave more progeny than an annual which depends upon a seed pool or widespread seed dispersal in order to colonize gaps. Prescott chervil *Chaerophyllum prescottii* is a monocarpic umbellifer of forest steppe in the USSR which behaves in this way. It has no seed pool in the soil but produces a dormant tuber which is stimulated into growth and flowering by soil disturbance (Rabotnov 1964). This is rare but probably not unique behavior among monocarpic perennials.

3) The monocarpic perennial habit may be an evolutionary stable strategy preventing the spread of annual "mutants" within a population. Populations of monocarpic perennials often seem to be composed of single cohorts of uniform age, possibly reflecting intermittent recruitment from temporary germination sites. When monocarpic perennials do colonize a vegetation gap they frequently form a dense ground cover of rosettes in the second year which would prevent new seedlings establishing there successfully in that season. Thus the seeds produced by a mutant annual genotype in a monocarpic perennial population are unlikely to survive to reproduce themselves. Those seeds or suppressed seedlings which do survive the period of a year while the perennials flower and die will have lost the advantage of early reproduction which the annual habit confers. This hypothesis, which depends to a large extent upon synchronous reproduction and death among monocarpic perennials in the same population, is at present being tested in the field. It is similar to the intercohort competition model for synchronous periodical reproduction in cicadas, produced by Hoppensteadt and Keller (1976).

We now come to the most interesting question of all. Why are biennials so much more common among composites and umbellifers than among grasses or sedges? I advance the hypothesis that this difference is the result of evolutionary constraints determined by plant architecture. By Hart's model, in either its original form or in the site-deterioration version, biennials must produce more seeds than either annuals or perennials. The number of seeds an umbellifer or a composite produces is regulated by components of yield which are subunits of the plant's vertical structure. A carrot for instance has a divaricating stem which may support anything from one to four orders of umbels, so that the total number of seeds a

carrot plant produces increases geometrically with each additional order of branching. Studies of the regulation of seed yield in goldenrods show that these plants also adjust or increase seed production by varying the number of branches per stem, capitula per branch, or seeds per capitulum (Primack et al. 1981). Stems, which are subunits of horizontal structure, appear to be unimportant in the regulation of seed number in composites. In these two families of plants seed number increases allometrically with the size of an individual stem. Seed number increases by simple iteration of vertical architectural units. Therefore the step toward the biennial life history is a simple allometric one.

The architecture of grasses and sedges makes increased seed production a quite different affair in these families. By contrast with the umbellifers and composites, grasses regulate seed yield by variation in tiller number, a component of horizontal structure. Changes in components of seed yield such as panicle size and number of spikelets per panicle appear to affect total seed yield per plant much less than changes in tiller number (e.g., Clements et al. 1929; Wilson et al. 1981). Cyperaceae, having the same basic architecture as grasses, probably regulate seed yield in the same way, though I can find no data. The consequence of this type of architecture is that a member of either family which increases its seed production is likely to do so by ramification of its horizontal structure. While increased seed production seems to be a necessity for the biennial habit to evolve, the means by which it is achieved in the grasses and sedges is also a step toward perennation. A plant which produces additional tillers will probably gain a greater advantage by continuing the process of horizontal ramification and becoming a polycarpic perennial than by stopping half-way as a short-lived monocarpic perennial. In circumstances where monocarpy itself is favored by the benefits of "big-bang" reproduction (1, above) the largest possible concentration of reproductive output can be achieved by prolonging the pre-reproductive period during which clonal spread may occur. Thus in the monocarpic bamboos which are the only major group of monocarpic perennial grasses, pre-reproductive periods of 20 yr are commonplace and the record is 120 yr (Janzen 1976).

Another anatomical difference between the Gramineae and Cyperaceae and the Umbelliferae and Compositae may be important in determining the relative success of the "biennial" habit in the contrasting families. The large bout of reproduction necessary in biennials for them to raise their fecundity to at least four times that of an equivalent annual demands a storage organ in which the necessary resources can be accumulated during the prolonged pre-reproductive phase. Biennials in the Compositae and Umbelliferae generally use their tap roots for this purpose but grasses and sedges have no equivalent storage organ. It is true that rhizomes which are very common among grasses and sedges may act as storage organs, but these carry vegetative buds and are mainly organs of perennation. So, in this aspect of morphology, too, a necessary condition of the biennial habit also turns out to be a feature of perennation in the grasses and sedges.

It seems that there are architectural constraints on the evolution of the biennial life history among grasses and sedges which operate in addition to the disadvantages of the habit which affect all plants. Ignorance of the former type of constraint appears to have led to an overestimate of the importance of the latter constraint in explaining why, in the angiosperms as a whole, biennials are so few.

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## LITERATURE CITED

- Charnov, E. L., J. J. Bull, and S. T. Mitchell-Olds. 1981. A note on sex and life histories. *Am. Nat.* 117:814-818.
- Charnov, E. L., and W. M. Schaffer. 1973. Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* 107:791-792.
- Clements, F. E., J. E. Weaver, and G. C. Hanson. 1929. Competition in cultivated crops. *Carnegie Inst. Wash. Publ.* 398:202-233.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old field in Michigan: experiments on the effects of vegetation. *J. Ecol.* 68:919-927.
- Grubb, P. J. 1976. A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biol. Conserv.* 10:53-76.
- Hart, R. 1977. Why are biennials so few? *Am. Nat.* 111:792-799.
- Hoppensteadt, F. C., and J. B. Keller. 1976. Synchronization of periodical cicada emergences. *Science* 194:335-337.
- Janzen, D. H. 1976. Why bamboos wait so long to flower. *Annu. Rev. Ecol. Syst.* 7:347-391.
- Law, R. 1981. The dynamics of a colonizing population of *Poa annua*. *Ecology* 62:1267-1277.
- Primack, R. B., A. R. Rittenhouse, and P. V. August. 1981. Components of reproductive effort and yield in goldenrods. *Am. J. Bot.* 68:855-858.
- Rabotnov, T. A. 1964. The biology of monocarp perennial meadow plants. *Bull. Moscow Soc. Nat.* 69:57-66. Russian Translation Service 8739, British Library.
- Salisbury, E. J. 1942. *The reproductive capacity of plants*. Bell, London.
- Schaffer, W. M., and M. V. Schaffer. 1979. The adaptive significance of variation in reproductive habit in the Agavaceae II: pollinator foraging behaviour and selection for increased reproductive expenditure. *Ecology* 60:1051-1069.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* 14:235-250.
- Symonides, E. 1979. The structure and population dynamics of psammophytes of inland dunes. I. populations of initial stages. *Ekol. Pol.* 27:3-37.
- Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, and D. A. Webb, eds. 1964-1980. *Flora Europaea*. Cambridge University Press, Cambridge.
- Waller, D. M., and D. Green. 1981. Implications of sex for the analysis of life histories. *Am. Nat.* 117:810-813.
- Wilson, A. M., R. L. Cuany, J. G. Fraser, and W. R. Oaks. 1981. Relationships among components of seed yield in blue grama. *Agron. J.* 73:1058-1062.

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