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0521373506 - Fruit and Seed Production: Aspects of Development, Environmental Physiology and Ecology

Edited by C. Marshall and J. Grace

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H. W. WOOLHOUSE

Plant reproductive biology: an overview

Biological principles of fruit and seed production

The life cycles of flowering plants can be generalized, with a few exceptions in which sexual reproductive capacity has apparently been lost to clonal vegetative reproduction or distorted by such devices as apomixis (Fig. 1). Within this simple framework, however, the variation is enormous: the duration of the life cycle may range from days to centuries, and the proportion of the biomass invested in reproduction varies with species, genotype, age of the plant and environmental conditions (Baker, 1972). For a given reproductive investment, species may trade off large numbers of tiny seeds from a single flower, as in many orchids, as against a few bulky seeds with large reserves from a large number of flowers, as in the pome fruits. There is abundant evidence that the evolution of these details of plant reproductive biology has been influenced by a wide variety of physical factors such as availability of nutrients, light and water (Mooney, 1972) and biological factors such as the nature, availability and energetics of pollinators (Heinrich, 1975), the agents of fruit and seed dispersal (Gautier-Hion *et al.*, 1985) and the activity of pathogens and predators (Janzen, 1977). One may trace in the literature of plant reproductive biology a process of gradual description and elucidation of factors which may influence reproductive behaviour (Lloyd, 1980; Lloyd, Webb & Primack, 1980; Sutherland, 1986; Primack, 1987; Stephenson, Devlin & Horton 1988) and a steadily increasing sophistication in the 'telling of adaptive stories' which purport to 'explain' observed behaviour (Gould & Lewontin, 1979).

The search for generalizations in the mass of observational data is exemplified in studies such as those of Sutherland (1986) who analysed fruit set values in 447 species, relating them to compatibility, breeding system, life form, latitude, type of fruit and type of pollination. One could envisage extending the list of species by orders of magnitude and the number of parameters to be considered many-fold, but it seems

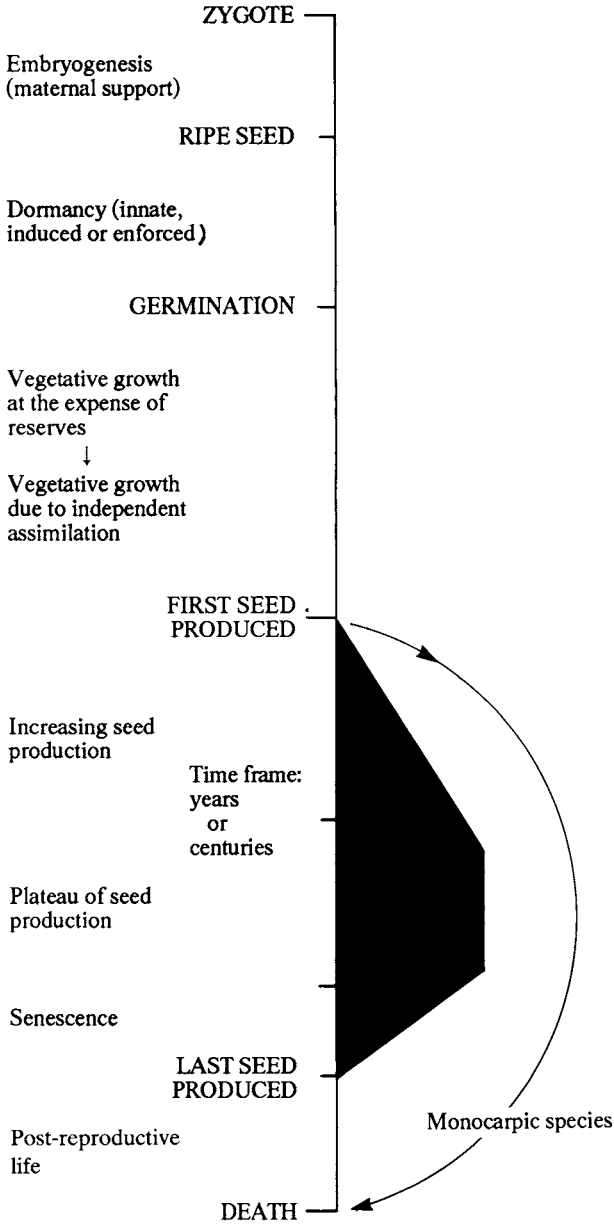


Fig. 1. Diagram of the life cycle of a higher plant.

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doubtful to the present author that there is any guarantee of significant generalizations emerging from this approach.

Reproductive effort

In an attempt to push the study of plant reproductive biology into a more quantitative and formal mould in a theoretical sense, several authors have sought to apply the ideas of MacArthur (1962) concerning r and K selection. At the heart of this approach is the notion that species or sub-specific taxa can be compared with respect to their allocation of resources to reproductive effort under density-dependent and density-independent conditions of mortality. Populations in habitats which give rise to high density-independent mortality (r -strategists) will be selectively favoured to allocate more of their resources to reproductive activities, which will prejudice their capacity to reproduce under crowded conditions. By contrast, populations in habitats which generate high density-dependent regulation (K -strategists) will be selectively favoured to allocate more of their resources to non-reproductive growth and development, at the expense of their capacity to reproduce in environments where there is a high level of density-independent mortality. Examples of this approach with plants are to be found in Gadgil & Solbrig (1972) for *Taraxacum*; Abrahamson & Gadgil (1973) on *Solidago*; and the series of papers on *Plantago* from Antonovics' group (cf. Primack & Antonovics, 1982). Studies such as these serve to provide some description of the ways in which populations respond under a variety of conditions. One intrinsic weakness of this approach is that it encourages the generation of comparative data and the extent to which these offer the prospect of any deeper understanding of the mechanisms involved tends to be ignored.

At the root of the practical problems which are soon encountered in applying theories of reproductive effort is the problem of definitions. Over the past twenty years ecologists and evolutionary biologists have approached the problem of reproductive effort from the standpoint that there must be a trade-off between the consumption of resources by an individual to meet its current reproductive activity and the use of resources for its own survival in order to achieve future reproduction. These notions lead in several directions: (i) intensive mathematical modelling by population geneticists to represent this trade-off in terms of fitness sets (see, for example, Stearns, 1976; Goodman, 1979; (ii) detailed considerations of the allocation of resources to the sub-sets of attributes of seed production, i.e. how many, how big and then how much for dispersal, dormancy, establishment, predator protection and environmental protection, etc. (for a review of this approach, see Foster, 1986).

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Reproductive effort and the question of currency

Bazzaz & Reekie (1985), in a discerning review of work to date on reproductive effort in plants, express serious doubts as to whether the theoretical predictions alluded to above are borne out for a variety of plants in a variety of environments. They lay emphasis on the practicalities of measuring reproductive effort: as, for example, is biomass allocation to flowers and fruits a good indicator of allocation to reproduction; and what proportion of the respiration of a plant can one sensibly allocate to its reproductive effort? It is my view that this last little practical difficulty exemplifies a fundamental error in this whole approach. It may be technically convenient (Bazzaz, Carlson & Harper, 1979) or intellectually satisfying to suppose that one can use biomass or energy as a common currency for the costing of reproductive effort but there is absolutely no *a priori* reason why such a relationship should exist (Trivers, 1972; Dawkins, 1989). In many environments photosynthate is not limiting to growth; the elaboration of attributes of flowering response, floral development, embryogenesis, seed morphology, protection and dispersal mechanism can be amply provided for. The key elements in the development of this complex reproductive apparatus are the genes which control its developing and functioning. The task then becomes one of unravelling the genetic control of flowering and fruiting attributes in all their manifestations, a task further complicated by the fact that the genes involved do not act in isolation, they interact with one another.

New approaches to the study of plant reproductive biology

In suggesting the need for new approaches to plant reproductive biology I do not presume to advocate the abandonment of established lines of investigation; though I do imply that the slavish adherence of many ecologists to facile and inappropriate notions of reproductive effort could usefully be dropped.

If one produces haploid barley from anther culture, the plants that develop will produce an inflorescence but meiosis being blocked, there is no subsequent embryo development or filling of the grain. Under these circumstances axillary buds at the base of the stem grow out and the plant develops as a vegetative perennial. In *Poa annua*, races developing in hot dry microhabitats such as suburban streets or dry rock crevices produce a few tillers which carry an abundance of flowers and seeds and then die. From habitats such as well-watered lawns and cool damp montane locations, races of the same species have been described in which only a few of the tillers develop a weak inflorescence bearing few flowers and seeds,

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whereas other tillers adopt a horizontal habit, forming runners which root at the nodes and thereby promulgate the vegetative spread of the plant. The genetics of these race differences have yet to be determined but we may presume that, as in haploid barley, they relate to the genetic determinants of the relative sink strengths of the developing seeds and the axillary buds. In a recent review, Ho (1988) has discussed genetic factors influencing sink size and strengths, pointing to ways in which genes affecting the enzymes of starch biosynthesis and abscisic acid metabolism may influence these attributes (see also chapters by Ho and Duffus, this volume).

Recent studies with *Arabidopsis thaliana* (Meyerowitz, Smythe & Bowman, 1989) and *Antirrhinum majus* (Almeida *et al.*, 1989) have illustrated the successful application of transposon tagging to the isolation of genes controlling floral morphogenesis. It has also been established that transposon-mediated modification of promoter sequences of genes encoding enzymes on the anthocyanin biosynthetic pathway in *A. majus* can alter both the intensity of pigmentation and the pattern of pigment distribution over the surface of the petals (Martin *et al.* 1985). Studies such as these, and analogous work with mobile elements in bacteria and insects, carry implications of a role for these elements in the evolution of attributes of the reproductive system (Syvanen, 1984). Similar approaches are now being used with the Ac transposable elements from maize introduced into *Arabidopsis* for the isolation of genes involved in the vernalization response, timing of flowering and development of the silique. In these studies one sees the beginnings of combined molecular biological and genetic approaches to the study of the reproductive biology of plants. Further instances could be cited; for example, new work on gene expression in the ripening of fruits (Brady, 1987). It may be objected that this is a symposium of the Plant Environmental Biology Group of the SEB; but such an evasion will not do. My point is that both environmental and intrinsic developmental factors govern the expression of the genes affecting the reproductive biology of plants. The tools for identifying and measuring the activity of genes controlling reproductive behaviour are now developing rapidly; one hopes that this may lead to a new synthesis in which ecologists will align themselves with colleagues involved in these developments, for it is along this track that I believe that we shall come to a more comprehensive and convincing account of what constitutes the reproductive efforts of plants and a clearer view of the determinants of reproductive fitness.

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R.F. LYNDON

The environmental control of reproductive development

Environmental control of flowering

The simple observation that many plants flower at a particular season or time of year implies that flowering is influenced and perhaps controlled by changes in the environment. All plants require conditions in which they can grow and develop in order to reproduce and so the ultimate environmental controls are those that determine plant distribution, and the main one may very often be temperature (Grace, 1987). But in all habitats, variations in the environment provide potential cues for the plant to make use of, so that the transition to reproductive growth coincides with the conditions most likely to lead to successful completion of flowering, fruiting and seed dispersal. Even in plants that do not respond to specific environmental changes, the onset and rate of progress of reproductive development will be determined by the general environment of the plant.

Are there any habitats in which the environment is constant and optimum so that growth and reproductive development are governed entirely by factors internal to the plant? The nearest approach to this is probably the tropical forest of SE Asia, which is virtually non-seasonal. However, even here flowering can be controlled by environmental changes, but because these are infrequent, mass flowering is also infrequent. When it does occur, up to 88% of the species may flower simultaneously (Appanah, 1985). The close correlation between an environmental change and subsequent flowering has been shown for the rain forest in Singapore, one of the least seasonal places in the world (Corlett, 1990). Two episodes of mass flowering were recorded a few months after an unprecedentedly dry, sunny month (Fig. 1). The two peaks of flowering (Fig. 1) also show that a single environmental event may subsequently result in flowering at different times for different species, presumably because, even in the same environment, flower development takes longer in some species than others. In other tropical forests

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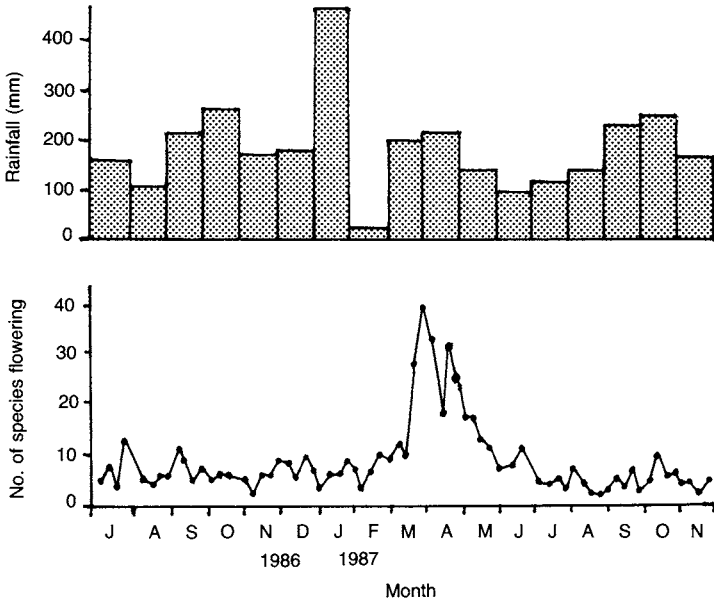


Fig. 1. Monthly rainfall and numbers of species in flower along a 5.1 km route through the forest in Singapore between July 1986 and November 1987. From March to May 1987, after a dry month (Feb. 1987), more than 150 species (out of a total of 787) flowered, with up to 40 species and 81 individuals flowering simultaneously. Normally in the otherwise uniform climate only about 6 species and 10 individuals were in flower at any one time. (After Corlett, 1990.)

the environment is less constant and flowering usually seems to be seasonal and to follow rainy or dry periods (Frankie, Baker & Opler, 1974). Mass flowering in tropical forests may occur only where the environment is normally very uniform and so when irregularities do occur many species respond.

Flowering at all times of the year may occur in cool temperate as well as in tropical environments. Some weeds and ornamentals can be in flower in the middle of winter in Edinburgh, Scotland (56° N) even after frosts if they have not been injured. Such plants can potentially flower all year round if they can grow, however slowly. The environment is controlling flowering only in so far as it allows or prevents growth. All-year flowerers in a very seasonal climate may be individuals that are either self-fertilized or apomictic (if wild plants) or ornamentals that do not depend upon the natural environment for cross-fertilization and propagation.

Why should plants use environmental cues to regulate flowering?

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Plants may use environmental signals either to promote flowering, so that a favourable environment for reproductive growth can be quickly and successfully exploited, or to delay it until it can be achieved optimally as, for instance, in biennials. The critical parts of the reproductive process are pollination, fertilization and fruit and seed formation. The whole process has to be set in train, by the transition to flowering, several weeks or months in advance of eventual culmination. Not only must individuals be able to complete their reproductive development under favourable conditions but, for successful outcrossing, they must also flower synchronously with others of the same species. Those plants relying on specific animals or insects for dispersal may also require their seeds or fruits to reach ripeness at fairly precise times, which may depend on the timing of the previous stages of reproductive development.

If, however, the season is an abnormal one then the environmental changes, on which a plant may normally depend to promote flowering, may not occur. In this case the plant may need a fall-back position where internal controls can be overriding so that the plant reproduces, albeit suboptimally (Fig. 2). This would be consistent with the observation that most plants eventually flower, however unfavourable the conditions may be, so long as they can support some growth (Bernier, 1988) and with the view that, in the last resort, plant growth substances may provide a fail-

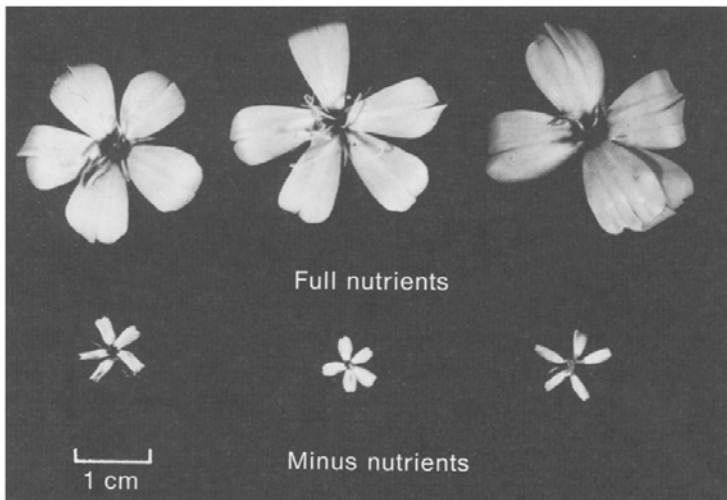


Fig. 2. Flowers of normal plants of *Silene coeli-rosa*, and of nutrient-deprived plants (grown in sand and watered only with distilled water). Without nutrients the flowers are very small, and only a single, small flower is formed instead of a many-flowered inflorescence (R.F. Lyndon, unpublished).