news & views

A binary classification of plant life history and some possibilities for its evolutionary application

by Jonathan Silvertown*

Introduction

The evolution of semelparity in plants has been one of the more active areas of recent research in plant life history (e.g. Janzen, 1976; Hart, 1977; Young, 1981; Lacey et al., 1983; Silvertown, 1983, 1986; de Jong et al., 1987).The apparent fascination with this phenomenon arises from the paradox that, though many plants appear to be capable of virtual immortality as genets, individuals of semelparous perennial species live for several to many years, flower only once and then die. Although this is not a common type of life history, semelparity is taxonomically widespread and occurs in bamboos, palms, dicot trees, agaves, and is scattered among many families of temperate herbs. The evolution of semelparity in perennials has also attracted attention because it is an extreme life history whose fitness consequences are easy to calculate, thus lending itself to analysis by relatively simple, tractable mathematical models. The conveniently short lifespan of many semelparous, perennial herbs has meant that these models can be tested in the field (Werner and Caswell, 1977; Kachi and Hirose, 1985; Meijden and Waals-Kooi, 1979). This fortunate conjunction of an interesting evolutionary problem with ample means to analyse it has yielded satisfying results which explain the particular ecological conditions in which semelparity may be favoured over iteroparity.

This paper proposes a new approach to the analysis of plant life history by looking at the morphology of semelparous plants in the context of other life histories. A binary classification of life history that is independent of taxonomic classification is described and some of its evolutionary implications are suggested.

The morphology of plant reproduction

In all plants, sexual reproduction consumes the meristems from which the reproductive organs arise. By contrast, vegetative growth results in the multiplication of meristems. Several authors have suggested that the

*Biology Dept., Open University, Milton Keynes, MK7 6AA, UK.

relative magnitude of the opposing rates of meristem consumption in reproduction and meristem production in growth are fundamental determinants of plant life history (Watson, 1984; Silvertown, 1985; Torstensson and Telenius, 1986; Watkinson, 1988), but few attempts have been made to analyse life histories on this basis (Sackville Hamilton, Schmid and Harper, 1987).

Simmonds (1980) distinguished between plants that are semelparous 'by morphology' and those that are semelparous 'by adaptation'. This distinction is itself based upon morphology. The plants Simmonds calls semelparous by morphology have determinate growth and die when the apical meristem flowers. Plants that are semelparous 'by adaptation' have a genet with a branched structure or one composed of many ramets. Species with such a structure are generally iteroparous, but in a few cases, such as the tree *Tachigalia versicolor*, or in semelparous bamboos, the genet is semelparous because all its semelparous branches or ramets flower simultaneously. It is clear from the distinction between these two forms of semelparity that the syndrome as a whole has two components: a morphological one, and a temporal one, the latter only becoming important for plants with an indeterminate growth form.

Meristems, which may potentially give rise to either vegetative or repoductive organs, are the extremities of a morphological hierarchy consisting of the components: genet; ramet; branch; meristem, where a genet is defined as a plant arising from a seed and a ramet is a clonally produced offshoot with its own roots (attached or unattached to other ramets). When a meristem develops into reproductive organs two more levels may be added to the hierarchy which now becomes: genet; ramet; branch; inflorescence; flower; gametes. Depending upon the species, some architectural components of the full hierachy may be missing. For example most palms lack branches, most trees (with notable exceptions) do not have clonally produced ramets and there are plants whose flowers are borne singly rather than in an inflorescence.

Reproduction always involves the sacrifice of plant parts, if only because flowers, ovules and pollen are organs that can only be used once. Each of the other components of the structural hierarchy may also be disposed of when a plant reproduces. For example it is common for the ramets of grasses (tillers) to die after producing seed but, in iteroparous species, the genet survives by the production of new ramets. Each of the parts of a plant (genet, ramet, branch, etc.) may be coded according to whether they survive a reproductive event (1) or not (0), as shown in Table 1.

The life history of an entire plant can be described synoptically using a six-bit code, with one bit for each of the levels in the structural hierarchy. Ovules (and pollen) and flowers are always once-off structures, thus reducing the information-containing segment of the code to only four bits. Because plant organs are hierarchically organized, the death of an organ at one level in the hierarchy necessarily involves the loss of all the organs above it (i.e. those it bears) as well. Hierarchical construction therefore limits the possible number of life histories, as classified in the binary scheme, to four — corresponding to the four levels of the morphological hierarchy for which repeated reproduction is an option.

The synchronicity of reproduction among ramets (or branches) is not explicit in this code, but is indicated by whether a genet with semelparous ramets is itself semelparous or not. A genet with semelparous ramets which flower synchronously dies, a genet with semelparous ramets that flower asynchronously must (by definition) survive. In this case the synchronous loss of all organs at one level causes the loss of the unit in the hierarchy at the next lowest level. The downwardly-acting constraint caused by synchronous flowering of semelparous parts adds two more types of life history to those that are morphologically possible. Some coded examples of different life histories are given in Table 2.

The binary classification of plant life histories makes it easy to see that semelparity is but an extreme expression of a phenomenon seen in all plants: the loss of organs after reproduction. Furthermore, for a species with semelparous ramets, the evolutionary step between iteroparity and semelparity (or the reverse) may involve only a slight change in the behaviour of meristems at the bottom of the structural hierarchy. An iteroparous species can become semelparous if it is reduced to a single ramet, or if all ramets flower simultaneously. The ease with which this evolutionary change may be accomplished is demonstrated by the frequency with which semelparous and iteroparous species occur in the same, or in allied genera. There are many examples of this: in the palms (Table 3), giant lobelias (Young, 1984), yuccas and agaves (Schaffer and Schaffer, 1977), bamboos (McClure, 1966), bananas, shrubs in the genus *Strobilanthes* (Acanthaceae) (Simmonds, 1980) and herbs in the genera *Verbascum* (Scrophulariceae) and *Oenothera* (Onagraceae) to name only some.

Discussion

The binary classification of plant life history based upon

Table 1. The hierarchy of plant structural components (parts) involved in reproduction, each of which may hypothetically survive (1) or be lost (0) during reproduction. Structural components shown in parentheses may be absent from the architecture of some species

Part	Survive reproduction
6. Ovule & pollen	0
5. Flower	0
4. (Inflorescence)	0/1
3. (Branch)	0/1
2. (Ramet)	0/1
1. Genet	0/1

Table 2. Coded examples of different life histories in plants. 'Missing' structural components are indicated by dashes. Ovules, pollen and flowers are always once-off structures and for brevity are left out of the code specifying a particular life history. Abreviations are Genet, Ramet, Branch, Inflorescence

Life History	GRBI	Examples
Aclonal plants		
Semelparous, no branches	0- -0	*Dipsacus fullonum*[1]
Tree with synchronously flowering semelparous branches	0- 00	*Tachigalia versicolor*[2]
Iteroparous 'tumbleweed' that sheds the whole shoot	1- 00	*Psoralea argphylla*[3]
Iteroparous tree with semelparous branches	1- 00	*Nannorrhops ritchiana*[4]
Iteroparous vine with an indeterminate inflorescence	1- 11	*Psigura* spp.[5]
Clonal plants		
Clonal, synchronously flowering semelparous ramets	0000	*Phyllostachys bambusoides*[6]
Clonal, with asynchronously flowering semelparous ramets	10- 0	*Senecio jacobaea*[7]
Clonal, with iteroparous ramets	11- 0	*Ranunculus repens*[8]
Clonal tree with iteroparous ramets & semelparous branches	1100	*Rhus typhina*[9]
Clonal tree with iteroparous ramets and iteroparous branches	1110	*Populus tremula*

Sources: 1. Werner (1975); 2. Foster (1977); 3. Becker (1968); 4. Tomlinson and Moore (1968) [and pp. 130−1 in Hallé *et al.* 1978]; 5. Gilbert (1980); 6. Janzen (1976); 7. Meijden and Waals-Kooi (1979); 8. Sarukhán (1974); 9. Hallé *et al.* (1978:151).

Table 3. Examples of intra-generic variation in life history in the palms

Code	Genus Metroxylon[1]	Arenga[2]	Caryota[2]	Raphia[2]
0--0	M. salomonense M. upolense M. vitiense M. warburgii	A. pinnata	C. urens	R. regalis R. humilis R. taedigera
1--0	M. amicarum			
1000	M. sagu		C. mitis	R. gigantea

Sources: 1. Moore and Uhl (1982); 2. Hallé et al. (1978).

structure makes the relationship between plant architecture and life history explicit and offers a means of analysing the constraints of one upon the other during the course of evolution. So, for example, using the binary classification it is possible to reinterpret Raunkiaer's (1934) scheme of classification of plant life forms and to see how geographical constraints on life form will also affect life histories.

Raunkiaer's (1934:18) scheme of plant life form classification is based upon the position of meristems during the resting period of the seasonal cycle and upon the parts of plants which are shed at the end of the growing season. It is thus concordant with the binary classification. His *phanerophytes* shed twigs and inflorescences (1110). Some *chamaephytes* shed a proportion of their branches (1100), and all *hemicryptophytes* and *cryptophytes* shed the aerial part of shoots, but not necessarily the ramet itself (1[1/0][1/0]0). Raunkiaer showed that there is a correlation of these forms with geography and climate with, for example, hemicryptophytes poorly represented in tropical lowland floras. We may expect geography and climate to constrain the distribution of certain binary classes of life history too. For instance, such an approach may help explain the recurrent evolution of semelparity among giant rosette plants of tropicalpine floras.

These plants, which include the tree Senecios and Lobelias of African mountains, and *Puya raimondii* of the Andes, occur in habitats typically devoid of phanerophytes (Hedberg and Hedberg, 1979) and appear to have evolved from low-altitude hemicryptophyte ancestors which are tolerant of cold. It has been pointed out elsewhere that semelparity is peculiarly common in certain, largely herbaceous, plant families by virtue of their morphology (Silvertown, 1983). Although the gigantism of tropicalpine rosette plants places them among the phanerophytes, they retain a morphology typical of their hemicryptophyte ancestors, and therefore susceptible to the evolution of semelparity. This argument does not

Table 4. The binary classification applied to some of Hallé et al.'s (1978) models of plant architecture

Model	Code	Examples
Holttum	0--0	Corypha umbraculifera
Leeuwenberg Petit Chamberlain Koriba Fagerlind	1-10	Senecio keniodendron Gossypium hirsutum Philodendron selloum Catalpa bignoniodes Magnolia grandiflora
Corner	1--0	most palms
Prevost	1-00	Cordia tetrandra
Aubreville	1-10	Terminalia superba
Scarrone Stone	1-00	Carlina salcifolia Pandanus pulcher
Tomlinson	1100 or 1000	Euterpe oleracea Metroxylon sagu
McClure	10-0 or 00-0	Iteroparous bamboos Semelparous bamboos
PART:	GRBI	

attempt to explain the selective advantages of semelparity in tropicalpine plants, but only to point out that, for morphological reasons, it is more easily evolved in plants with hemicryptophyte (1000) than with phanerophyte (1110) ancestry.

The binary classification is also consistent with Hallé et al.'s (1978) models of plant architecture (Table 4), and may be useful in analysing the constraints or architecture on life history evolution. In an analysis of the yield characteristics of tropical crops, Verheij (1985) observed that seed yield was more stable in species with an

unbranched growth habit (11−0, 10−0, 1−−0) as compared with branched species (1110).

The binary classification of plant life history based upon structure by no means provides a complete specification of life history variables. For example it does not specify the age of first reproduction, which is an important determinant of fitness for life histories. This is an unavoidable problem for a morphologically based classification because age of first reproduction is not constrained by morphology. This is indicated by the fact that annual species as a group comprise those that are semelparous and those which Kirkendal and Stenseth (1984) suggest should be called uniseasonally iteroparous.

It has only been possible to outline the potential of a binary classification of life histories based upon plant morphology and it has not been possible to apply it rigorously to a group of plants. To do this would require a phylogeny for a large, well described plant taxon whose species exhibit a range of life histories. Individual species could be codified by the binary scheme, and the phylogenetic relationships between species could then be used to calculate the frequency of transitions between different life history states during the course of evolution. The usefulness of the proposed binary classification will depend upon the insights obtained from such an exercise.

Acknowledgements

References

Becker, D.A., 1968. Stem abscision in the tumbleweed, *Psoralea. American Journal of Botany*, **55**: 753−756.

Foster, R.B., 1977. *Tachigalia versicolor* is a suicidal neotropical tree. *Nature*, **268**: 624−626.

Gilbert, L.E., 1980. Ecological consequences of a coevolved mutualism between butterflies and plants. In: *Coevolution of Animals and Plants*. 2nd Edition. L.E. Gilbert and P.H. Raven (eds). University of Texas Press: Austin.

Hallé, F. Oldeman, R.A.A. and Tomlinson, P.B. (1978) *Tropical Trees and Forests*. Springer-Verlag: Berlin.

Hart, R., 1977. Why are biennials so few? *American Naturalist*, **111**: 792−799.

Hedberg, I. and Hedberg, O., 1979. Tropical-alpine life-forms of vascular plants. *Oikos*, **33**: 297−307.

Janzen, D.H., 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics*, **7**: 347−391.

Jong, T.J.de., Klinkhamer, P.G.L. and Metz, J.A., 1987. Selection for biennial life histories in plants. *Vegetatio*, **70**: 149−156.

Kachi, N. and Hirose, T., 1985. Population dynamics of *Oenothera glazioviana* in a sand-dune system with special reference to the adaptive significance of size-dependent reproduction. *Journal of Ecology*, **73**: 887−901.

Kirkendal, L.R. and Stenseth, N.C., 1985. On defining 'breeding once'. *American Naturalist*, **125**: 189−204.

Lacey, E.P., Real, L., Antonovics, J. and Heckel, D.G., 1983.

Variance models in the study of life histories. *American Naturalist*, **122**: 114−131.

Meijden, E. van der and Waals-Kooi, R.E. van der, 1979. The population biology of *Senecio jacobaea* in a sand dune system. *Journal of Ecology*, **67**: 131−153.

McClure, F.A., 1966. *The Bamboos: A Fresh Perspective*. Harvard University Press: Cambridge, Mass.

Moore, H.E. and Uhl, N.W., 1982. Major trends of evolution in the palms. *Botanical Review*, **48**: 1−69.

Raunkiaer,C., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press: Oxford.

Sackville Hamilton, N.R., Schmid, B. and Harper, J.L., 1987. Life-history concepts and the population biology of clonal organisms. *Proceedings of the Royal Society of London*, B., **232**: 35−57.

Sarukhán, J., 1974. Studies on plant demography: *Ranunuculus repens* L., *R. bulbosus* L. and *R. acris* L.: II. Reproductive strategies and seed population dynamics. *Journal of Ecology*, **62**: 151−177.

Silvertown, J., 1983. Why are biennials sometimes not so few? *American Naturalist*, **121**: 448−453.

Silvertown, J., 1984. Death of the elusive biennial. *Nature*, **310**: 271.

Silvertown, J., 1985. Survival, fecundity, and growth of wild cucumber *Echinocystis lobata. Journal of Ecology*, **73**: 841−849.

Silvertown, J., 1986. 'Biennials': A reply to Kelly. *American Naturalist*, **127**: 721−724.

Simmonds, N.W., 1980. Monocarpy, calendars and flowering cycles in Angiosperms. *Kew Bulletin*, **35**: 235−245.

Tomlinson, P.B. and Moore, H.E., 1968. Inflorescence in *Nannorrhops ritchiana* (Palmae). *Journal of the Arnold Arboretum*, **49**: 16−34.

Torstensson, P. and Telenius, A., 1986. Consequences of differential utilization of meristems in the annual *Spergularia marina* and the perennial *S. media. Holarctic Ecology*, **9**: 20−26.

Verheij, E.W., 1985. Towards a classification of tropical tree fruits. *Tropical Crops Coomunication No. 9*. Agricultural University: Wageningen, Netherlands.

Watkinson, A.R., 1988. On the growth and reproductive schedules of plants: a modular viewpoint. *Acta Oecologica Oecologica Plantarum*, **9**: 67−81.

Werner, P.A., 1975. Prediction of fate from rosette size in teasel. (*Dipsacus fullonum* Huds.) *Oecologia*, **20**: 197−201.

Werner, P.A. and Caswell, H., 1977. Population growth rates and age vs stage-distribution models for teasel (*Dipsacus fullonum* Huds.) *Ecology*, **58**: 1103−1111.

Young, T.P., 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist*, **118**: 27−36.

Young, T.P., 1984. The comparative demography of semelparous *Lobelia telekii* and iteroparous *Lobelia keniensis* on mount Kenya. *Journal of Ecology*, **72**: 637−650.