

both cases, the separate effects of uncertainty without dispersal and with encompassive dispersal, and of competition, were considered. What has yet to be tackled is the combined consequences of these factors. Venable & Lawlor (1980) tried germination and moderate dispersal. Dan Cohen told me that he is working with Simon Levin on some models which include germination, dispersal and competition. The rest is silence, so far, but the door is presumably open. Invitations are not required to enter, I suppose.

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11

When plants play the field

J. SILVERTOWN

Although mixed evolutionarily stable strategies (ESSs) are of uncertain importance in animal behaviour (Maynard Smith, 1982) there are many ways in which plants simultaneously or successively display multiple growth strategies (Lloyd, 1984). In this chapter I review some examples of two of the commonest kinds of multiple strategies in plants: multiple germination responses and multiple dispersal types in seeds.

Seed germination

Germinating seeds very often show the type of behavioural variety which suggests that a mixed strategy of response is favoured by natural selection. In laboratory tests it is unusual to find that a single type of treatment produces germination in all the viable seeds of a sample (e.g. Grime *et al.*, 1981) and even amongst those seeds which do respond it is rare for them all to germinate simultaneously. Field studies of germination frequently report a staggered pattern of seedling emergence which in populations of annual plants is often separated into distinct cohorts that emerge at different seasons of the year.

In the vast majority of populations displaying this type of behaviour, we do not know whether the observed variety is the product of variety within the seed clutches of individual parents or is due to differences between the seed clutches of different parents or both. Such data as exist suggest that the former is the likeliest source of variable behaviour in most cases (Silvertown, 1983). A number of theoretical studies have shown how environments which vary in time and space may select for bet-hedging and differential seed dormancy amongst a plant's progeny (Cohen, 1966, 1967; MacArthur, 1972; Jain, 1979; Venable & Lawlor, 1980; Schoen & Lloyd, 1983; León, this volume).

Table 1. Pay-off matrix for a contest between seedlings emerging in two cohorts 30 days apart^a

	Early	Late
Early	0.32	1
Late	0.01	0.45

Data from Abul-Fatih & Bazzaz, 1979.

^a Pay-offs are values of relative fitness calculated from the life-time sum of $l_x \cdot m_x$.

Seedling emergence and plant fitness

Parallels exist between game theory treatments of animal conflict, in those cases where strategies are played against the field, and the situation for seeds germinating in a population with mixed environmental response. Established plants occupy space and thereby hold access to resources which are denied to other individuals in a very similar manner to the way in which territory holders defend space against intruders. Contests between territory holders or established plants and intruders are both strongly asymmetric. An example of a pay-off matrix for a contest between early- and late-germinating seedlings is given in Table 1. The pay-offs in the matrix are actual values of relative fitness (calculated from the lifetime sums of $l_x \cdot m_x$) for seedlings of an annual plant, *Ambrosia trifida*, emerging in two cohorts 30 days apart. Although these values are derived from an experiment in which the alternative 'strategies' of early and late germination are artificially produced by sowing the two cohorts at different times, the result typifies field situations in which differences in emergence time occur naturally. A difference of as little as one day in emergence time between seedling cohorts can have a significant effect on the fitness of the later-emerging seedlings (see Silvertown, 1982, for examples). Other things being equal, an early-germinating strategy is the ESS.

In such circumstances, where contests are strongly asymmetric, game theory predicts that the asymmetry should be used as a cue to settle the conflict (Maynard Smith & Price, 1973). In the present plant case the penalties for a conflict between early- and late-emerging seedlings fall exclusively on the later contestant. Thus, in many species, there is a mechanism which induces dormancy in a seed when it is exposed to the characteristic spectral quality of light filtered by a leaf canopy (Gorski, 1975; Silvertown, 1980). Leaf-canopy-induced dormancy is a seed's way of assessing an asymmetric contest and withdrawing from it. León (this

volume) presents a model which predicts that seed dormancy may be favoured in competitive situations.

Germinating seeds have to contend with environmental hazards as well as playing against a field of alternative germination strategies. Both physical hazards and predation are often seasonal and place costs on an early-germination strategy which may alter or even reverse the balance of advantage which usually favours early germinators. In experimental populations in Alaska, early-germinating plants of *Thidasp arvense* reached greater size than late-germinating ones and had more than twice the fecundity, but fitnesses were nearly equal due to high mortality amongst early germinators (Table 2).

In other cases, the variety of germination responses found among the seed progeny of individual plants (which we suppose is the main source of variety in seed populations) clearly creates large differences in fitness between siblings (Table 2). Since the germination behaviour of seeds is under the control of the maternal tissue in which the embryo is encased, variable behaviour in a clutch can be viewed as a parental strategy. This may conflict with the best strategy of the embryo (Westoby, 1981; Queller, 1983).

However, apparently diverse germination behaviour in a clutch might also be the result of some variance in germination response with low heritability. For example, seeds in enforced dormancy (Harper, 1977) may germinate whenever soil moisture and temperature rise above a threshold. If the speed of germination response is normally distributed, individuals in one tail of the distribution may germinate as soon as conditions permit, say the autumn, but those in the rest of the distribution might miss a brief period of suitable weather and actually not emerge till the spring. It would be wrong to interpret a bimodal distribution of seedling emergence as evidence of a mixed parental strategy if it is simply the consequence of a bimodal distribution of soil temperature (Popay & Roberts, 1970).

Mixed germination strategies

How then are we to distinguish a genuine mixed parental germination strategy and a true ESS from a situation of Hobson's choice in which parental fitness would be raised if all seeds germinated early but in which some simply fail to manage it? For some plants (e.g. those in Table 2) the resolution of this problem is just as difficult as it is for analogous cases in animal behaviour (Maynard Smith, 1982) but there is a category of plants which are unmistakably mixed strategists. These are the species with strong structural dimorphisms among the progeny of a single clutch. Structural seed dimorphisms are almost invariably linked to germination differences (but not vice versa) and/or to differences in their dispersal and longevity in

Table 2. Relative fitness for short-lived plants (annuals or biennials) germinating in early (1) or late (2) cohorts in the same populations

Species	Type of study population	Relative fitness (cohort 1: cohort 2)	Cohort 1			Cohort 2			Source
			l_x^a	m_x^b	$l_x \cdot m_x$	l_x^a	m_x^b	$l_x \cdot m_x$	
<i>Ambrosia trifida</i>	E ^c	1:0.01	0.22	320	70.4	0.13	5	0.65	Abul-Fatih & Bazzaz (1979)
<i>Lactuca serriola</i>	N ^d	0.91:1	0.10	1226	122.6	0.28	482	135	Marks & Prince (1981)
<i>Papaver dubium</i>	E	1:0.02	0.84	1206	1013	0.98	17	16.7	Arthur, Gale & Lawrence (1973)
<i>Thlapsi arvense</i>	E	1:0.99	0.50	11 220	5610	1	5565	5565	Klebesadel (1969)
<i>Leavenworthia stylosa</i>	N	1:0.27	0.38	45	17.1	0.78	6	4.7	Baskin & Baskin (1972)
<i>Lobelia gattingeri</i>	N	0.13:1	0.05	8.5 ^f	0.43	0.36	9.1 ^f	3.3	Baskin & Baskin (1979a)
<i>Vulpia fasciculata</i>	N	1:0.57	0.86	4.09	3.52	0.20	2	0.4	Watkinson (1981)
<i>Pastinaca sativa</i>	N	1:0.50	0.02	* ^e	*	0.01	*	*	Baskin & Baskin (1979b)
<i>Senecio vulgaris</i>	N	1:0.05	0.84	*	*	0.04	*	*	Putwain, Scott & Holliday (1982)

^a l_x = Survivorship from seedling emergence to flowering.

^b m_x = Fecundity (number seeds or f = number of fruits).

^c E = Experimentally sown population.

^d N = Natural population.

^e *No fecundity data, fitness values are based on relative values of l_x only.

Table 3. Number of European taxa in the genus *Crepis* with monomorphic or polymorphic achenes, divided by lifespan ($p < 0.001$, $G = 12.93$, G Test)

Number of achene types in a clutch	Lifespan	
	Annual or annual/biennial	Perennial or perennial/biennial
1	5	15
2 or 3	6	0

Data from *Flora Europaea*, vol. IV (Tutin *et al.*, 1976).

^a The editorial rules used in this compilation were: 1. All species in the same section of the genus and having the same syndrome were scored as a single case. 2. Species with different syndromes in the same section were scored independently. 3. Species with the same syndrome in different sections were scored independently. There are 71 species in 21 sections of *Crepis* in Europe.

the soil (Becker, 1913; Silvertown, 1983). Many examples are found in the Compositae and amongst annual and short-lived plants in particular.

I have tabulated the occurrence of structural seed polymorphism in the European members of the genus *Crepis* (Compositae) in Table 3. It clearly illustrates the occurrence of mixed parental strategies in short-lived plants as predicted by Cohen's (1967) theoretical treatment of bet-hedging. Structural polymorphism within seed clutches also occurs in many species in the genus *Leontodon* and in the tribe *Calenduleae* (both Compositae), but it does not correlate with lifespan in either of these taxa (Silvertown, unpublished data; Norlin, 1943; Heyn, Dagan & Nachman, 1974). Correlations between polymorphism and lifespan do crop up in other plant families but these also contain exceptions. The constraints which operate on this kind of mixed strategy require investigation.

Seed dispersal

Plastic adjustments of investment in alternative strategies

The existence of clearly identifiable mixed strategies in plants and the fact that parental investment in each of the alternatives can be measured by counting the number of seeds of each type in a clutch, means that we can begin to ask questions about what determines the level of relative investment in each. Schoen & Lloyd (1984) have approached this problem

with a model that assumes differential dispersal distances for two seed types. As clutch size increases, the seed type dispersed near the plant rapidly fills available space and encounters density-dependent competition from sibs. Thus the fitness gain by a parent which produces more near-dispersed morphs is a decreasing function of clutch size and the ESS is to bias the ratio in favour of the far-dispersed morph as seed production increases.

Plants producing a polymorphic clutch can be divided into two groups according to how they alter the ratio of seed types as reproductive expenditure (usually related to plant size) rises. In the first group the ratio of morph types remains constant and in the second it changes in favour of one particular morph.

Likely candidates for species in the constant-ratio group are plants such as *Cakile maritima* (Cruciferae) which produces a bi-locular fruit containing one small seed and one large one and the grass *Aegilops kotschyii* which bears a large and a small caryopsis with different germination behaviour in the same spikelet (Wurzbarger & Lesham, 1967). It might be difficult for such plants to vary the ratio of morph types allometrically with the size (and reproductive expenditure) of the plant, even if this could raise parental fitness, because of close developmental association of the two seed types. On the other hand, there is at least one species which could easily alter its morph ratio as it grows larger but which has an elaborate mechanism that appears to conserve the ratio. *Aethionema saxatile* (Cruciferae) produces indehiscent one-seeded fruit (nucamenta) and dehiscent many-seeded fruit (siliques) in alternating groups along its branches as they grow (Pursh, 1970). No neo-Darwinist could resist speculating that such disciplined behaviour raises parental fitness in some way! The questions of whether it does and, if so, how, are ripe for experiment.

Changes in morph ratio with clutch size have been studied in the annual *Hypochoeris glabra* (Compositae) which produces fruit (achenes) with dimorphic dispersal abilities but similar weight and germination responses. Small plants produce small clutches with a ratio of about 2:1 in favour of the more dispersible morph. In plants with a larger clutch, the number of poorly dispersed morphs rises only slightly and the ratio of achene types is about 3:1 in favour of the more dispersible morph (Baker & O'Dowd, 1982). This shift in morph ratio with clutch size accords well with Schoen & Lloyd's (1984) prediction that sib competition amongst poorly dispersed morphs should favour the far-dispersal strategy as clutch size increases.

The two-achene types produced by *H. glabra* develop from different flowers in the fruiting head (capitulum). The near-dispersed achenes develop around the circumference of the capitulum and far-dispersed ones from the disc. Dimorphic achenes with differential dispersal ability have evolved independently in a number of other Composite genera and in all of these show the same arrangement of dispersal type within the capitulum

Table 4. Pay-off matrix for alternative parental strategies of seed production by *Emex spinosa* at low density^a

	Subterranean	Aerial
Subterranean	0.90	0.90
Aerial	0.02	1

Data from Weiss, 1980.

^a Pay-offs are values of relative partial fitness calculated from total seed production (m_x) per plant.

(Zohary, 1950). The contrast in allometric relationships between achene number and clutch size for the two-achene types in *H. glabra*, which is responsible for the shift in the ratio of types, is the result of their different positions in the capitulum. A small increase in the radius of a capitulum allows only a small increase in its circumference and in the number of marginal achenes. However, the area of the capitulum disc and hence the number of disc achenes, increases with the square of the radius. Thus ratio adjustment with clutch size has an architectural basis. The similarity of structure between *H. glabra* and other composites with dimorphic fruit suggest that there are many independent examples of morph ratio adjustment in this family which all corroborate Schoen & Lloyd's (1984) hypothesis.

This model is also excellently corroborated by another, taxonomically very heterogeneous, group of species which vary morph ratio with clutch size. Plants which produce subterranean fruit and also aerial ones from separate flowers (behaviour known as amphicarp) occur in at least nine different families but show remarkable similarities. Nearly all appear to be annual, have subterranean fruit larger than aerial ones and, where investigated, initiate their clutch by producing near-dispersed (subterranean) fruit and progressively change the ratio in favour of far-dispersed (aerial) fruit as clutch-size increases (Zeide, 1978; Loria & Noy-Meir, 1980; Cheplick & Quinn, 1982, 1983).

Thus far, plant behaviour agrees with theoretical prediction but it still remains to test the change in parental fitness as the morph ratio shifts with clutch size and seed density, and to establish whether an ESS is achieved. The only remotely relevant experiment published is for *Emex spinosa* (Polygonaceae) a Mediterranean amphicarp studied by Weiss (1980) in Australia, where it has become a weed. A replacement series competition experiment between seedlings from subterranean and aerial fruit demonstrated that subterranean fruit production is an ESS (Table 4). This experiment was conducted only at low density and so, as far as it goes, the

observed result is consistent with theory. A complete test of Schoen & Lloyd's (1984) model would involve measurements of fitness at a range of densities and proportions of the two seed types.

Evolutionary changes in mixed strategies

Taxonomists have paid a great deal of attention to angiosperm fruit structure and diversity and have traced putative lines of evolutionary relationship between species with monomorphic and with polymorphic fruits or seeds. The studies reveal a recurring association between the evolution of the annual habit and mixed strategies in seeds. The 50 or so species in the genus *Aethionema* divide into a group of perennials, mostly with a single fruit type (silicles), and two groups of annual which are considered more recently evolved. Species in one annual group have two fruit types, dehiscent silicles and indehiscent nucamenta (e.g. *A. saxatile*, above); those in the other annual group have only nucamenta. The same evolutionary trend appears in the family Fumariaceae, where a perennial genus with monomorphic dehiscent fruit (*Corydalis*) is thought to be antecedent to annuals in the genus *Ceratocarpus* – which have both dehiscent and indehiscent fruit – and annuals in the genus *Fumaria* which have only indehiscent fruit. *Fumaria* is the most recently evolved of the three genera (Zohary & Fahne, 1950).

The evolutionary association of mixed seed strategies with the annual habit is predicted by the theory of bet-hedging (see above) but the loss of one strategy type in some annual species seems, at first sight, surprising. The annuals with monomorphic fruit have lost the dehiscent fruit type which aids the long-range dispersal of seeds. This would normally be expected to increase sib competition and hence to lower fitness compared with the annuals with polymorphic fruit from which they appear to have evolved. The evolution of a monomorphic, near-dispersal strategy could be favoured in conditions where sib competition is reduced. Ellner & Shimida (1981) have suggested that this is the case in deserts, where density-independent mortality is severe. A reasonable prediction, not yet tested, is that density-independent mortality is greater, and sib competition is less, in natural populations of both *Aethionema* with monomorphic fruit and *Fumaria* than in natural populations of their dimorphic relatives. Annuals with monomorphic fruit do occur in deserts (Ellner & Shimida, 1981). This does not contradict the expectation that desert annuals should hedge bets by a mixed-germination strategy since polymorphic seed behaviour may be selected independently of dispersal type.

Polymorphic fruit types (and by inference mixed-germination or seed-dispersal strategies) have evolved repeatedly, have been lost, and have evolved again in the Compositae. These changes have been traced in the

taxonomy of the tribe Calenduleae by Norlin (1943). The genus *Dimorphotheca* contains both annual and perennial species which all have two (sometimes more) fruit (achene) types within a head (capitulum). Different types of achenes are produced from female ray florets around the circumference of the capitulum and from hermaphrodite disc florets.

Two lines of development have occurred from this 'primitive' state. In the genus *Casalis*, with three perennial species, the female ray florets have become sterile and only one achene type is produced by the disc florets. In the four remaining genera of the tribe the disc florets are female-sterile and there are varying degrees of polymorphism in the achenes produced by ray florets. *Gibbaria* species are perennial and have only one achene type. There is no correlation between lifespan and the occurrence of achene polymorphism among either *Calendula* spp. or *Osteospermum* spp., which are variable for both these traits. The fifth genus produces drupeaceous animal-dispersal fruits.

The Calenduleae illustrate the complex shifts in the occurrence of mixed strategies and in the ratio of types of strategy which have occurred during plant evolution. The causes behind some of these kinds of changes may yet be revealed as we learn more about what happens when plants with different strategies play the field.

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