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Seed heteromorphism and the life cycle of plants: a literature review

Úloha heteromorfismu semen v životě rostlin: přehled literatury

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The species which produce two or more seed types represent groups where divergent strategies usually existing in different taxa are combined by one individual. In such groups, there is a tendency for seed functions to diverge, each type specializing on some aspect of environmental variation to which it is predisposed while being buffered by the other seed type. Two main types of this behaviour are distinguished, i.e. heterodiaspory and amphicarpy, based on the morphology of diaspores, their spatial distribution on a plant, dispersibility, and other ecological functions. Ecology of heterodiasporic and amphicarpic plants is reviewed in relation to particular life cycle stages and habitat conditions. It is concluded that seed heteromorphism represents (a) a form of bet-hedging in the face of temporal variation in environmental suitability in habitats where changes of environmental conditions from season to season and year to year are very frequent and no single pattern of ecological behaviour can ensure successful survival, (b) escape from negative effects of density or (c) sib competition and occurs because intermediate adaptation have low fitness.

Keywords: Heterodiaspory, heterocarpy, heterospermy, amphicarpy, dispersal, seed bank, germination, dormancy, competition, predation, evolution, bet-hedging

Introduction

Many species possess special mechanisms which contribute to the increase of a plant's fitness in different stages of their life cycle and under different conditions. Seed polymorphism, representing one of these mechanisms, has been increasingly studied over the past two decades (Ungar 1979, Venable 1985b, Wertis et Ungar 1986, Tanowitz et al. 1987, Cheplick 1988, Kigel 1992, Venable et al. 1995). Although most plants have normal or skewed frequency distribution of seed size and shape, some produce two or more sharply defined types of fruits (Dalby 1962, Ungar 1979, Berger 1965, see Fig. 1). Effect of such heteromorphism on dispersal, germination, recruitment, and survival under both laboratory and field conditions have been repeatedly described (Baar 1912, Beadle 1952, Cook et al. 1971, Flint et Palmblad 1978, Venable 1985a, Venable et Levin 1985a, b, McEvoy et Cox 1987, Ungar 1987, Kigel 1992, Burke 1995).

This paper aims at (1) reviewing the relevant literature on the behaviour of heterocarpic and amphicarpic plants at different life stages which is still a poorly understood phenomenon, and (2) emphasizing the further research avenues of this area of population ecology of plants.

Terminology

Somatic polymorphism of seeds can be defined as a production of two or more "genetically identical" (on the intra-specific level), but morphologically or physiologically distinct

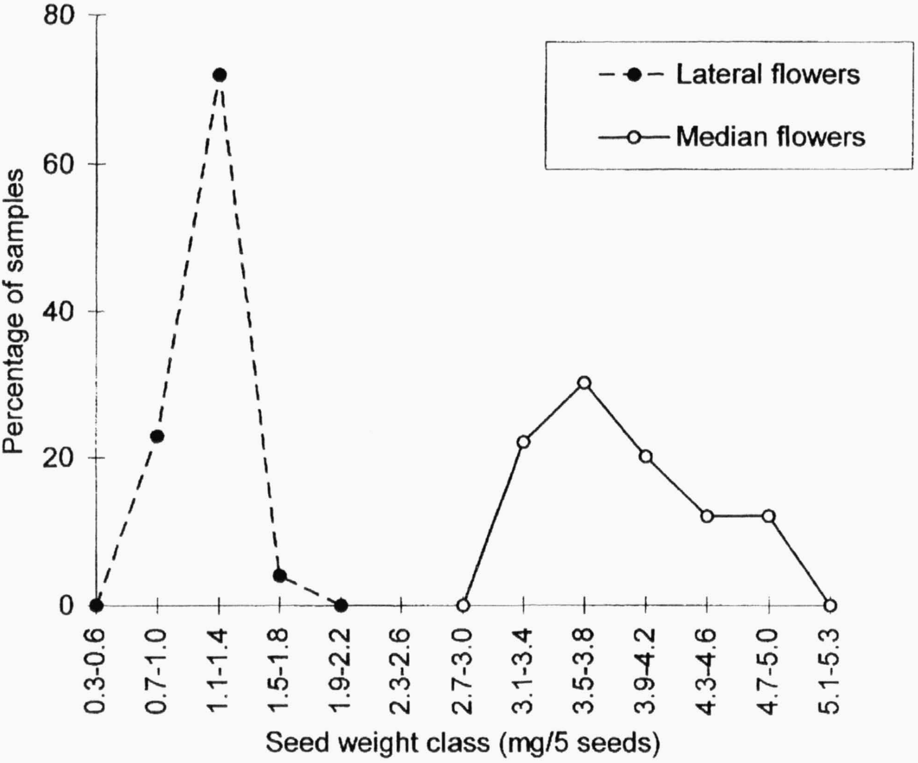

Fig. 1. – The weight of seeds (mg) developing from median and lateral flowers of *Salicornia europaea* (adapted from Ungar 1979). In this case, the heterocarpy is represented by the size of seeds and the frequency is clearly disruptive. Seeds from the larger median flowers were 1.8±0.1 mm long, and those from lateral flowers were 1.1±0.1 mm (mean ± SE).

types of seed by one plant. The phenomenon may take a variety of forms in morphological or ecological point of view, and is common namely in *Asteraceae, Chenopodiaceae, Poaceae* and *Brassicaceae* (Harper et al. 1970, see Table 1).

Somatic polymorphism, where all individual plants are monomorphic and each of them bears polymorphic diaspores, contrasts with the genetic polymorphism of seeds found in, e.g. *Spergularia* (Sterk et Dijkhuizen 1972) when two kinds of diaspores are born but on genetically different individuals.

The main problem in classification of somatic seed polymorphism is that particular authors use different terms for the same phenomena; it is being called "somatic seed polymorphism, diaspore heteromorphism, heterodiaspory, heterocarpy, heteromericarpy, heteroarthrocarpy, heterospermy, heteroblasty" or, in same cases, "amphicarpy". Furthermore, many authors use wrong morphological terms for various types of diaspores, e.g. the term seed is commonly used for achene or nutlet. I screened 25 papers and in 40% the term "seed" was used for various types of fruits. When pericarp or accessory parts contribute substantially, the distinction between seed and fruit is not merely academic but frequently plays an important role in principal ecological functions such as dispersal, germination, and dormancy.

Table 1. – Percentage of heterodiasporic and amphicarpic species in relation to family (see Fig. 4 for data sources for heterodiasporic species, data for amphicarpic species are adapted from Cheplick 1987).

Family	Percentage of species	
	Heterodiasporic	Amphicarpic
Aiozaceae	6.5	–
Asteraceae	35.5	6.9
Brassicaceae	16.1	6.9
Caryophyllaceae	3.2	–
Commelinaceae	–	6.9
Euphorbiaceae	3.2	–
Fabaceae	3.2	38.0
Fumariaceae	3.2	–
Chenopodiaceae	29.0	–
Poaceae	–	27.7
Polygalaceae	–	3.4
Polygonaceae	–	3.4
Scrophulariaceae	–	3.4
Urticaceae	–	3.4

The opinions on the classification of heterocarpic plants differ by various authors. The crucial problem represents the question: Which type of within-plant seed variation may be considered as seed heteromorphism? To illustrate the complexity of the problem, I will review several classification schemes that I consider as influential and inspirative in conception and/or depth of elaboration.

Venable et al. (1995) consider as heteromorphic only those plants producing "extreme and often discrete forms that demand further functional and evolutionary explanation". They propose that within-plant seed variation caused by (a) the time of production and (b) position on the parent plant be called "cryptic heteromorphism" defined as "continuous variation in size, shape, or germination time" (Venable 1985b).

In contrast, Levina (1967) published a very extensive survey of types of somatic seed polymorphism, but some of her types of somatic seed polymorphism belong to genetic polymorphism. Moreover, to use this detailed classification in practice would require very comprehensive information on every species to be classified which is certainly not available.

A detailed survey of types of somatic seed polymorphism in *Brassicaceae* was published by Voytenko (1968). He distinguished three main groups, the former two being (1) **heterocarpy** comprising plants that produce two or more types of fruit, and (2) **heteroarthrocarpy** for those producing a single type of fruit composed of two parts. Within both groups, **equivalent** and **unequivalent heterocarpy** is distinguished depending on whether all the fruits (in the former) on the plant or both parts of the same fruit (in the latter case) contain one or more seeds. The third main group distinguished, i.e. (3) **heterospermy** is the case if the fruit contains seeds different in color, size, shape or development, and includes two subgroups called (a) **heterospermy in different parts of the fruit** (i.e. cases where differences beetwen fruits go hand in hand with differences between seeds from different fruits – *Aethionema carneum,*[1] *Diptychocarpus strictus*) and (b) **heterospermy**

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[1] The nomenclature of species used in examples given throughout the paper was taken consistently from the original resources. Authors names are not given as in some cases these are missing from the respective papers.

within fruit (the seeds within a fruit possess variability in shape, size, color, etc. – *Hesperis* sp., *Sinapis arvensis*, *Sisymbrium* sp.).

The classification of van der Pilj (1982) is based on the mode of dispersal, using the terminology of Zohary (1962). According to this classification, dispersal mechanisms relevant to plants with heteromorphic diaspores are (1) geocarpy consisting of two subgroups, i.e. **geocarpy** *sensu stricto* ("the burying near the mother plant of all diaspores") and **amphicarpy** ("the burying ... of a number of them"). For this category it is typical that one type of fruit is undispersiable. The second term is (2) **heterodiaspory** when "both kinds of diaspores are functioning in dispersal, albeit dispersal by different methods". Heterodiaspory is further classified into four subgroups, i.e. heterocarpy, heteromericarpy, heterospermy and heteroblasty (see van der Pilj 1982 for details).

Another classification (Gutterman 1994c) focused on variability in size and ecological behaviour (namely germinability) of diaspores in relation to position effect. The scheme is based on the fact that in different parts of the plant body, diaspores of different quality develop. The following classification criteria were adopted for the classification: position in fruit, position in inflorescences, position of amphicarpic aerial and subterranean inflorescences, position of dimorphic capsules, position of inflorescences, position of dispersal units, and position of heteromorphic fruits.

The classification of seed polymorphic plants should be based on (a) diaspore morphology, (b) spatial distribution of diaspores in plant body (corresponding partly to the position effect sensu Gutterman 1994c), (c) dispersal mode (partly sensu van der Pilj 1982), and (d) other ecological functions (i.e. germination, dormancy, survival of seedlings, vulnerability to predation, etc.). With these criteria in mind, I propose the following classification:

(1) **Amphicarpy** (sensu Cheplick 1987) – some of the fruits are produced below the soil surface on specialized reproductive structures, in addition to aerial fruits on the same individual.

(2) **Heterodiaspory** (corresponding in part to the term used by van der Pilj 1982) – all of the fruits are produced above ground level and both kinds of diaspores are functioning in dispersal, albeit dispersal by different methods, and have different ecological functions. Three subgroups can be distinguished:

(a) **Heterocarpy** (sensu Voytenko 1968) – one plant bears two or more types of fruit, which differ in shape, size, color and ecological properties. The examples include: *Heterosperma pinnatum* (Venable 1987, Venable et al. 1995), *Hypochoeris glabra* (Baker et O'Dowd 1982), *Hedypnois rhagadioloides* (all *Asteraceae*) (Kigel 1992) or *Atriplex dimorphostegia* (*Chenopodiaceae*) (Koller 1957).

(b) **Heteroarthrocarpy** (sensu Voytenko 1968, corresponds also to the term heteromericarpy as used by van der Pilj 1982) – one type of fruit is produced, consisting of two parts; each part produces seeds which are different in form and ecological function from those produced by the other part e.g. *Cakile, Rapistrum* or *Sinapis* (all *Brassicaceae*) (Voytenko 1968).

(c) **Heterospermy** (sensu Voytenko 1968) – one type of fruit is produced containing seeds different in terms of size or ecological functions. *Sinapis arvensis, Aethionema carneum, Isatis bossieriana* (Voytenko 1968) or *Raphanus raphanistrum* (all *Brassicaceae*) (Stanton 1984) can serve as examples.

In some cases the heterospermy may be combined with heterocarpy and heteroarthrocarpy. For example the seeds in the heterocarpic fruit can be different in size in relation to different maturation in time or heteroarthrocarpic fruits may contain seeds which are different in size and function in relation to upper and lower parts of fruit.

Characteristic of amphicarpy

Seeds produced by self fertile subterranean flowers are always large, less numerous, usually possessing a very low dispersal potential and high ability to survive under unfavourable conditions. Seeds from aerial cross-pollinated flowers are more vulnerable in terms of survival, but possess a greater potential for long-distance dispersal (Koller et Roth 1964, Mattatia 1976, 1977, Evenari et al. 1977, Haines et Lye 1977, McNamara et Quinn 1977, Cheplick 1983, 1988, Cheplick et Quinn 1982, 1983, 1987, 1988, Schnee et Waller 1986, Trapp 1988, Momose et Inoue 1993, de Clavijo 1995). For the list of amphicarpic plants see Cheplick (1987).

Amphicarpic plants are rather rare; altogether, only 29 species from many families are known (Cheplick 1987, see Table 1). This is certainly not the final figure, as more amphicarpic species will be discovered in the future. This assumption is justified by amphicarpic species added to Cheplick's list during the last decade, e.g. *Glycine pindanica, G. hirticaulis* (*Fabaceae* – Tindale et Craven 1993), *Glycine arenaria* (*Fabaceae* – Tindale 1986), *Macroptilium gracile* (*Fabaceae* – Pengelly et Eagles 1993), *Eleocharis caespitosissima* (*Cyperaceae* – Bruhl 1994). Also, many amphicarpic species occur in deserts (Cheplick 1987), which have been less thoroughly investigated than e.g. temperate zones from the taxonomic point of view.

In the majority of amphicarpic plants, subterranean or basal flowers are cleistogamous but species with basal flowers that are not cleistogamous and produce seeds with apomictic embryos are also known, e.g. *Eleocharis caespitosissima* (*Cyperaceae* – Bruhl 1994).

Amphicarpic plants represent the opportunity for studying different dispersal modes, cleistogamous breeding systems and making evolutionary predictions. In addition, the common presence of cleistogamy and chasmogamy provides us with an opportunity to study the trade off between energetically more expensive chasmogamy, which is generally favoured (Silvertown et Lovett-Doust 1993) and energetically cheaper cleistogamy (Schemske 1978, Waller 1979).

Four hypotheses have been proposed to account for the selection processes leading to the evolution of amphicarpy (Cheplick 1987): (1) placement of the basal fruits in a suitable site, as defined by the occurrence of the parent plant; (2) protection of the basal fruits from extremes of microclimate, with higher maintenance of viability over time of basal seeds relative to the aerial seeds; (3) protection of the basal fruits from predation; and (4) protection of the basal fruits from perturbations, such as fire. I will discuss these points later in relation to particular life cycles and habitats.

Characteristic of heterodiaspory

Heterodiaspory is rather common in annuals, plants of arid and semiarid regions, and among weeds, though not restricted to these particular groups (Harper 1977, van der Pijl 1982). The screening of 31 studies on heterodiasporic species (see Fig. 3 for the list of references) revealed that of the species studied, 38.7% inhabited desert, 22.6% disturbed sites, 9.7% grasslands, 9.7% salt marshes, 9.7% shorelines and only 6.5% woodlands.

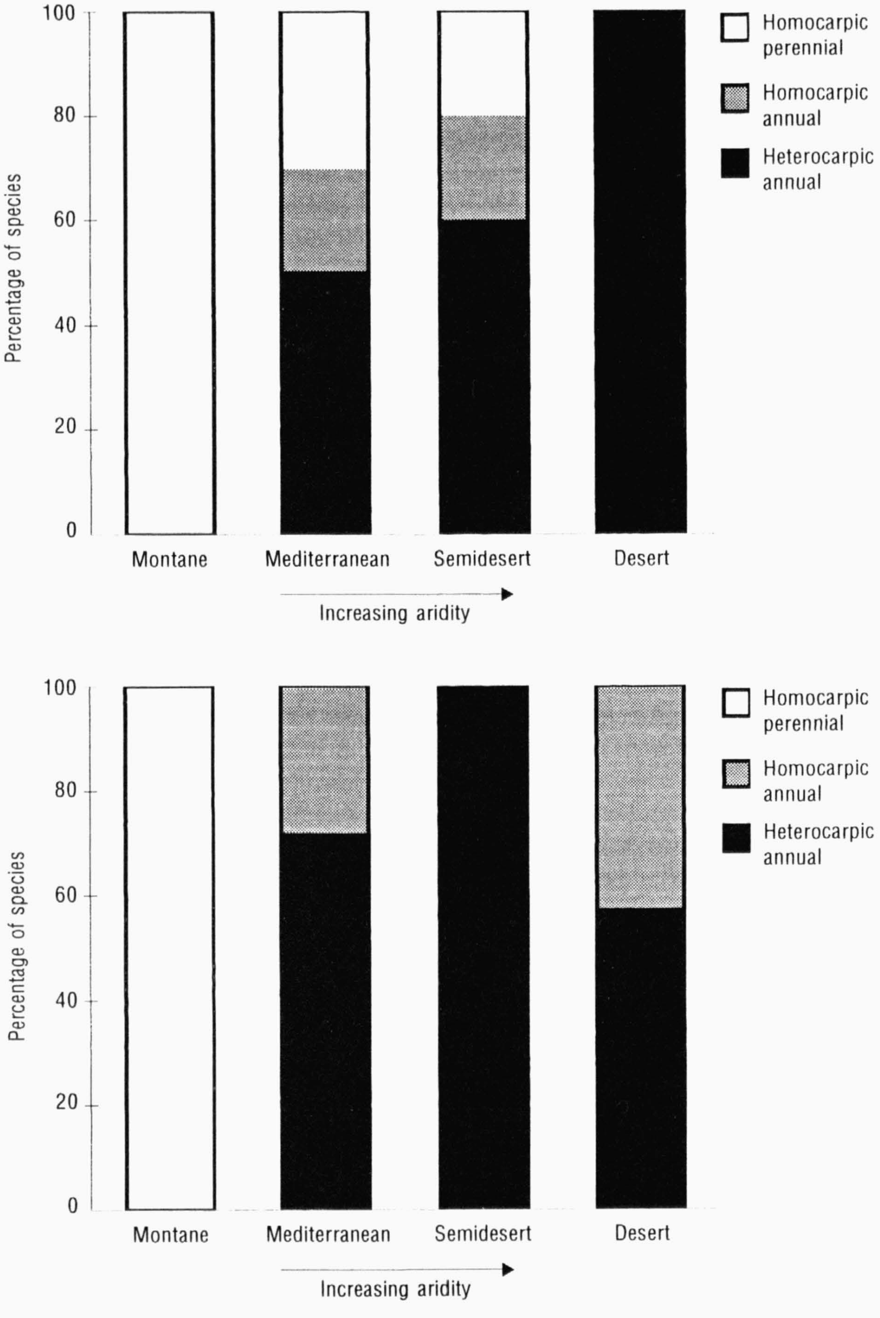

Fig. 2. – Lifespan and heterocarpy/homocarpy status of seven *Picris* species of the (a) Old World and (b) Middle East classified according to habitat. Aridity is increasing from left to right, i.e. from mesic to extreme desert habitats. The desert species may be restricted either to washes (the channels in which rainfall collects and flows) or to sandfields. The sandfield species are predominantly heterocarpic, while the wash species are generally homocarpic in the case of Middle East; species whose distribution includes several habitats are included in each habitat (based on the data from Ellner et Schmida 1984).

On a within-generic level, the pattern was nicely demonstrated in *Picris* (Ellner et Schmida 1984, Fig. 2a, b). The increased presence of seed heteromorphism among weeds and plants of arid regions has traditionally been interpreted in terms of the environmental variability inherent in these habitats (Stebbins 1974, Harper 1977). Habitats with a high level of stress are supposed to have led to the evolution of heterocarpy (Harper 1977, van der Pilj 1982, Ellner et Schmida 1984).

Many studies recorded species with two diaspore morphs differing in both shape, size and colour. These properties are often associated with different ecological functions,

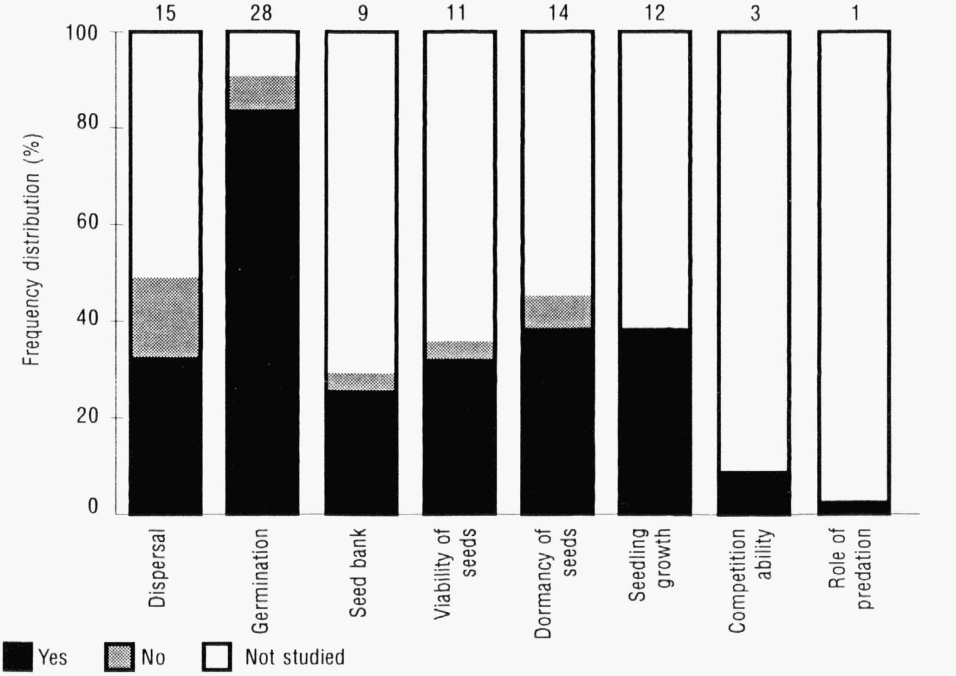

Fig. 3. – Research focus on particular phases of the life cycle and heterodiaspory aspects, expressed on the basis of screening studies on 31 heterodiasporic species. Yes – there was a difference in ecological behaviour of particular fruit types, No – no difference found, Not studied – means that the difference in behaviour beetween fruit types with respect to particular phase was not analysed. Numbers of studies related to a particular phase appear on top. The following species were included: *Aellenia autrani* – Negbi et Tamari (1963), *Aethionema carneum* – Zohary et Fahn (1950), *Aethionema heterocarpum* – Zohary et Fahn (1950), *Alysicarpus monilifer* – Maurya et Ambasht (1972), *Atriplex dimorphostegia* – Koller (1957), *Atriplex sagittata* – Baar (1912), Kopecký et Lhotská (1990), Mandák et Pyšek (unpubl.); *Atriplex triangularis* – Philipupillai et Ungar (1984), Wertis et Ungar (1986), Ellison (1987), Drake et Ungar (1989), Khan et Ungar (1984, 1985); *Bidens pilosa* – Forsyth et Brown (1982); *Cakile edentula* var. *edentula* – Maun et Payne (1989); *Cakile edentula* var. *lacustris* – Payne et Maun (1981), Maun et Payne (1989); *Cakile maritima* – Maun et Payne (1989); *Ceratocapnos heterocarpa* – de Clavijo (1995); *Eremocarpus setigerus* – Cook et al. (1971); *Gaigeria alata* – Burke (1995); *Grindelia squarrosa* var. *serrulata* – McDonough (1975); *Halogeton glomeratus* – Williams (1960); *Hedypnoides rhagadioloides* – Kigel (1992); *Hemizonia increscens* – Tanowitz et al. (1987); *Heterosperma pinnatum* – Venable (1987), Venable et al. (1987), Venable et al. (1995); *Heterotheca grandiflora* – Flint et Palmblad (1978); *Heterotheca latifolia* – Venable et Levin (1985a, b), Venable (1985); *Hypochoeris glabra* – Baker et O'Dowd (1982); *Chenopodium album* – Baar (1912), Williams et Harper (1965); *Mesembryanthemum nodiflorum* – Gutterman (1994a); *Picris echioides* – Sorensen (1978); *Salicornia europaea* – Ungar (1979), Philipupillai et Ungar (1984); *Salicornia patula* – Berger (1985); *Salsola volkensii* – Negbi et Tamari (1963); *Senecio jacobaea* – McEvoy (1984), McEvoy et Cox (1987); *Spergularia diandra* – Gutterman (1994b).

i.e. one seed type germinates better and is more easily dispersed than the other (Flint et Palmblad 1978, Baker et O'Dowd 1982, Forsyth et Brown 1982, Venable et Levin 1985a, b).

Of 31 species on which detailed case studies are available, most concentrated on a particular phase of life cycle; hence the information is somewhat scattered and incomplete (Fig. 3). The focus was mostly on germination, dispersibility and dormancy, whereas studies dealing with seed bank and competitive ability of particular heteromorphic types of diaspores are poorly represented. An almost complete life cycle was studied only in three species, e.g. *Heterosperma pinnatum, Heterotheca latifolia, Atriplex triangularis* (see Fig. 3 for references). More studies on the ecological functioning of particular seed types in particular phases of life cycle are therefore needed.

Dispersal

Amphicarpy

In amphicarpic plants, two reproductive strategies usually existing in different taxa are combined by one individual. Such plants are convenient for studying the effects of selection on the evolution of plant dispersal system and testing theoretical assumptions, e.g. on self-fertilization being associated with long-distance dispersal and colonizing ability (Stebbins 1957). Natural selection thus forces plants into producting two dispersal modes, i.e. dispersed and "stay-at-home" seeds (Begon et al. 1986, Silvertown et Lovett-Doust 1993). This type of behaviour was described by the "bet-hedging hypothesis" (Venable 1985b) and can be illustrated in a desert annual *Gymnarrhena micrantha* (*Asteraceae*). This species produces light aerial seeds with pappus, spread by wind a long distance, and 1–3 large subterranean seeds, which are non-dispersed. In very dry years, plants produced only undispersed subterranean seeds while in wetter years, a number of aerial seeds were produced (Koller et Roth 1964). Thus, in terms of bet-hedging theory, plants can increase their fitness in wetter years due to aerial seeds, which are products of cross-fertilization and may play a role in evolution. In unfavorable years, only self-pollinated flowers are formed, and the population is maintained in the site where successful survival is probable as tested previously by the mother plant (mother-plant theory).

Trapp (1988) tested this assumption on *Amphicarpea bracteata* (*Fabaceae*), an amphicarpic species producing three types of seeds, i.e. chasmogamous, aerial cleistogamous and subterranean cleistogamous. Only 3% of the subterranean seeds were deposited more than 200 cm from the parent plant, whereas it was 31% in chasmogamous and 25% in aerial cleistogamous seeds. The subterranean seeds are restricted to microsites tested by the parent plant in the past, increasing hence the probability of successive germination and seedling survival. A similar phenomenon has also been observed in *Lathyrus ciliolatus* or *Pisum fulvum* (both *Fabaceae*) from Israel (Mattatia 1976, 1977).

Heterodiaspory

Some plants produce seed types differing in a simple aspect of dispersal. *Picris hieracoides* (*Asteraceae* – Sorenson 1978) and *Hypochoeris glabra* (*Asteraceae* – Baker et O'Dowd 1982) may serve as examples; in these species two types of fruit are present with different mode of dispersal. In the former, one fruit type is dispersed by wind, the other by animals.

Venable et Levin (1985a) in their studies of achene structure, germination and dispersal in *Heterotheca latifolia* (*Asteraceae*) reported strict differences in dispersibility by wind between two fruit types. Well dispersed disc achenes germinated rapidly to high percentages while poorly dispersed ray achenes germinated at a much lower rate to lower final percentages. This is a typical example of "colonizer" and "maintainer" types of seed. The "colonizer" type expands the range and facilitates gene flow while the "maintainer" type remains in the parental environment of proven suitability (Koller et Roth 1964). Simply, one of them keeps the population in mother site (a high level of dormancy makes it possible to prolong the germination period over time) and the second one colonizes new habitats and extends the distribution range.

Senecio jacobea (*Asteraceae*), a biennial or short lived perennial native to Europe and introduced to the North America, has heterocarpic fruits (McEvoy et Cox 1987). Central (disk) florets yield achenes that are lighter, more numerous, and bear a pappus that aids wind transport, and a row of trichomes that aid animal transport. Marginal (ray) florets yield achenes that are heavier, less numerous, and lack obvious dispersal structures. Whereas disk achenes are released shortly after they mature, ray achenes remain on the parent plant for a month following maturity. These differences should result in differential dispersal in nature. McEvoy et Cox (1987) reported that the differences in dispersibility due achene morphology were affected by site and surroundings. At a coastal site, disk and ray achenes dispersed similar distances, probably because dispersal of disk achene was sharply reduced by wet wheather (high atmospheric humidity reduces dispersal distances by causing the pappi to become matted and phyllaries to close around the achenes) and tall vegetation. At an inland site, disk achenes dispersed farther than ray achenes on the mown sites, but on the unmown sites the surrounding vegetation reduced the dispersal distances of disk achenes, and differences between achene types were not significant. Thus achene differences appear to yield dispersal differences only in dry, open habitats. Nevertheless, in all sites the range in dispersal distances of disk achenes was greater than that of the ray achenes.

Dispersal of fruits by water flow or waves is crucial for heterocarpic plants inhabiting sea coast or lake shores. *Cakile edentula* var. *lacustris* (*Brassicaceae*) grows on beaches along Canadian lakes and produces a siliqua consisting of the upper and lower segments (i.e. heteroarthrocarpy). Payne et Maun (1981) suggest that the upper fruit segment of this species disperses a long distance, while the lower one remains on the parent plant in the proven habitat.

To summarize the examples given, the basic difference between heteromorphic diaspores lies in their ability to disperse. Other ecological properties are often additional, being related to dispersibility or non-dispersibility. For example, easily dispersed diaspores are more germinable, with low level of dormancy and low ability to survive. The undispersable diaspores are often dormant, but chances of surviving for the seedlings are high.

Seed bank

Amphicarpy

Subterranean seeds, buried under soil level, form a persistent soil seed bank, whereas aerial seeds form a transient seed bank (Cheplick 1987).

Heterodiaspory

Few data on the dynamics of the soil seed bank of heterocarpic species are available. Principle information comes from an excellent study of seed production, seed rain and soil seed bank dynamics of *Atriplex triangularis* (Wertis et Ungar 1986). Two distinct types of seeds were recognized, i.e. large brown and small black. Large brown seeds germinated very fast in favourable conditions in spring and formed a Type II transient seed bank (i.e. after dispersal seeds require a period of chilling before germination can take place – Thompson et Grime 1979), whereas small black seeds that were less germinable usually formed a persistent soil seed bank (Type IV – few of the seeds germinate in the period immediately following dispersal and the species maintains a large seed bank the size of which changes little with season and is large in relation to the annual production of seeds) and were present throughout the summer (Fig. 4). This germination polymorphism may be understood as an adaptation to alternative temporal and spatial germination situations, i.e. salinity or water availability (Wertis et Ungar 1986), at least partly eliminating the environmental hazard in time. A similar phenomenon was observed by Philipupillai et Ungar (1984) in *Salicornia europaea*.

Seed bank dynamics was monitored also for disc and ray achenes of *Heterotheca latifolia* (*Asteraceae* – Venable et Levin 1985a) which differ morphologically and anatomically in a number of features. The former possess a pappus while the latter do not. The most striking difference is in the structure of achene pericarp: the ray pericarps have thick, highly lignified layer of fibres while the disc pericarps are thin. Disc achenes germinate early and rapidly with a high final germination percentage. Ray achenes germinate later,

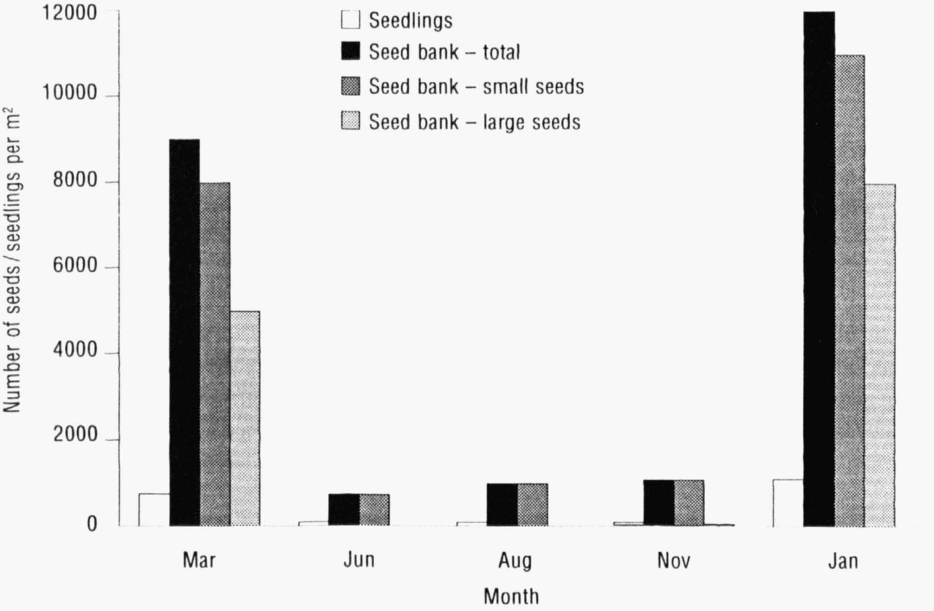

Fig. 4. Seasonal changes in the number of *Atriplex triangularis* seeds / m^2 extracted from the soil and number of germinable seeds/m^2 (seedlings/m^2) in the greenhouse soil sample (adapted from Wertis et Ungar 1986).

more slowly and have a low final germination percentage (Venable et Levin 1985a). The seed bank of disk achenes approached zero in the spring while 24% of the ray seed bank were still viable after one year (Venable et Levin 1985b).

These examples probably reflect a general trend in species with seed heteromorphism. One type of seed does not develope a persistent seed bank, the other one, usually smaller, cannot successfully emerge from deep burial and have evolved a light requirement for germination. This light requirement incidentally leads to the production of between-year seed banks (Bewley and Black 1982).

Dormancy and germination

Germination and dormancy are still one of the least understood phenomena in the seed research but their importance is underscored by a growing body of literature (Roberts 1972, Thompson et Grime 1979, Grime et al. 1981, Bewley et Black 1982, 1985, Baskin et Baskin 1985, 1988, 1989, Fenner 1992, Hilhorst 1995, Vleeshouwers et al. 1995). Heterocarpic species provide us with a unique opportunity to study different dormancy-breaking mechanisms on a single plant (Williams et Harper 1965, Forsyth et Brown 1982, Venable et Levin 1985a, Tanowitz et al. 1987, Venable 1987, Kigel 1992, Venable et al. 1995), removing thus bias in results accounted for by differences between species.

Amphicarpy

Aerial and subterranean seeds differ sharply in seed germination. *Emex spinosa (Polygonaceae)* has subterranean fruits at the stem base near the root neck; these do not disperse and germinate in the close surroundings of the dead mother plant (Evenari et al. 1977). Functionally, they could be considered as equivalent to dormant vegetative regenerative buds of a perennial as pointed out by Koller (1968, quoted by Evenari et al. 1977) for *Gymnarrhena micrantha* (*Asteraceae*). The subterranean propagules of *Emex spinosa* keep their full viability for many years; in contrast to aerial propagules, the germination of a whole set of subterranean propagules of a single mother plant is spread over a long period of time (Evenari et al. 1977).

Germination response to light and temperature was studied in two seed types of *Gymnarrhena micrantha*. The final percentage germination was higher in light than in the dark. The effect of high temperature on germination was more restrictive in darkness than in light. The achenes differed in that (a) final germination percentage of the aerial achenes was much more temperature-dependent in both light and dark than those of subterranean ones, and (b) start of germination of subterranean achenes was more rapid than that of the aerial ones (Koller et Roth 1964).

In *Amphicarpea bracteata* (*Fabaceae*) the rate at which subterranean and aerial seeds germinated differed considerably. Germination of aerial seeds was slower and insensitive to temperature, with only 0.5–2% of the seeds sown germinating per day, while subterranean seeds germinated faster, particularly at higher temperatures, reaching 33.5% per day at 25°C (Schnee et Waller 1986).

There are alternative germination strategies in amphicarpic plants. These include (a) germination of different types of seed is separated in time and allows survivorship in different seasons, or (b) germination is not separated in time, but particular types differ in response to light and temperature which makes it possible for the species to occupy a wider range of habitat types.

Heterodiaspory

Germination behaviour represents the most frequently addressed aspect of the population biology of heterocarpic species (Fig. 3) and the association of seed heteromorphism with difference in germination has been repeatedly observed (Williams et Harper 1965, McDonough 1975, Flint et Palmblad 1978, Ungar 1979, Baker et O'Dowd 1982, Venable et Levin 1985a, Tanowitz et al. 1987, Kigel 1992). The most important aspects are documented by the following examples.

In *Alysicarpus monilifer*, a perennial *Fabaceae* herb of open, sunny sites common in India, Africa and Australia, two types of seed can be recognized: yellow-mottled and brown-smooth. Seeds produced in the rainy season have lower immediate germination capacity than those produced in the summer season but even amongst the seeds produced in a single season, the two colour forms differ in their readiness to germinate – freshly collected brown seeds give a greater immediate percentage germination than yellow seeds. Dormancy is apparently broken during storage in the soil and this property, taken together with heteromorphism, seems to be advantageous in an environment that has unpredictable elements and two distinct periods of seasonal growth (Maurya et Ambasht 1973).

Achene morphology of *Heterosperma pinnatum* (*Asteraceae*) varies from periphery to the center of each head and is not determined by floret type as in most *Asteraceae* with achene heteromorphism. Venable et al. (1995) grouped the achenes into three "types" for experimental convenience. Central achenes are long, very narrow, possess a beak, have little or no wing, and are usually 5 to 15 times as long as wide. Peripheral achenes are short, wide winged, concave, and usually at least half as wide as long. Intermediate achenes represent a range of morphologies including anything not conforming to the "pure" central or peripheral types (Venable et al. 1987). Venable et al. (1987) studied the germination ecology which includes two important aspects: within-year and between-year timing of germination. When achenes of different morphologies have been germinated at the same time, no difference in seedling size, growth rate, or competitive ability was found. However, there was a difference between central and peripheral achenes in the within-year timing of germination. All the achenes produced possessed innate dormancy, but the central ones lose theirs earlier in the spring. In general, central achene tend to emerge earlier than peripheral achenes. Early emergence usually results in lower survival but greater size and reproduction of survivors. However, the magnitude of these differences varies, resulting in shifts in relative success of achene types. As to the between-year timing of germination, there was no difference because seed banks diminish to zero during the germination season. Thus, polymorphic seeds need not necessarily differ in their germinability as pointed out by Venable et Levin (1985a), Ungar (1979) and others, but within-year timing of germination may be very important. Moreover, if germinability is similar under laboratory conditions, there is no reason to assume that it is also similar under natural conditions.

Germination of heteromorphic seeds may also be regulated by the concentration of internal hormones. This germination pattern could be due to differential response of heteromorphic seeds to both salinity and temperature and their interaction (Khan et Ungar

Table 2. – Effect of NaCl, giberellic acid – GA_3 (2.9 mM), and kinetin (4.7 μm) on germination of heterodiasporic seeds of *Atriplex triangularis* after 20 days (%); mean ± SE (based on data from Khan et Ungar 1985).

NaCl (mM)	Additions (mM GA_3)	Seed size Small	Seed size Medium	Seed size Large	Additions (μM kinetin)	Seed size Small	Seed size Medium	Seed size Large
0	None	97±2	94±2	99±1	None	99±1	97±3	98±2
	2.9	95±2	89±1	99±1	4.7	100±0	100±0	100±0
172	None	70±9	63±7	100±0	None	46±2	57±4	61±8
	2.9	77±11	47±14	25±4	4.7	90±2	72±4	84±7
345	None	8±2	33±13	33±9	None	7±2	11±1	22±3
	2.9	27±5	30±7	36±3	4.7	69±5	39±4	39±4

1984). Biotic factors influencing germination include changes in internal hormone balances and variation in the thickness of seed coat. Seed dormancy induced by salt stress in halophytes *Suaeda* and *Salicornia* can be alleviated by application of giberellic acid (GA_3) (Ungar et Binet 1975, Boucaud et Ungar 1976, Ungar 1977, 1984). Kinetin is reported to have the same effect, i.e. stimulating germination at all salinities and seed sizes tested (Khan et Ungar 1985). In addition, GA_3 and kinetin generally increased seedling growth at all concentrations of salinity studied but higher concentration of the latter were found to be inhibitory (see Table 2).

In *Atriplex triangularis*, the testa is formed by a single layer of cells regardless of seed size, and the thickness of seed coat increases with decreasing size of the seed. Small seeds have larger diameter of epidermal cells than medium and large seeds (Khan et Ungar 1985). Osmond et al. (1980) suggested that the mechanical resistance of these large epidermal cells in *Atriplex* provides a resistance to germination and may induce dormancy in small seeds. Dormancy due to mechanical resistance of testa was closely associated with low levels of giberellin-like activity in seeds of *Suaeda* sp. (Boucaud et Ungar 1973) and mechanically-induced dormancy was broken by an external application of GA_3 (Boucaud et Ungar 1976).

Regulation of germination and dormancy in *Atriplex* can be influenced by other factors such as fruiting bracts covering the seed in all heterocarpic representatives of the genus. Beadle (1952) found a high concentration of NaCl in bracts of five Australian species of *Atriplex*, completely inhibiting germination of naked seeds (Table 3). He suggested that this high salt content may prevent germination and allow it only under favourable circumstances, i.e. after rainfall. The same effect was observed in *A. hortensis* (Osmond et al. 1980), a species possessing three types of seed. One type is not covered by fruiting bracts and originates from female or bisexual flowers with 5-lobed perianth; these seeds are dormant. The other two types of seed are produced by female flowers and are enclosed in fruiting bracts; the former is small and dormant while the latter is relatively big and non-dormant. Leaching of salt from bracts is necessary for germination to occur, because water uptake in NaCl solution is very low compared to distilled water (Osmond et al. 1980). This holds only for non-dormant seeds, because in the dormant ones the testa is thick and water uptake in distilled water is similarly low as in high salt concentrations. The thin testa of non-dormant seeds is very sensitive to NaCl concentration. Similar phenomenon was found in *A. dimorphostegia* (Koller 1957).

Leaching of chloride from bracts stimulated germination of arid shrubland *Atriplex* species and some other representatives of sect. *Dimorphostegia* exhibited a similar

Table 3. – NaCl concentration in water-satured bracteoles of *Atriplex* species and concentration of NaCl required to inhibit germination of naked fruits (based on data from Beadle 1952; for different seed batches).

Species	NaCl in saturated bracteoles (M)	NaCl preventing germination (M)
A. nummularia	0.72	0.6
	0.48	0.4
	0.48	0.4
A. vesicaria	0.48	0.4
	0.55	0.5
A. semibaccata	0.61	0.4
	0.45	–
A. inflata	0.90	0.7
	0.61	0.5
	0.44	0.4
A. spongiosa	0.62	0.8
	0.69	0.4

response. Khan et al. (1985) found a remarkably low concentration of NaCl in seeds of *A. canescens*. It may well be that the bracts act as a salt accumulation area but the problem certainly requires further study; a comparative study of a number of species inhabiting various habitats would be most useful for explaining the role of high salt concentrations in fruiting bracts of *Atriplex*.

Fruiting bracts can play another role in germination ecology of *Atriplex* species. Since there is a diffusive resistance of O_2 movement in germinating seeds, it is possible that water-saturated bracteoles of some species restrict O_2 exchange and inhibit germination (Burbidge 1945 quoted by Osmond et al. 1980, Beadle 1952). High salt concentration cannot be thus taken as the only explanation of inhibition of germination in non-dormant seeds. Underlying reasons for differential germination of particular seed types are, however, in their anatomy, the most frequently found anatomical difference being pericarp thickness (Baar 1912, Osmond et al. 1980, Venable et Levin 1985a). The pattern is not restricted to *Chenopodiaceae* (McEvoy 1984, Tanowitz et al. 1987). In general, fruit anatomy can influence germination by (a) physically impeding germination, (b) blocking gas diffusion, (c) restricting water intake or (d) containing chemical inhibitors.

Seedling recruiment and survival

Amphicarpy

The survivorship of plants arising from aerial and subterranean seeds was studied experimentally in *Amphicarpum purshii*, an annual North American grass, under different conditions (Cheplick et Quinn 1982). Seedlings from subterranean seeds survived better in both dry and wet sites and at low and high densities, whereas those grown from aerial seeds showed significantly less total growth and seed production. In addition, the former began early to allocate considerable energy to subterranean production (ca 40% of the total plant dry weight); the allocation to aerial culms and flowers did not begin until mid-August and never exceeded 3%. Plants arising from aerial propagules produced only subterranean flowers, because they were too small to be capable of producing aerial chasmogamous flowers.

Seedlings arising from subterranean diaspores of *Amphicarpum purshii* (*Poaceae* – Cheplick et Quinn 1982), *Emex spinosa* (*Polygonaceae* – Evenari et al. 1977) and *Gymnarrhena micrantha* (*Asteraceae* – Koller et Roth 1964) tolerated stressful conditions (in terms of water availability) better than those arising from aerial diaspores.

Heterodiaspory

Variation in seed size is correlated with environmental factors. Both within and among species, a larger seed size is associated with less-disturbed habitats (Werner et Platt 1976), dryness (Baker 1972, Schimpf 1977), decrease in altitude (Baker 1972) and increase in latitude (McWilliams et al. 1968). Consequently, seedlings from larger seeds are supposed to have a higher rate of root extension which makes them more drought-tolerant. Also, if larger seeds produce larger seedlings they may have a competitive advantage over those from smaller seeds, especially if the two types of seedlings are grown in mixed stands (Black 1958). The assumed positive correlation between seed and seedling size, however, does not always seem to hold. Melzack et Wats (1982) found no correlation between seed size and seedling dry weight. The initial differences in seedling size, produced by different seed sizes, may soon disappear owing to different growth rates among seedlings from different sizes of seeds (Zimmerman et Weis 1983). Seed size may have no effect in dense stands where seedling's success is largely determined by order of emergence (Ross et Harper 1972). Similarly, Ellison (1987) studied an effect of seed dimorphism on density-dependent dynamics of experimental populations of *Atriplex triangularis* (*Chenopodiaceae*). Larger seeds produced larger and more fecund plants than small ones. However, the effect of seed size on final biomass and fecundity was only indirect, operating via emergence time. Because, for many species, seedling size is correlated with seedling survival – smaller seedlings having higher chances of mortality than the larger ones (Cook 1980) – seed size may only affect seedling survival if it affects both emergence ability and final seedling size.

Autumn-germinated brown seeds of weedy *Chenopodiaceae* suffer high winter mortality from frost and disturbances due to agricultural practices, but those that survive have much higher reproductive outputs than plants germinating from black seeds in spring (Harper 1977). Brown seeds form only 3 % of the total seed production by parent plants, and are usually the first to mature. There is a strong evidence for environmental control (particularly by photoperiod) in this and other chenopodiaceous seed heteromorphism, i.e. the ratio between particular seed types differs with changing daylength (Macdonald et Smith 1990).

Competition, growth and fecundity

Amphicarpy

Plants reduce flower and seed production with increasing density (Harper 1977). In *Amphicarpum purshiion* on plants grown under intraspecific competition, a depression of weight of subterranean and aerial spikelets that emerged from subterranean or aerial seeds was strongly associated with increasing density (Cheplick et Quinn 1983, see Fig. 5). Cheplick et Quinn (1983) also studied percentage of allocation to reproductive structures in cultures grown from mixtures of aerial and subterranean seeds, and found that weight of plants from aerial seeds was reduced by the presence of plants from subterranean seeds. These results might be explained in relation to size of different seed types: the bigger seeds usually have higher growth rate and survive better in the mixture (Black 1958, Harper et al. 1970). The significant reduction of the weight of plants from aerial seeds by plants from subterranean seeds has also been observed by Weiss (1980) in *Emex spinosa* (*Polygonaceae*).

Heterodiaspory

Competitive ability of seedlings arising from different seeds depends on (a) physiological characteristics, (b) time of emergence, and (c) differences in relative growth rate. Seedlings from seeds of different sizes have different relative growth rates (Wulff 1986). Growth rates are usually positively correlated with size; however, sometimes seedlings from smaller seeds have higher growth rates than those from larger seeds during early stages of development as reported for, e.g. *Xanthium strumarium* (*Asteraceae*) (Zimmerman et Weis 1983).

Vulnerability to predation

Amphicarpy

The only work on vulnerability of amphicarpic plants to predation is that of Engler from 1895 (reviewed by Cheplick 1987). Comparative data on the impact of herbivory on both aerial and subterranean flowers and seeds are needed to support or refuse the theory that in desert, animals can be a major cause of seed mortality. It is expected that herbivore pressure may be of some evolutionary importance, because subterranean seeds are protected from foraging animals and hence the plant fitness is increased.

Heterodiaspory

Differential predation of heterocarpic plants has been relatively rarely studied. The only detailed work focusing on this aspect was that of Cook et al. (1971) who studied interactions between the North American species *Eremocarpus setigerus* (*Euphorbiaceae*) and mourning dove (*Zenaidura macroura*). Discontinuous genetic variation in the seed coat pattern was found to influence the predation of seeds by birds. The *Eremocarpus* plants produce several colour morphs of seed, and plants from desert produced different types than those growing on the coast. Grey seeds differ from mottled, black and striped seeds in their visual, chemical, structural and germination characteristics. Doves usually ate all mottled and striped seeds but refused grey seeds which contain toxic compounds. In addition, grey seeds were less germinable than the other types. Populations lacking grey seeds would thus have no chemical immunity to dove predation, and conversely, in a population with complete chemical immunity, no seeds with the germination advantages of other seed types would be produced (Cook et al. 1971).

Unfortunately, almost no data are available about the impact of herbivory by insects on the dynamics of particular seed types in heterocarpic plants. These interactions may

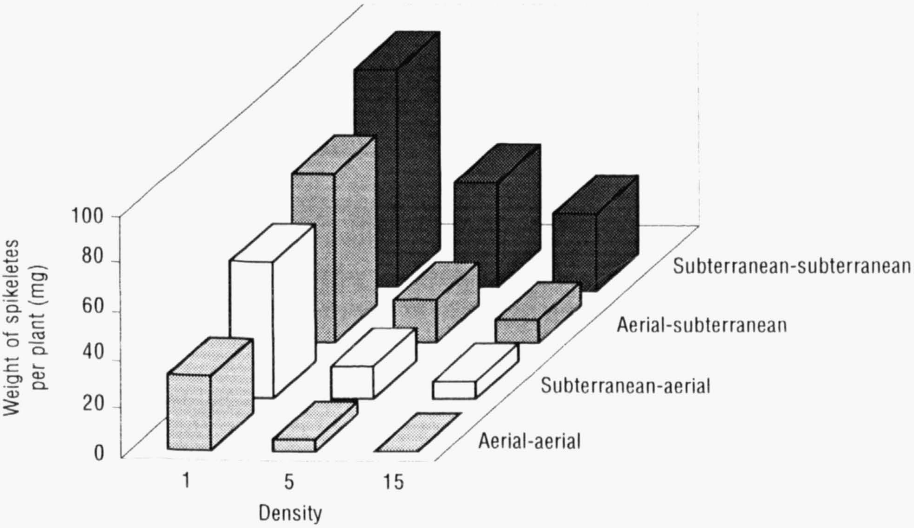

Fig. 5. Weight (mg) of two type of spikelets produced in *Amphicarpum purshii* plants subjected to varying levels of density. Subterranean-subterranean – subterranean spikelets arising from subterranean seeds; aerial-subterranean – aerial spikelets of plants arising from subterranean seeds; subterranean-aerial – subterranean spikelets of plants arising from aerial seeds; aerial-aerial – aerial spikelets of plants arising from aerial seeds (based on data from Cheplick et Quinn 1983).

influence production of particular seed types and consequently the chance of a plant to survive. This interaction was found by Kopecký et Lhotská (1990), but they only stated, that in *Atriplex sagittata*, one type of fruit is usually damaged by insects (albeit without quantitative data and the insect name is not given either).

Factors affecting the proportion of particular diaspore types produced

Amphicarpy

For amphicarpic plants, the knowledge of this aspect is rather poor. One of the few studies available revealed that the shift in aerial/subterranean fruit ratio in *Amphicarpum purshii* was affected by (a) competition and (b) depth of burial of subterranean seeds in the soil (Cheplick et Quinn 1983). The allocation to aerial seeds decreased with increasing plant density. Greater depth of sowing lead to decreased emergence rates and increased percentage allocation to subterranean seeds. This example shows that the increasing abundance of plants in succession may force amphicarpic species to produce more and more subterranean seeds which would germinate if the vegetation cover is removed and/or the soil is disturbed (Cheplick et Quinn 1983). In the same vein, the ratio of the number of *Amphicarpum purshii* aerial/subterranean caryopses increased with recentness and/or frequency of disturbance (McNamara et Quinn 1977).

Gymnarrhena micrantha, an annual *Asteraceae* species from the Negev Desert increased production of aerial, long-distance diaspores under favourable conditions (in terms of water supply) in comparison to subterranean, short-distance diaspores (Koller et Roth 1964).

Heterodiaspory

Influence of environmental conditions

Most frequently, the shift in the ratio of particular seed types produced by heterocarpic plants reflects variation in environmental conditions. In this section, I review some of the examples available.

In *Heterotheca pinnatum* (*Asteraceae*), genetic variation in achene proportions provides the species with a flexible seed biology that has permitted apparently adaptive population differentiation. Populations with a high proportion of awned achenes tend to be found in vegetation types where they are likely to be ephemeral. In contrast, a high proportion of central achenes tend to be found in sites with little pre-rainy season precipitation (Venable et al. 1995).

Interaction between intraspecific competition, seed dispersal and proportion of two types of diaspores was studied by Baker et O'Dowd (1982). In *Hypochoeris glabra* (*Asteraceae*), two distinctly different achene types are produced: beaked and unbeaked. The latter have a low dispersal potencial (they are animal dispersed and more adherent to wool sock) while the former are wind dispersed. At high parent-plant density, the plant weight and scape height are reduced. Plant size in *Hypochoeris glabra* regulates allocation to reproduction through receptacle size. In turn, receptacle size mediates both total achene production and the proportion of each achene type. When the competition is low, plants produce more beaked achenes. Proportion of beaked achenes decreases as a function of the area of receptacle; consequently, larger receptacles have greater proportion of beaked achenes. The existence of two major differences between the types of achene may reflect adaptation to two separate dispersal mechanisms, wind and animal (Baker et O'Dowd 1982).

In *Heterotheca latifolia* (*Asteraceae*), when plentiful water was available, achenes favouring long-distance dispersal were more successful in germination than achenes favouring short-distance dispersal (Venable et Levin 1985a, b, Venable 1985a).

A similar phenomenon was observed in *Hedypnois rhagadioles* (*Asteraceae* – Kigel 1992). This species produces three types of diaspores differing in size, structure and dispersal capacity: (1) inner achenes with pappus, (2) outer achenes without pappus, and (3) compound diaspores developed from marginal row of achenes. There was a trend for a reduced production of pappose achenes and a concomitant increase in less-dispersed (epappose) achenes with increasing aridity while the proportion of compound diaspores remained relatively stable. Thus, assuming that the smaller pappose achenes behave as long-range dispersal achenes, it can be concluded that *H. rhagadioloides* plants invest less biomass and produce less long-range diaspores with increasing aridity. A similar trend was found in the genus *Picris* (*Asteraceae*) if various types of habitats are compared (Ellner et Schmida 1984). In more arid regions this phenomenon also represents a partial shift from wind dispersal to animal dispersal, as barbs on the involucral bracts facilitate dispersal of marginal achenes by the attachment to the fur of mammals (Schmida et Ellner 1983).

Ungar (1987) disscussed the ratio of small (<1.5 mm) to large (>1.5 mm) seeds in *Atriplex triangularis* (*Chenopodiaceae*), changing from 1: 1 to 1: 60. If plants grew under more stressful conditions, the ratio was lower than at lower density or reduced soil salinity. In contrast, Ellison (1987) found, that regardless of density conditions and parentage (i.e. whether the plant originated from large or small seeds), large and small seeds were produced in equal proportions by *Atriplex triangularis* plants.

These studies indicate a rather consistent trend. Under unfavourable conditions, plants tend to produce relatively more seeds with low dispersibility, germinability and high level of dormancy. However, some factors may negatively affect survival of stay-at-home progeny, such as intraspecific competition (notably sib-competition – for review see Cheplick 1992) in biologically saturated environments. Under these conditions, the "escape" from the mother site by means of long distance dispersal diaspores might always be favoured. This theory was tested by Burke (1995) on *Geigeria alata* (*Asteraceae*) in the eastern part of the central Namib desert; seed heteromorphism was studied in relation to increasing aridity. However, the theory of more long-range dispersal units being produced under less favourable conditions was not proved. With decreasing aridity, plants produced more long-dispersal units enhancing thus the chance of escape from parental site.

Two general trends in production of particular seed types emerge with respect to the habitat:

1. Dispersibility and germinability are generally reduced in semi-arid and arid regions compared to more mesic regions. The plants thus tend to produce diaspores with low dispersibility and high level of dormancy.
2. In salt marshes, the species tend to produce more stress-tolerant seed types when the conditions are unfavourable (but note *Atriplex triangularis*).

Influence of photoperiod

In some plants, the day length during seed maturation affects seed germinability and subsequently has an influence on the occurrence of long- and short-lived seeds in the seed bank (Gutterman 1994c). If seeds of *Trigonella arabica* (*Fabaceae*) mature under long days, their coats are yellow or yellow with green spots; they are well-developed and impermeable to water (rapid germination can be triggered by scarification). Seeds that mature during short days are green or brown, have less-developed coats and germinated more readily because of being permeable to water (Gutterman 1978).

In *Chenopodium polyspermum* (*Chenopodiaceae*), the thickness of the seed coat is quantitatively dependent on the number of long days after flowers begin to appear; the more long days, the thicker the seed coat. The shorter day length therefore stimulates the thinner seed coat and higher level of seed germination and vice versa (Pourrat et Jacques 1975). The same influence of photoperiod was observed by Williams (1960) on *Halogeton glomeratus* (*Chenopodiaceae*), a species producing brown and black achenes. Seeds of black achenes germinated more rapidly, while seeds of brown achenes were viable, but germinated very poorly. Under short days *Halogeton* produced black achenes and under long days it produced brown achenes.

Kigel et al. (1979) studied germination pattern in relation to the day length and age of maternal plants in *Amaranthus retroflexus* (*Amaranthaceae*). Germinability of seeds produced by plants induced to flower in long days by 1, 2, or 3 short days was lower than that of seeds produced by plants grown continuously in short days, and decreased with the age of the parent plants at the time of flower induction. On the contrary, in *Spergularia diandra* (*Caryophyllaceae*) the longer day length, the higher the percentage of germination

(Gutterman 1994b). These results indicate, that although the growth under shorter days leads to the production of more readily germinated seeds compared to longer days, the pattern is not unequivocal.

Seed heteromorphism in relation to environment

Most of the heteromorphic plants studied are annuals, often pioneer species or plants faced with stochastic environment such as desert and semidesert. This chapter reviews the available knowledge on how amphicarpy and heterodiaspory relate to the main types of enviroment inhabited by these species.

Amphicarpic plants and their environment

Cheplick (1987) published a survey of 29 amphicarpic species and showed that they occured in dry habitats, being very frequent in deserts. The case of *Fleurya podocarpa* var. *amphicarpa* (*Urticaceae*), native in tropical Africa, however, indicates that amphicarpy need not necessarily be restricted to this type of environment.

Amphicarpy is advantageous for successfull survival in desert conditions. This was demonstrated in studies carried out on *Emex spinosa* var. *minor* (*Polygonaceae*) in the Negev desert in Israel (Evenari et al. 1977). The aerial propagules are spiny, small and light and the subterranean ones are large, smooth and heavy, each type performing different ecological functions. In drought years there will be only few such microsites where runoff collects and correspondingly, only few *Emex* plants derived from aerial propagules are produced. In years with much rain and floods "aerial" plants will be spread over large areas. As conditions vary remarkably between years, the *Emex* populations expand or contract around safe sites which are sufficiently wet.

Based on studies of seed dispersal and germination in arid environment, Gutterman (1992, 1994a, b, c) distinguished the "escape" and "protection" strategies of seed dispersal that are very important in the life of desert plants. The former strategy has nothing to do with heterocarpy: some species produce plenty of tiny, dust-like seeds, which are very easily dispersed after maturation. The "protection" strategy, however, is represented by many desert amphicarpic plants: the subterranean diaspores are not dispersed, whereas aerial ones are dispersed very easily. The ecological importance of amphicarpy has been discussed for the following species occurring in deserts of Israel or surrounding regions: *Emex spinosa* (Evenari et al. 1977), *Gymnarrhena micrantha* (Koller et Roth 1964), *Lathyrus ciliolatus* (*Fabaceae* – Mattatia 1976), *Pisum fulvum* (*Fabaceae* – Mattatia 1977).

Heterodiasporic plants and their environment

Haline environment

Plants growing in a haline environment possess many special ecological adaptations. To cope with salinity, not only halo-succulence or special bladder hairs (Freitas et Breckle 1993, 1994, Breckle 1995) but also heterodiaspory is important. The germination and establishment is probably the most precarious stage in the life of a halophyte and a plant in this phase of life cycle is more sensitive to salinity than at other periods of development as demonstrated by Millington et al. (1951) with *Atriplex semibaccata.*

Halophytic species are frequent in *Chenopodiaceae* and *Poaceae* (Flowers et al. 1986). I will focus on the *Chenopodiaceae*, in which salt tolerance is most widespread and best investigated (e.g. Millington et al. 1951, Ungar 1962, 1967, 1977, 1979, Berger 1965, Rivers et Weber 1971, Osmond et al. 1980, Khan et Ungar 1984, 1985, Drake et Ungar 1989, Yokoishi et Tanimoto 1994).

Koller (1957) found that "flat" seeds of *Atriplex dimorphostegia* germinate very early compared to the "humped" type. In *Atriplex nummularia,* the germination ability of heavier seeds was 93%, corresponding figure for lighter seeds being 10% (Uchiyama 1981). Ungar (1979) reported interactions between seed size and germinability at various levels of salinity. Large seeds of *Salicornia europaea* were more salt-tolerant than small seeds and germinated better at various concetrations of NaCl. Seeds which did not germinate under salinity stress germinated with high percentages (86%) after immersion in distilled water for 42 days. So, inhibition of germination evoked due to salt stress was transitory. Similarly, large seeds of *Atriplex triangularis* had higher germination percentages in saline medium than small seeds and the rate and percentage of germination decreased with increased salinity stress. In general, different seed sizes have different tolerance limits to salinity, i.e. large seeds are more tolerant to salinity at a wide range of temperatures and smaller seeds possess more specific temperature requirements for germination under saline conditions (Khan et Ungar 1984).

These studies clearly suggest the ecological significance of seed polymorphism in a haline environment. Particular seed types play different roles in plant's life and allow advantages in alternate temporal and spatial situations for seed germination and growth which are evoked by changing environment.

Desert environment

Variation in dispersal and dormancy strategies of diaspores has been suggested to represent an adaptive response to desert conditions (Venable et Lawlor 1980, Venable et Brown 1988). For a desert plant, the germination period is a crucial stage and a number of mechanisms are known that time the germination to suitable conditions. A desert plant waits for the rain and then germinates within a very short time (Gutterman 1972).

In general, the germination can be affected by a relatively large number of factors (Fenner 1992). One of them is maternal influence affecting seed germination in relation to the "position effect" (see Gutterman 1994c for a review). Seed germinability is influenced by the position of the seeds in the fruit or in the inflorescences or by the position of the inflorescence on the plant (Gutterman 1994c).

Effect of polymorphism on plants in desert environment was demonstrated on *Spergularia diandra* (*Caryophyllaceae*), an annual plant inhabiting the Negev desert of Israel (Gutterman 1994b). In this species, nine types of seed are known: 3 genotypes (i.e. genetic polymorphism) combined with 3 colour phenotypes (i.e. somatic polymorphism of seeds). The seeds were divided into three groups (genotypes): the first group produced only smooth seeds, the second group produced only "partially hairy" seeds, and the third group produced only hairy seeds. Each genotype produced black, brown or yellow seeds (i. e. heterospermy), which differed in capsule position and the age of a plant when a particular seed matured. The seeds which matured in the first capsule that appeared on a plant were black. Later on, brown seeds appeared. At the end of the growing period, when symptoms of senescence appeared, yellow seeds were produced. Each of the three genotypes differed from the other two in weight, hairiness, dispersibility, seed coat structure, colour and germinability.

A similar phenomenon is known in *Mesembryanthemum nodiflorum* (*Aizoaceae*), a South African annual of saline deserts (Gutterman 1994a). In this species, the position of a seed in the capsule (i.e. terminal, central and basal seeds) affects its germinability. In these long-living seeds that germinate to low percentages even under optimal conditions, seed heteromorphism is an important survival strategy in unpredictable extreme environments such as deserts, as it reduces the risk of germination failure.

The position effect was demonstrated for a number of desert species (see Gutterman 1992, 1994c for reviews). The position of capsules (central or peripheral) in the canopy affected seed germinability in the perennial South African shrub *Glottiphyllum linguiforme* (*Aiozaceae* – Gutterman 1990). The effect of position on seed germinability was observed in *Pteranthus dichotomus* (*Caryophyllaceae* – Evenari 1963), *Aegilops geniculata* (*Poaceae* – Datta et al. 1970, 1972), and *Aegilops kotschyi* (*Poaceae* – Wurzberger et Koller 1976). The position of achenes in the different whorls of the capitulum influenced the germinability in *Asteriscus hierochunticus* (*Asteraceae* – Gutterman et Ginott 1994).

The main question, however, remains unanswered: Is there a general biochemical pathway at the relevant stage of maturation which is affected by the maternal position and/or environmental factors resulting in differences in seed germinability or, in the different plant species, are there different biochemical pathways that are affected by different maternal position and environmental factors (Gutterman 1992)?

Evolution of seed heteromorphism

Seed heteromorphism is frequently found in highly variable environments such as disturbed habitats (Harper 1977) and arid and semiarid habitats (van der Pijl 1982, Ellner et Schmida 1981, 1984). Functional differences among seed types are necessary for the existence of temporal or spatial variation in their relative success. Many cases have been known of dramatic seed heteromorphism with extreme and often discrete forms that demand further functional and evolutionary explanation (e.g. *Asteraceae* – Zohary 1950, and *Brassicaceae* – Voytenko 1968).

Current explanations of seed heteromorphism are largely adaptionist. Variable seed functions are usually explained in terms of either bet-hedging (Venable 1985b), escape from negative effects of density (Levin et al. 1984, Ellner 1985), or escape from the negative effects of sib competition (Schoen et Lloyd 1984, Cheplick et Clay 1989, Cheplick 1992, Venable et Brown 1993).

Making more than one type of seed may achieve the reduction in temporal fitness variance characteristics of **bet-hedging** by ensuring that at least some offspring function appropriately in a variety of environmental circumstances. The species *Amphicarpum purshii* follows this strategy; it allocates resources into a limited number of large seeds with high probability to survive and any spare resources above a threshold into as many small seeds as possible. So, when conditions are more stressful, there is a high uncertainty as to which kind of seed size will be suitable (Cheplick et Quinn 1982, 1983).

Variable progeny may also result in escape from the **negative effect of crowding** in variable environments by being spread out in space or time, i.e. dispersive vs. nondispersive fruit types (spread in space) or dormant vs. nondormant seed types (spread in time) (Venable et al. 1995).

Sib competition can be reduced by spreadings offspring in space and time in such a fashion that they tend to interact less with relatives and more with non-relatives (regardless of whether any reduction in density is achieved or even whether density varies or not). This is a component of fitness that may favour heteromorphism above and beyond the general crowding effect. Environmental variability in time or space tends to enhance the selective advantage of multiple strategies, at least with regard to the first two factors (i.e. bet-hedging and negative effect of crowding) (Venable et Brown 1993, Venable et al. 1995).

The production of two seed types should decrease temporal variation in offspring success. Thus, the theory suggests that seed heteromorphism is favoured in temporally variable environments when variation in reproductive success is high for any single seed morph but lower for heteromorphism because morphs are successful under different conditions (Venable 1985b). Seed heteromorphism can also be favoured by spatial heterogeneity in microsite availability to progeny if seedling success is microhabitat-specific and if greater allocation to either seed type results in diminishing fitness gains from that type because of local density dependence (Lloyd 1984). In both of these scenarios, each seed type must yield greater fitness at some time or place and hence the types must differ ecologically.

Various theoretical arguments and some empirical data suggest that natural selection might often favour a negative correlation between seed dispersal and dormancy. This negative correlation is predicted because dispersal and dormancy have partially substituable effects on bet-hedging, escape from high density and escape from sib competition: more dormancy results in less selection for dispersal and vice versa (Venable et al. 1995).

Venable (1985b) developed a model of the ecology and evolution of seed heteromorphism. In most heterocarpic species, seeds dispersed locally display delayed germination i.e. spread over time, and thus establish themselves with a high degree of success, even in poor years. These seeds exhibit a "low-risk" strategy. Seeds dispersed over large distances show less control over germination and may germinate quickly, which can be advantageous if subsequent environmental conditions are favourable, but the fast germination may also be hazardous because of unpredictable and unfavourable environmental conditions at the site of germination. This type represents the "high risk" strategy. On the bases of "low-risk" and "high-risk" concept he divided heterocarpic plants into two main groups: (a) high-risk-low-risk (HRLR) heteromorphism (e.g. *Atriplex dimorphostegia, Chenopodium album, Halogeton glomeratus, Salicornia europaea, Grindelia squarrosa, Gymnarrhena micrantha, Heterotheca latifolia, H. grandiflora, Heterosperma pinnatum, Senecio jacobaea, Xanthium canadense, Alysicarpus monilifer* – for references see legend of Fig. 3), and (b) high-risk-high-risk (HRHR) heteromorphism (e.g. *Hypochoeris glabra, Emex spinosa* – for references see caption of Fig. 3). These two kinds of heteromorphism may arise when evolution of seed morph behaviour is constrained by a different way in different seeds on the same plants. The HRLR heteromorphism is (defined by Venable 1985b) "inferred when the conditions for germination are similar for two seed morphs but more restricted for one of them". For example, the disk achenes of *Grindelia squarrosa* germinate more rapidly and over a broader temperature range than the ray achenes (McDonough 1975). The HRHR heteromorphism is "inferred when the germination of one seed morph is controlled by one environmental factor, while germination of the other seed type is controlled by a different factor". An example of a species classified as HRHR heteromorphism is *Hypochoeris glabra*. Beaked achenes are more light sensitive, whereas unbeaked achenes are more temperature sensitive (Baker et O'Dowd 1982).

Dramatic seed heteromorphism often occurs in such taxa where seeds on different parts of the plant have different preexisting constraints on their evolution, such as in the frequently mentioned ray vs. disc flowers in *Asteraceae* (McEvoy et Cox 1987, Kigel 1992). The second possibility are chasmogamous (CH) vs. cleistogamous (CL) flowers in many grasses and other groups (Cheplick et Clay 1989). Potentially cross-pollinated CH flowers are often produced in addition to the CL flowers on an individual. Besides differences in breeding system, there may be differences in floral phenology (Schemske 1978, Waller 1980, Cheplick et Quinn 1982, Schoen 1984), development (Lord 1981), and/or morphology (Lord 1981, Campbell et al. 1983, Ellstrand et al. 1984) between CH and CL flowers. Morphological differences often include size dimorphism between seeds from CH and CL flowers (Schoen 1984, Cheplick 1987) which may also differ in their germination requirements (Baskin et Baskin 1976, Evenari et al. 1977, Flint et Palmblad 1978, Weiss 1980, McEvoy 1984, Venable et Levin 1985a, Venable et al. 1987). However, the ontogeny of flower and seed differences in dimorphic species has rarely been investigated (Silvertown 1984).

The two types of structure may occur simultaneously on one individual and constitute a multiple strategy, or occur separated in time and compose a conditional strategy (sensu Lloyd 1984). One example of a strategy that is either multiple or conditional is the production of both open and potentially outcrossed CH flowers, and closed, selfed CL flowers. This strategy has been recorded in 56 angiosperm families (Lord 1981). Concerning the regulation of flower-type it is possible to discern at least two different types of cleistogamous species: those in which allocation to CH and CL flowers is mediated largely by plant growth and plant size, and those where photoperiod and temperature determine the floral form produced (Lord 1981).

The production of genetically diverse offsprings via sexual reproduction (CH flowers) may mitigate potential selective disadvantages linked to intense competition among the genetically similar offsprings produced by alternative modes of reproduction that restrict genetic recombination. Possible selective advantages to cleistogene production include reproductive insurance, retention of seed in the parental microhabitat, protection from herbivores, predators, or pathogens, low resource/energy expenditure, and other advantages traditionally linked to inbreeding (Cheplick et Clay 1989, Cheplick 1993).

Future avenues of research

By viewing heterocarpy through particular phases of a plant's life, it appears that some aspects have been investigated intensively (namely germination and dispersal), while our knowledge of the others remains very incomplete (see Fig. 3). Studies following the complete life cycle of heteromorphic species, taking into account different ecological roles of particular diaspore types, are still very rare (*Atriplex triangularis* – Philipupillai et Ungar 1984, Wertis et Ungar 1986, Ellison 1987, Drake et Ungar 1989, Khan et Ungar 1984, 1985; *Heterosperma pinnatum* – Venable 1987, Venable et al. 1987, Venable et al. 1995; *Heterotheca latifolia* – Venable et Levin 1985a, b, Venable 1985a). However, much needs to be done with respect to particular phases of the life cycle; the major gaps and opportunities for further research are still numerous:

Dispersal

So far, relatively little is known about the ecological significance of particular diaspore types in relation to the structure of surrounding vegetation (although most heteromorphic species are typical of arid communities with low cover, some do inhabit closed vegetation), e.g. the availability and features of gaps, type and intensity of disturbances.

Seed bank

Data on long-term dynamics of seed bank, which would provide us with field data on seed persistence, depletion of seed bank due to germination dynamics, factors affecting temporal shifts in germination between particular types, etc, are missing.

Germination

Detailed studies of secondary dormancy and dormancy pattern within one year, i.e. does the dormancy pattern differ between particular types of dormant seeds during a single growing period? Little is known about the competitive ability of plants originated from particular seed types (though indirect information via difference in size is available), i.e. how do the changes in proportions of particular seed types affect fitness of the population? Does the strength of maternal effect (expressed as a gradient of density and nutrient availability) differ between particular seed types with different dormancy-breaking mechanisms? Production of another seed type as a mean of escape from sib-competition also deserves further attention (number of heteromorphic species that are self-pollinated or produce cleistogamous flowers).

Predation

It has been almost unknown so far whether there is a differential predation on particular diaspore types of a single heteromorphic plant and if so, is it determined by a seed position on a plant? Also, the possible effect of herbivory on the shifts in ratio of diaspore types remains unknown.

Apart from particular problems related to the phases of life cycle, studies of behaviour of heteromorphic plants on a wide geographical gradient are urgently needed, including comparisons of natural and adventive distribution in the case of aliens. Studies of both phenotypical plasticity and genetic variation would be most useful. Also, the study of seed heteromorphism represents a very convenient opportunity for investigation of the ecology and evolution of seed traits. Comparative ecology of a reasonably large set of heteromorphic species, performed on a wide geographical gradient, appears to be a promising tool for better understanding the ecology and evolution of this fascinating group of plants.

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Souhrn

Tato práce je přehledem našich znalostí o somatickém polymorfismu semen, který je definován jako produkce dvou nebo více typů semen či plodů na jedné rostlině. Z hlediska terminologického je možno tyto druhy rozdělit do dvou základních skupin – (a) druhy amfikarpní vytvářejí vedle chasmogamních nadzemních květů a plodů ještě kleistogamní květy a plody , které se vyvíjejí pod zemí, (b) druhy heterodiasporní, které vytvářejí dva nebo více typů diaspor v nadzemním květenství. Heterodiasporii můžeme dále dělit na (i) heterokarpii – produkce různých typů plodů, (ii) heteroarthrokarpii, kdy dochází k tvorbě jednoho typu plodu, který však obsahuje dva nestejné díly a (iii) heterospermii, tedy produkci různých typů semen v jednom plodu.

Velká pozornost je věnována rozdílnému ekologickému chování polymorfních diaspor v rámci jednotlivých životních stádií rostliny. Diskuse je zaměřena zejména na šíření, banku semen, dormanci, klíčení, vzcházení a přežívání semenáčků, kompetiční schopnosti a predaci různých typů diaspor.

Poté následuje přehled vlivu abiotických podmínek na výsledný poměr jednotlivých typů diaspor a současně zhodnocení ekologického významu těchto změn pro rostliny. Závěrem jsou diskutovány naše znalosti a názory na evoluci amfikarpních a heterodiasporních druhů.

Produkce několika typů diaspor na jedné rostlině je jev, který můžeme nejčastěji zaznamenat u zástupců čeledí *Asteraceae*, *Chenopodiaceae* a *Poaceae*. Většinou jsou to jednoleté druhy obývající aridní nebo semiaridní oblasti či slaniska, tedy biotopy, kde přežití do reproduktivního stadia je velmi nejisté. Tvorba několika typů diaspor je pak ideální strategií, jak se vyrovnat s velmi variabilními podmínkami prostředí. Každý typ diaspory je přizpůsoben jinému aspektu prostředí, což je velmi výhodné pro úspěšné vyklíčení a dokončení životního cyklu.

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