Chapter 3

Maternal Effects on Seeds During Development

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Introduction

In most plant species, the seeds vary in their degree of germinability between and within populations and between and within individuals. Some of this variation may be of genetic origin, but much of it is known to be phenotypic. That is, it is caused by the local conditions under which the seeds matured. These conditions consist of a combination of the microenvironment experienced by the seed due to its position on the parent plant and the abiotic environment of the plant (e.g. the ambient temperature, day length, water availability, etc.).

In different plant species, maternal factors, such as the position of the inflorescence on the mother plants or the position of the seeds in the inflorescence or in the fruit, can markedly influence the germinability of seeds (Evenari, 1963; Koller and Roth, 1964; Datta *et al.*, 1970; Evenari *et al.*, 1977; Thomas *et al.*, 1979; Jacobsohn and Globerson, 1980; Gutterman, 1980/81a, b, 1990a, 1993, 1994a, b, 1996b; Grey and Thomas, 1982). The age of the mother plant during flower induction (Kigel *et al.*, 1979) or seed maturation (Gutterman and Evenari, 1972; Do Cao *et al.*, 1978; Gutterman, 1978a) and, in the case of certain grasses, even the order of the caryopsis that the mother plant originated from can

all have an influence on seed germinability (Datta *et al.*, 1972a).

There are numerous cases recorded of seed germinability being modified by environmental factors operating during development and maturation. Examples include day length (Lona, 1947; Jacques, 1957, 1968; Koller, 1962; Cumming, 1963; Wentland, 1965; Evenari *et al.*, 1966; Gutterman, 1969, 1973, 1974, 1978a, b, 1982a, 1985, 1992b, 1993, 1994b, 1996a, b; Karssen, 1970; Gutterman and Evenari, 1972; Gutterman and Porath, 1975; Pourrat and Jacques, 1975); temperature (Juntila, 1973; Heide *et al.*, 1976); parental photothermal environment (Datta *et al.*, 1972b; Wurzburger and Koller, 1976; Kigel *et al.*, 1977); light quality (Cumming, 1963; McCullough and Shropshire, 1970; Gutterman, 1974, 1992b; Gutterman and Porath, 1975; Jacobsohn and Globerson, 1980; Cresswell and Grime, 1981); and altitude (Dorne, 1981). Achenes of *Lactuca serriola* (which mature during summer and autumn), as well as summer- and winter-maturing seeds on the same mother plants of some biseasonal-flowering perennial shrubs of the *Aizoaceae*, have been found to differ in germinability (Gutterman, 1991, 1992a). Fenner (1991, 1992) reviews environmental effects on seed size, chemical composition and germination.

The maturation of different seeds with different germinability on one mother plant has a very important ecological advantage, especially under extreme habitats, such as deserts (Gutterman, 1980/81b, 1982a, 1983, 1985, 1992a, b, 1993, 1994a, b, c, 1998a; Roach and Wulff, 1987; Fenner, 1991). In such areas, the time (day or night) of the first rains of the season that cause germination may affect the emergence of plants with seeds that require light or dark for germination (Gutterman, 1996a, b). The date, the amount and the distribution of rain, and the temperatures during and following these rains may be completely unpredictable. For example, in the Negev Highlands of Israel, the date of appearance of a rainfall that causes germination could range from mid-November to the end of February (3.5 months). In one season, one to three rains could cause germination (Gutterman, 1982a) when, in most years, the long, hot, dry summer starts towards the beginning of May (Evenari *et al.*, 1982; Gutterman, 1993, 1998a). In many plant species occurring in the Irano-Turanian and Saharo-Arabian phytogeographical regions, including large areas of the Negev and Judaean Deserts, the phenotypic plasticity of seed germination decreases the risk to species survival by increasing the diversity of seed germination (Gutterman, 1993, 1997, 1998a, b). In *Pteranthus dichotomus* (*Caryophyllaceae*) (Evenari, 1963), even seeds from the same inflorescence may germinate in different years. A similar phenomenon of intermittent germination is also found in the germination of some other plant species, including weeds, that survive under unpredictable conditions (Harper, 1977; Gutterman, 1985; Cavers, 1995; Baskin and Baskin, 1998). In many plant species, different maternal and environmental factors may increase the phenotypic diversity. This ensures that, during or after a rainfall, only a portion of the total seed bank of a certain plant species will germinate.

It has been found that, in many plant species, the fate of the next generation or generations, as far as the germination of seeds is concerned, is dependent, at least to a certain degree, on the maturation conditions of the seeds when they are still on the mother plant (Datta *et al.*, 1972a, b).

Seed position affecting seed germination

Position in capsules, pods and fruit

Seed position in different organs on the mother plants can affect seed colour, size, morphology and germination in many plant species. Even within a single capsule, the position of a seed may influence its germinability. *Mesembryanthemum nodiflorum* L. (*Aizoaceae*) is an annual desert plant originating in South Africa, with very wide phytogeographical distribution, including the Saharo-Arabian, Mediterranean and Siberian regions. Plants collected from populations in the Judaean Desert near the Dead Sea were studied. This area is in the Saharo-Arabian phytogeographical region, receiving an average rainfall of about 100 mm year^{-1}. The *M. nodiflorum* fruit, which contains about 60 seeds, is a dry capsule and the seeds are dispersed by rain. When the fruit is wetted, the terminal seeds are shed first (after 15 min), followed by the middle and lower seeds, which are shed after 200 and 320 min, respectively. The terminal seeds germinate much more readily than those lower in the fruit. Germination was 61, 5.5 and 1% in the terminal, middle and lower seeds, respectively, after 8 years of storage. These differences persist indefinitely (Fig. 3.1) and can be demonstrated in laboratory-stored seeds even after 28 years. In addition, the terminal seeds have an endogenous annual cycle of dormancy, resulting in high levels of germination in winter and spring and low levels in summer and autumn (Gutterman, 1990a, b, 1994a). The combination of the position effect and the annual rhythm of germination ensures that seed dispersal and germination are spread over time and occur at the right season (Gutterman, 1980/81b).

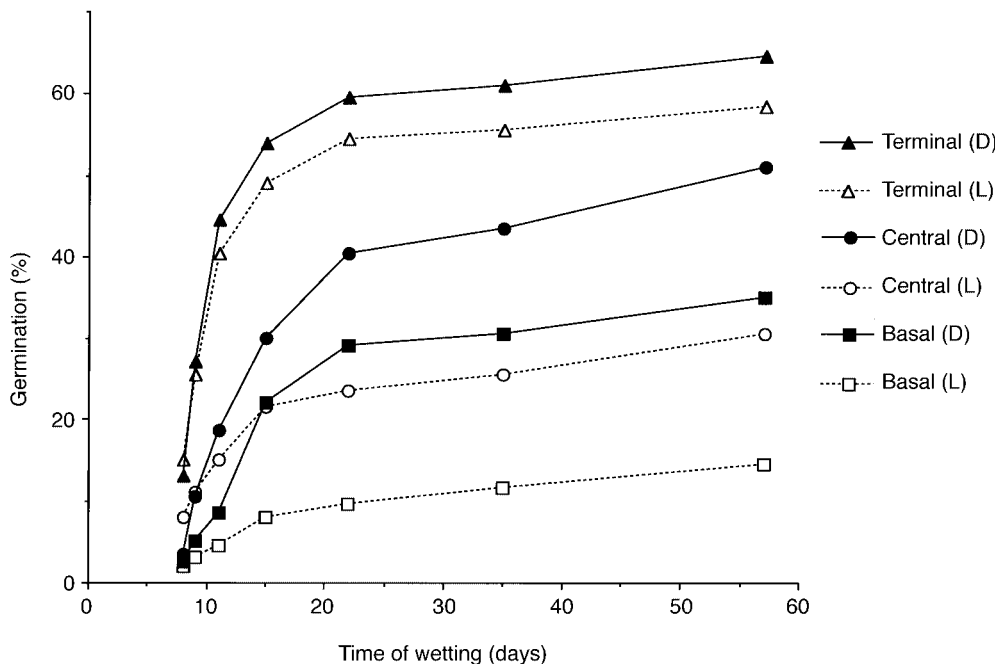In *Medicago* spp. (*Fabaceae*), the spiral pods are multiseeded dispersal units.

Fig. 3.1. *Mesembryanthemum nodiflorum* seed germination according to their position in their capsules – terminal, central and basal groups of seeds – after 19 years of dry storage and up to 60 days of wetting at 15°C in dark and light (from Gutterman, 1990b).

Seed weight and impermeability to water decrease from the calyx to the stylar end (Kirchner and Andrew, 1971; McComb and Andrews, 1974). In *Platystemon californicus* (*Papaveraceae*), the seeds that mature in the carpels of the fruit are much more dormant than seeds formed in the central chamber (Hannan, 1980). In *Cakile edentula* var. *lacustris* (*Brassicaceae*), the pods are divided into two segments. At sub- or supra-optimal temperatures of 25/5 or 15/5°C, in the dark, seeds of the lower segment germinate to higher percentages than seeds of the higher segment (Maun and Payne, 1989; Baskin and Baskin, 1998).

Effect of position of capsules or fruit

In some species, there are often marked differences between seeds from different capsules on the same plant. For example, on one individual of the South African shrub *Glottiphyllum linguiforme* (*Aizoaceae*)

occurring in the Karoo Desert (Herre, 1971), there are central and peripheral capsules that are different in size, number of loculi valves and number of seeds. In Petri dishes, seeds from capsules from the centre, incubated at 25°C for 18 days, germinated to very low percentages, in the light and in the dark. In the same time, under the same conditions, the seeds from the peripheral capsules reached about 80% germination. When seeds from central capsules that had matured during the previous 3 years of the experiment were placed in wet soil, they did not germinate. However, approximately 20% germination was counted in seeds from the peripheral capsules that were placed under the same conditions. The capsules in the central part of the plant are much bigger and contain approximately 200 seeds, whereas the peripheral capsules are smaller and contain approximately 125 seeds. The peripheral capsules are easily separated from the mother plant and it is possible that they act

as a dispersal unit, which could be dispersed by wind or floods. The central capsules remain below the canopy in the central part of the shrub, covered by a hillock that forms below the shrub. These capsules may provide the long-living seeds of the local seed bank, supplying seedlings to replace the dead mother plant (Gutterman, 1990a).

Neotorularia torulosa (= *Torularia torulosa*) (*Brassicaceae*) is common in the Irano-Turanian phytogeographical region. It develops two types of pods, according to the position of the flowers in the inflorescence. On the upper part of the inflorescence, the yellow pods are less lignified and the seeds are dispersed after a light touch to the pod or by wind during the summer following seed maturation. The dark brown pods that develop from the lower flowers of the inflorescence are lignified and the seeds are dispersed only after periods of wetting by rain. The seeds from the yellow pods of the upper part germinate faster and to higher percentages than those from the lignified pods (Gutterman, 1998b).

Heteromorphism (the bearing of seeds of different sizes, shapes or colours) is found in a number of species. In some cases, two types are produced (dimorphism), in others, three (trimorphism). A case of the former is seen in *Salicornia europaea* (*Chenopodiaceae*). This species is one of the highly salt-tolerant annual halophyte pioneers that occupy dried-up saline marshes. It flowers in groups of three, with the middle flower situated above two laterals (Zohary, 1966). The single seed of the median flower is larger and heavier than the single seed produced by the lateral flowers. The large seeds germinate to about 90% after 59 days of wetting and the small seeds germinate to only 50% in the same time. It was also found that, after 6 weeks of stratification and 1 week of wetting, large seeds germinate to 74% in light and to 53% in the dark. In contrast, the small seeds germinate to 30% in light and only 16% in the dark. The recovery of seeds after 56 days in 5% NaCl, when wetted by distilled water for 42 days, was 91%

germination for the large seeds and only 16% for small seeds. The small seeds appear to be much less salt-tolerant than the large ones. Germination percentages in NaCl concentrations were higher for large seeds than for small ones (Ungar, 1979; Philipupillai and Ungar, 1984).

In *Salsola komarovii* (*Chenopodiaceae*), the fruits at the distal position have longer wings and faster after-ripening than the fruits at proximal positions (Yamaguchi *et al.*, 1990). In *Halothamnus hierochutnicus* (= *Aellenia autrani*) (*Chenopodiaceae*), fruits that mature at the distal parts of the branches have narrow wings and produce green seeds that are non-dormant. Fruits at the basal position have thick and wide wings and their seeds are yellow and dormant. Fruits producing green or yellow seeds have also been found in *Salsola volkensii* (Negbi and Tamari, 1963; Werker and Many, 1974; Baskin and Baskin, 1998).

Atriplex dimorphostegia (*Chenopodiaceae*) is an Irano-Turanian and Saharo-Arabian annual desert plant of the sandy and/or saline areas (Zohary, 1966). Two types of dispersal units are formed on the same branch: flat or humped. The humped type appears on the distal ends of the branches and the flat type below them. The flat type appears and matures earlier. When the fruit is separated from the dispersal unit, the one seed of the flat type germinates to 20% at 20°C in light, compared with only 6% for the humped type. In the dark, 68 and 38%, respectively, germinate (Koller, 1954, 1957; Koller and Negbi, 1966). Dimorphic dispersal units are also formed in *Atriplex* species (*Chenopodiaceae*), such as *A. rosea* (Kadman, 1954), *A. semibaccata semibaccata* and *A. holocarpa* (= *A. spongiosa holocarpa*) F. Mueller (= *A. spongiosa*), as well as in *A. inflata* in Australia (Beadle, 1952), in which the fruits also differ.

In *Spergularia diandra* (*Caryophyllaceae*), three different seed types are found. The capsules that develop from the first flowers that terminate the main stem contain black seeds, which have low dormancy. They are the heaviest seeds that develop on this plant. On the hairy geno-

type, the hairs on the seeds are straight, ending in a round knob. The flowers on lateral branches of the main stem develop capsules that contain brown seeds, which are lighter than the black seeds and have a higher percentage of dormancy. The last seeds to mature are those in the capsules of the flowers that appear when the plant is in the process of senescence. These seeds are yellow and are lighter than the black and brown seeds. They have the highest percentage of dormancy and their seed-coat hairs are 'cobra-shaped'. The yellow seeds make up most of the long-term perennial seed bank of these species (Gutterman, 1994b, 1996b; Fig. 3.2).

Hedypnois cretica Dum.-Courset (= *H. rhagadioloides*; (*Asteraceae*), which is a winter annual composite that inhabits Mediterranean and desert areas of Israel, produces three different diaspore morphs: (i) the smallest (1.03 mg) inner achenes, which have a pappus and the highest percentage (77–86%) of germination at 15°C in light; (ii) the larger (2.14 mg) outer achenes, with the lowest germination (41–46%); and (iii) the largest (4.48 mg) marginal epappose achenes, with germination of 42–51% (Kigel, 1992). In *Dimorphotheca polyptera* (*Asteraceae*), found in the Namaqualand desert of South Africa, the three types of diaspores also enable the species to spread germination in time and location (Beneke, 1991).

Effect of seed position in the inflorescence

In *Pteranthus dichotomus*, a Saharo-Arabian annual plant, the whole inflorescence is the dispersal unit. The seed position on the inflorescence influences seed germination. In good conditions, the plant produces dispersal units containing seven pseudocarps, each consisting of a one-seeded fruit, in three orders. The first order contains one pseudocarp, the second order two pseudocarps and the third order four pseudocarps, which are the terminals. In unfavourable conditions, only one or two orders develop. The one to seven seeds are protected for many years in their ligni-
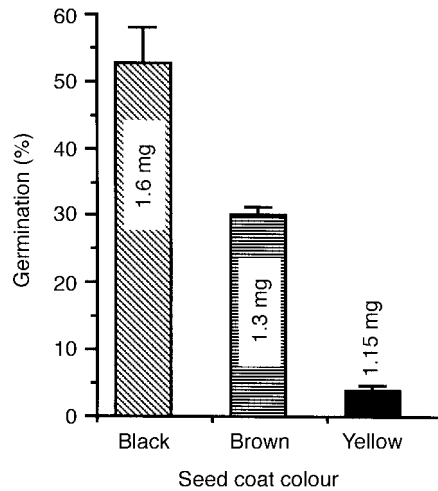

Fig. 3.2. Comparison of germination after 9 days of wetting (average % ± SE of 4 × 50) of black, brown and yellow hairy *Spergularia diandra* seeds harvested on 27 June 1989 from a natural population near Sede Boker. Seeds were wetted on 2 May 1994 at 15°C in the dark for 6 days. The average weight (mg) of 100 seeds is marked. (From Gutterman, 1994b.)

fied dispersal units and usually one seed germinates per year, depending on its position in the capsule. The terminals of each dispersal unit always germinate better than the subterminals. In dispersal units of one pseudocarp, the seed germinates as well as the terminals of order III (Evenari, 1963; Evenari *et al.*, 1982).

Aegilops geniculata (= *A. ovata*) (*Poaceae*) is common in the Mediterranean phytogeographical region. The spike, composed of two to four spikelets, is the dispersal unit (Fig. 3.3). In a dispersal unit spike with three spikelets, each of the lower spikelets contains two caryopses (grains), a_1, a_2 and b_1, b_2. The terminal spikelet contains only one caryopsis, c. Germinability, time of emergence and subsequent time to flowering all vary between spikelets. Even caryopses from the same spikelet differ in this way. Thus, when caryopses were sown under short days or long days, a_1 and b_1 caryopses gave higher germination and emerged and flowered more quickly than caryopses a_2 and b_2. Plants originating from caryopsis c had the lowest germination after the longest time
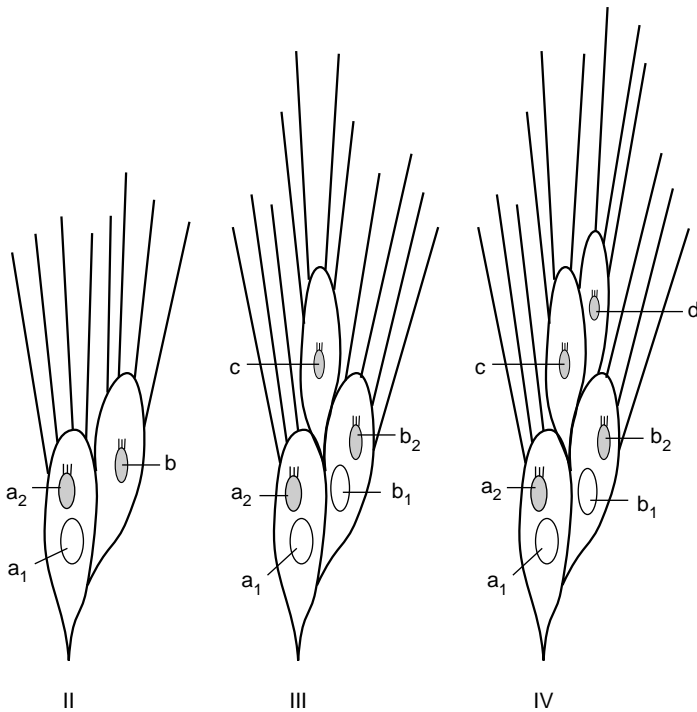
Fig. 3.3. Schematic drawing of the three types of spikes (II, III, IV) of *Aegilops geniculata*. Position and number of caryopses (a_1– d) shown in the different spikes containing II, III or IV spikelets. (Adapted from Datta *et al.*, 1970.)
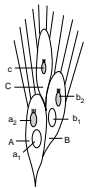
and also had the longest time to flowering. The position of the caryopses in the dispersal unit has an influence on their germination and the plant development for more than one generation (Datta *et al.*, 1972a; Table 3.1).

When lettuce, *Lactuca sativa*, achenes were imbibed in leachate from hulls of *A. geniculata* spikelets a, b and c of a three-spikelet dispersal unit (25.6 g hulls 300 ml^{-1} water), an inhibitory effect by the leachate was observed. The inhibitory effect is highest in hulls from c spikelets and lowest in hulls from a spikelets (Datta *et al.*, 1970). Under dark conditions, the inhibition is much smaller. The main inhibitor was found to be monoepoxylignanolid (MEL), which inhibits *L. sativa* cv. 'Great Lakes' in incandescent light but not in the dark (Lavie *et al.*, 1974; Gutterman *et al.*, 1980). The different caryopses of a dispersal unit are thus different in size, weight, colour and germinability. There is

also a difference in the inhibitory effect of the hulls of the different spikelets of the dispersal unit. All of these components are involved in the heteroblasty of the caryopses of this plant. This ensures the spread of germination of the caryopses of each spike in time. Only one or two caryopses out of any one spike were observed to germinate in one season in the field. Similar results were observed in *Aegilops kotschyi* (Wurzburger and Koller, 1976). Differing germinability has also been found in caryopses of *Aegilops neglecta*, *Aegilops triuncialis*, *Agrostis curtisii*, *Avenula marginata* and *Pseudarrhenatherum longifolium* (all *Poaceae*) (Gonzalez-Rabanal *et al.*, 1994). In the spikes of all of these grasses, the lower caryopsis is larger than the upper one and less dormant.

The position of a seed in an individual bur or capitulum can influence its germinability. For example, in *Xanthium canadense* (= *X. strumarium* var. *canadense*)

Table 3.1. Position effect on average weight (mg) and germination (% ± SE) after 24 h in light at 15°C on *Aegilops ovata* caryopses harvested from plants originating from a_1, b_2 and c caryopses and grown under 18 h long days at day/night temperatures of 15/10°C and 28/22°C (from Datta *et al.*, 1972b).

Three-spikelet (A, B and C) dispersal unit and position of caryopses (a_1–c)	Order of caryopses from which mother plant developed	Order of caryopses collected from mother plant	Average weight of caryopses (mg)		Germination (%)	
			15/10°C	28/22°C	15/10°C	28/22°C
	a_1	a_1	20.6 ± 0.7	13.9 ± 0.5	84.4	100.0
		b_2	9.5 ± 0.8	6.7 ± 0.3	10.0	60.0
		c	6.1 ± 0.6	3.0 ± 0.3	8.5	63.1
	b_2	a_1	22.9 ± 0.5	12.9 ± 0.4	55.0	100.0
		b_2	9.2 ± 0.2	7.1 ± 0.2	2.3	85.3
		c	3.8 ± 0.4	3.0 ± 0.2	0	90.0
	c	a_1	27.3 ± 1.9	14.7 ± 1.7	21.2	100.0
		b_2	13.0 ± 0.3	6.9 ± 0.8	0	76.0
		c	4.2 ± 0.7	3.5 ± 4.2	0	86.7

(*Asteraceae*), the upper seed of two in the dispersal unit germinates before the lower one (Crocker, 1906). However, in *X. strumarium*, after 12 weeks of cold stratification, the two seeds germinated together in 18% of the dispersal units or burs (Baskin and Baskin, 1998). In *Trifolium subterraneum* (*Fabaceae*), the larger seed in the bur germinates before the small one. In the three-seeded spikelet burs of *Cenchrus longispinus* (*Poaceae*), the seed in the central spikelet is largest and comes out of dormancy after dry storage much earlier than the smaller seeds of the lateral spikelets (Baskin and Baskin, 1998).

In *Asteriscus hierochunticus* (= *A. pygmaeus*) (*Asteraceae*), there are mechanisms that delay achene dispersal and spread dispersal and germination over time. The capitula are closed when dry and open when wet. During some rain events, a few of the peripheral achenes are dispersed (Fahn, 1947). Only disconnected achenes germinate (Koller and Negbi, 1966). The percentage germination of achenes from the peripheral whorls is much higher than that of achenes from the sub-peripheral whorls. Each year, some of the achenes are disconnected and dispersed by rain. The aerial seed bank of this desert annual can remain protected in the capitula of the lignified dead mother plant for many years (Gutterman and Ginott, 1994).

Where plants have hermaphroditic flowers and female-only flowers in the same inflorescence, their seeds may differ in germinability. For example, *Parietaria judaica* (= *P. diffusa*) (*Urticaceae*), a perennial herb found in shady habitats in the Mediterranean and Irano-Turanian regions, has an inflorescence of this type. The central female flower opens first and the hermaphroditic flowers 2–4 days later. Seeds from female flowers were found to have higher germinability than seeds from the hermaphroditic flowers. The same is true of their longevity: after maturation or 1–2 years of storage, the seeds from female flowers germinate earlier than those from hermaphroditic flowers, and the seeds from female flowers are mainly heterozygotic. The seedlings from these seeds are more resistant in unpredictable conditions than the seedlings from hermaphroditic flowers. Furthermore, the dispersal units of the seeds originating from the female flowers are more hairy and can be dispersed further. This correlates with the fact that the seedlings do not compete well with the adult plants. Seeds from female flowers produce plants that grow well, far away from the adult plants, and are more resistant to water stress in comparison with the seeds from the hermaphroditic flowers. The latter are dispersed over only short distances and their seedlings grow well near the adult plant (Roiz, 1989).

In the *Apiaceae*, seeds from different positions on the umbel vary greatly in size and degree of dormancy. In three cultivars of celery, *Apium graveolens*, a difference in the achene ('seed') weight and germination was found, depending on the position of the umbels on which they matured. Achenes were collected from primary (p), secondary (s), tertiary (t) and quarternary (q) umbels (Fig. 3.4). Achenes from the primary umbels are the heaviest but have the lowest percentage germination, in comparison with achenes from the other umbels. The highest percentage germination was observed in achenes from the tertiary or quarternary umbels, depending on the cultivar (Table 3.2; Thomas *et al.*, 1979).

Position of the inflorescence on the plant (amphicarpy)

The position effect of the inflorescence on the plant is most marked in species with amphicarpic fruit. One example is *Gymnarrhena micrantha* (*Asteraceae*), a desert annual plant that has telechoric aerial achenes. The hydrochastic capitulum and pappus are opened by rain, after which the achenes are dispersed by wind (Gutterman, 1990b). The aerial achenes differ in their germination requirements from the subterranean atelechoric achenes, which germinate *in situ* from the dead mother plant (Zohary, 1937). The aerial achenes, with a well-developed pappus, are much smaller (0.37 mg) than the subter-
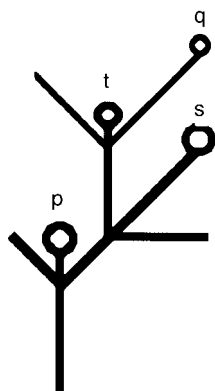
Fig. 3.4. Diagram of the structure of a celery (*Apium graveolens*) inflorescence. p, Primary; s, secondary; t, tertiary; q, quaternary umbels. (From Thomas *et al.*, 1979.)

Fig. 3.5. *Gymnarrrhena micrantha.* Comparison of aerial and subterranean achenes: a schematic drawing (from Gutterman, 1993).

ranean achenes (6.50 mg), which have an undeveloped pappus (Fig. 3.5). At 25°C in the light, final germination of the subterranean achenes was 87% in comparison with 38% for the aerial achenes. In the dark, the subterranean achenes germinated to 30% and the aerial to 4%. In the lower temperatures of 5 or 10°C, germination reached above 90% for both types of achene. However, the seedlings of the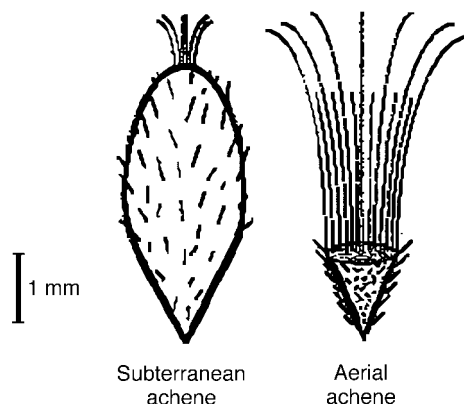 subterranean achenes were much more drought-tolerant than seedlings from the aerial achenes (Koller and Roth, 1964). In some years with above the average amounts of rain and lower temperatures, clusters of seedlings have emerged in the Negev Desert highlands (Evenari and Gutterman, 1976; Loria and Noy-Meir, 1979/80; Evenari *et al.*, 1982; Gutterman, 1993).

Emex spinosa (*Polygonaceae*), a Mediterranean species extending into

Table 3.2. Seed position on umbel, weight (mg) and germination (%) after 21 days at 18°C in light, in three celery (*Apium graveolens*) cultivars. Least significant difference at 5% in parentheses. (From Thomas *et al.*, 1979.)

Cultivars	Umbel position	Mean seed weight (mg)	Germination (%)
'Greensnap'	Primary	0.590	51
	Secondary	0.440	85
	Tertiary	0.386	94
	Quaternary	0.382	80
		(0.069)	(9.8)
'Lathom Blanching'	Primary	0.474	50
	Secondary	0.438	72
	Tertiary	0.380	94
	Quaternary	0.348	82
		(0.069)	(9.2)
'Ely White'	Primary	0.590	59
	Secondary	0.468	62
	Tertiary	0.490	80
	Quaternary	0.520	87
		(0.086)	(7.3)

Saharo-Arabian territories (Zohary, 1966), is another amphicarpic plant. The subterranean propagules, which germinate *in situ* from the dead mother plant, are smooth and much larger (75 mg) than the aerial ones, which are spiny and range from 2 to 24 mg, depending on position. The aerial propagules are dispersed by wind, floods or animals. In this case, the germinability of the aerial propagules is much higher than that of the subterranean ones in all conditions tested in populations that inhabit the Negev Desert (10 versus 0% at 15°C). The leachate of the aerial fruit contains germination inhibitors not found in the subterranean ones. When seeds were transferred for 8 h daily from 15 to 30°C in the dark, the aerial propagules germinated to a much higher percentage 7 days after wetting than the subterranean ones (60 versus 20%) (Evenari *et al.*, 1977). The lower germination of the subterranean atelechoric propagules and their low numbers may be important for preventing competition and ensuring dispersal of germination in time. Usually, only one of the subterranean propagules germinates in one season. The inhibitors that are in the aerial telechoric propagules could have an influence on the amount of rain or washing by floods that is needed before these propagules germinate. These germination inhibitors could act as a rain-gauge or rain clock, ensuring that the germination will take place only after sufficient rainfall has occurred for the establishment of the seedlings. This, in addition to the better germination in the dark and the long time (7 days) of wetting needed for germination, may give the buried propagules a better chance to germinate in more favourable microhabitats, such as depressions and porcupine diggings (Gutterman *et al.*, 1990).

Position effects in the following generation

The position effect can be detected even in the following generation and possibly beyond. An experiment that illustrates this is one in which *Aegilops geniculata* plants were grown from a_1, b_2 and c caryopses and the germination of their grains compared. Germinability of the second-generation grains was markedly influenced by the order of the caryopses from which the mother plant was originally derived. Under cool temperatures (15/10°C), similar to temperatures existing during the growing season of the plant in the natural habitat, large differences were found in germinability between grains from parents derived from caryopses of different orders. However, these were not found when the plants were grown at higher temperatures (28/22°C). It was found that the origin of the mother plant also has an influence on the weight of the different caryopses. It is interesting to note that, in this case at least, the position effect has a very strong influence on the next generation and that its expression is dependent on the environmental conditions under which the second-generation plants are grown (Table 3.1; Datta *et al.*, 1972b).

Age effects

The age of the mother plant can affect the germination of its seeds. For example, in *Amaranthus retroflexus* L. (*Amaranthaceae*), a widespread weed of summer crops (Zohary, 1966), germinability declines with the age of the parent plant at the time of flower induction (Kigel *et al.*, 1979). In *Oldenlandia corymbosa* (*Rubiaceae*), less dormant seeds develop on younger plants in comparison with those from older plants (Do Cao *et al.*, 1978). When these plants were grown under 16 h day lengths, the seeds that matured in July germinated to 80–90%. However, seeds that had matured between August and October germinated to only 1–15% (Attims, 1972). Senescence of the mother plant can affect seed germination too. Seeds of *Trigonella arabica* and *Ononis sicula* (Gutterman 1980/81a) that mature under long days, when the plant has started to dry out at the end of the season, have incomplete seed-coats, which are green or brown. The imbibition and germination of these seeds is much faster than in

the typical yellow seeds matured under long days in younger plants (see section below) (Gutterman, 1993).

In *Spergularia diandra*, the yellow seeds that develop on the plants at the senescence stage have the highest dormancy and are the lightest in weight, in comparison with the black or brown seeds that develop on these plants earlier (see section above) (Fig. 3.2; Gutterman, 1994b, 1996b). *S. marina* seeds matured in July germinated in the greenhouse to 4–8% and seeds that matured in August germinated to 80–82% (Okusanya and Ungar, 1983). However, in cases where seeds are collected from plants grown under natural conditions, it is difficult to distinguish between true age effects and the effect of the changed seasonal environment under which the later seeds develop.

Environmental effects

Effect of maturation under natural conditions

L. serriola (*Asteraceae*), a widespread annual (or biennial), is a long-day plant for flowering (Gutterman *et al.*, 1975). Ripe achenes, which were collected each month separately from July to October 1989 from a natural plant population near Sede Boker, differed in germinability when tested in October and December 1989 and January, March and May 1990. A difference was observed in each month of harvest as well as the period of storage (Fig. 3.6). The plants started to produce seeds from the first capitula in July, when the photoperiodic day length is the longest (15 h), and terminated in October, when the day length is much shorter (12 h), when the majority of the leaves are in senescence (Gutterman, 1992a).

In biseasonal-flowering perennial shrubs, such as *Cheiridopsis aurea* (*Aizoaceae*) from South Africa, which were grown in the Negev Desert highlands, large differences in seed germinability according to the season of seed maturation were found in natural day length and temperatures. Seeds matured in winter, when temperatures are mild and days are short (the shortest being *c.* 11 h on 21 December), or in summer, when temperatures are high and days are long (the longest being *c.* 15 h on 21 June), seem to differ in germination when this occurs in the following growing season (Gutterman, 1991).
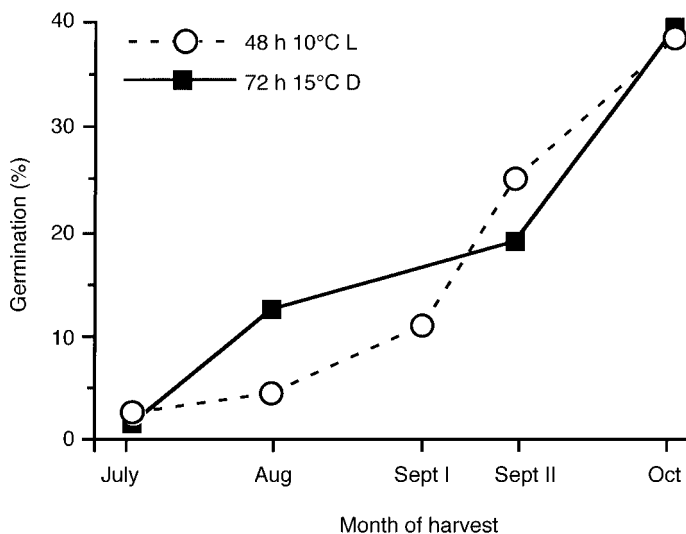

Fig. 3.6. Germination (%) of *Lactuca serriola* achenes after wetting for 48 h in light or 72 h in dark. Achenes harvested from July to October 1989, and tested on 21 January 1990 (after Gutterman, 1992a).

The germinability of *Chenopodium bonus-henricus* seeds that were collected from plants of natural populations from altitudes of 600 m differed markedly from that of seeds collected from plants from altitudes of 2600 m. The higher the altitude, the thicker the seed-coat, the higher the polyphenol content in the seed and the lower the germination. Plants transferred from one altitude to another matured seeds that were typical of the altitude to which they were transplanted. The polyphenols that accumulated in the thicker seed-coats of seeds matured at the higher altitude inhibit germination. It is possible that increase in the polyphenol content is due to increased visible radiation and the lower temperature at the higher elevation (Dorne, 1981).

Day length during seed development

Long- or short-day effect

Day length and other environmental factors may contribute to the phenotypic plasticity and diversity of seed germination in many plant species. The germinability of seeds of many species is affected by day length during seed development and maturation. In some plant species, short days result in higher germinability. For example, when seeds of *Chenopodium album* (*Chenopodiaceae*), a pluriregional plant and a common weed in irrigated crops (Zohary, 1966; Holm *et al.*, 1977), were matured under 8 h days from flower-bud formation, the germination was higher in comparison with seeds matured under 18 h days, when tested either in the light or in the dark. Alternating diurnal temperatures (22/12°C) during seed development also resulted in higher germination than in seeds developed under constant temperatures (22/22°C) (Table 3.3; Karssen, 1970).

In *Ononis sicula* Guss. (*Fabaceae*), an annual plant in the southern Mediterranean and Near East regions (Zohary, 1972), treatments of the mother plants during seed maturation affect the germinability of the seeds, through changes in the development of the seed-coat and its surface structure.

Table 3.3. The effect on seed germinability (% ± SE) of *Chenopodium album* of a daily temperature shift (22/12°C) or a continuous temperature (22°C) during the growth of the mother plant under 18 h (LL) or transferred from 18 h to 8 h days at flower-bud formation (LS). Germination was tested in continuous light or continuous dark at 23°C. (Adapted from Karssen, 1970.)

Temperature (°C)	Photoperiodic conditions	Light	Dark
22/12	LS	100	96
	LL	90	42
22/22	LS	85	61
	LL	71	22

Certain day-length treatments modify the seed-coat permeability to water, seed-coat resistance to fungus and seed longevity. Under long days (14.5 to 20 h), yellow seeds were produced with well-developed seed-coats. Under short days (8 to 11 h), there developed brown seeds with undeveloped seed-coats and/or green seeds with intermediate seed-coat structure and water permeability and higher germinability than the long-day seeds (Gutterman and Evenari, 1972; Gutterman and Heydecker, 1973; Gutterman, 1973, 1993).

In *Trigonella arabica* (*Fabaceae*), an annual desert plant with a Saharo-Arabian geographical distribution, yellow seeds or yellow seeds with green spots are developed during maturation under long days and green seeds or brown seeds are developed during maturation under short days. The seed-coat structure is well developed in the less permeable yellow seeds, in comparison with the less-developed seed-coat of the brown seeds, which also have the most permeable seed-coats (as in *O. sicula*) (Gutterman, 1978c). These day-length influences on the seed-coat are dependent on the last 8 days of maturation, when the fruit has reached its final size but is still green. At this stage it was shown that when seeds mature under 8 h days on plants in which half the fruits are covered with aluminium foil, seeds from both covered and uncovered fruits germinated to 100% after 3 weeks of wetting. In contrast, the seeds matured on plants under 15 h days, from both covered and uncovered fruit, swelled only 29 and 10%, respectively. This

indicates that the effect of the different day lengths is not due to action directly on the developing seeds, but is transmitted to the seeds from the vegetative parts of the mother plant (Gutterman, 1998a).

Seeds of *O. sicula* or *T. arabica* that mature on a young plant under long days have a well-developed seed-coat and are referred to as 'hard seeds' (impermeable to water). These are possibly the long-term seeds of the seed bank in the soil. The seeds that mature on the same mother plants during the short days have seed-coats that are more water permeable and are possibly the short-term seeds of the seed bank (Gutterman and Evenari, 1972; Gutterman, 1973, 1978c, 1993).

Quantitative short-day effect

Portulaca oleracea (*Portulacaceae*) is an annual plant of the warm-temperate regions of the world (Zohary, 1966) and is listed as one of the eight most common weeds on earth (Holm *et al.*, 1977). Seeds matured on plants grown under 8 h days germinate to a higher percentage than seeds from plants grown under 16 h days. This day-length effect is a quantitative short-day effect, and the critical time is the last 8 days of seed maturation. When plants were transferred from 16 h days to either 13 h or 8 h days during the last 8 days of maturation, the seeds increased their germinability. The shorter the day length, the higher the germination (Fig. 3.7; Gutterman, 1974). This also applied in the case of *Chenopodium polyspermum*, an annual plant of wasteland and cultivated ground. The shorter the day length (from 24 h to 10 h), the higher the germination and the heavier the seeds (Table 3.4). The seed-coat thickness of seeds matured under 8 h days is 20 µm, in comparison with 46 µm of seeds matured under 24 h days. Scarification of the seed-coat brings the seeds to 100% germination (Jacques, 1968). This was also seen in *C. album* (Karssen, 1970).

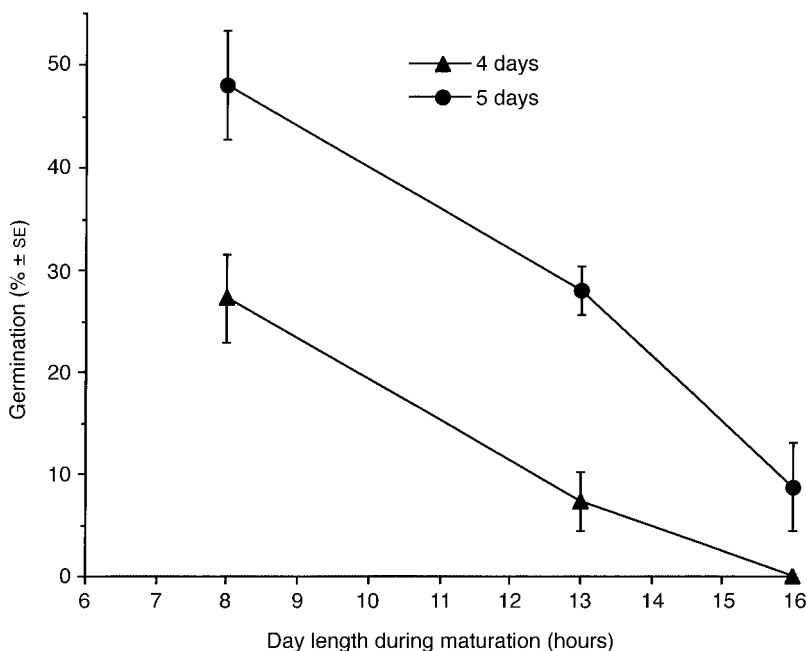**Fig. 3.7.** The influence of the change of day length during the last 8 days of maturation of *Portulaca oleracea* L. seeds, from 16 h to either 13h or 8 h days on germination at 40°C in the dark with 5 min of white light, once in 24 h. The first illumination was given 1.5 h after wetting (four batches of 50 seeds each per treatment). Germination (% ± SE) after 4 and 5 days. (From Gutterman, 1974.)

Table 3.4. The influences of 10, 12, 14 and 24 h day-length treatments of *Chenopodium polyspermum* plants during seed maturation on seed weight and seed germinability (from Jacques, 1968).

	Day length (h)			
	10	12	14	24
Weight (mg) of 100 seeds	63	54	45	23
% Germination	80	26	6	0

Day length also affects seed germination in plants with soft fruit. The tomato, *Lycopersicum esculentum* (*Solanaceae*), is a natural day-length plant for flowering but the day length has been found to affect the seed germination. Under 6 h days in over-ripe fruit, 38% of seeds were found to germinate in the fruit in comparison with only 0.2% that germinated when the plant was under a day length of 13 h. None of the seeds were found to germinate in fruit of plants under 20 h days. Tomato seeds harvested from plants that were under 6 h days germinated to a much higher percentage in comparison with seeds from plants grown under 20 h days. The differences in germination were found to be even greater when the fruit was covered with aluminium foil. Almost the same results were seen as in *T. arabica* (Gutterman, 1978c, 1998a). The day length during fruit maturation also has an influence on the inhibitory effect of the juice of the tomato fruit. When lettuce achenes were imbibed in half-strength tomato juice from fruit matured under 6 h days, the percentage of germination of the lettuce achenes was much higher than that in juice from fruit matured under 20 h days (58 versus 8%, respectively). Moreover, these soft fruits respond to day length when they are separated from the mother plant and there is an effect of the day length on the germinability of the seeds. In this situation, the isolated fruit responds in the same way as it does on the mother plant. In postharvested tomato fruit that were exposed to 6, 9 or 17 h of day length during fruit ripening and seed maturation, the ethylene amounts released were found to be affected quantitavely by the day length. The longer the day length, the higher the quantities of ethylene that were released from the fruit, even after a single photoperiod. This phenomenon lasted for a number of days until the fruits were fully ripe. The application of ethephon (which releases ethylene) to the tomato fruits during storage under the different photoperiods increased the effect of day length on ethylene release. These treatments also have an effect on the germinability of the seeds harvested from the fruits treated with ethephon under different day-length regimes (Gutterman, 1978b).

In cucumbers, *Cucumis sativus* (*Cucurbitaceae*), postharvested fruit stored for 15 days under different photoperiodic regimes were found to have an influence on the germination of their seeds even after the seeds had been kept for 270 days in dry storage. The seeds were wetted at 20°C in dark and the germination, after 24 h of wetting, was 84% for seeds from postharvested ripe fruit kept at 8 h days and only 12.5% for seeds from fruit held under long days. Injection of ethephon into the soft fruit of cucumbers affects the germination response to day-length treatments in the opposite direction: only 2% for seeds from fruit kept at 8 h days and 79% from fruit held under long days (Gutterman and Porath, 1975; Gutterman, 1978b). It is well known from other plant species that hormone application to plants during maturation has an influence on seed germinability (Zeevaart, 1966; Jackson, 1968; Ingram and Browning, 1979; Baskin and Baskin, 1998). Specific examples are *Avena fatua* (Black and Naylor, 1959), *Lactuca scariola* (Gutterman *et al.*, 1975), *Phaseolus vulgaris* (Felippe and Dale, 1968) and *Salsola komarovii* (Takeno and Yamaguchi, 1991).

Quantitative long-day effect

In contrast to all of the above cases, there are some species in which short days result in lower germinability. *Cucumis prophetarum* is a perennial desert plant distributed in the East Saharo-Arabian phytogeographical region. Seeds from postharvested soft fruit of *C. prophetarum* that had

been stored under day lengths of 8, 11, 13, 15 and 18 h were tested for germination. After 7 days of wetting at 20°C in light, the longer the storage day length of the fruit from which the seeds had originated, from day length of 8 to 15 h, the higher their germination percentages (Gutterman, 1992b).

Polypogon monspeliensis (*Poaceae*) plants were grown under six different day lengths, outdoors as well as in the greenhouse, during vegetative growth and seed maturation. In seeds harvested both outdoors and from greenhouse conditions, the longer the day length, the higher the percentage of germination at 25°C in continuous light (Table 3.5; Gutterman, 1982a). Similarly, after 7 days of wetting at 10°C in the dark, *Schismus arabicus* (*Poaceae*) 'seeds' that had developed and matured under constant day lengths of 8, 12 or 18 h showed a facultative long-day response in natural outdoor conditions at Sede Boker. This response was less pronounced in greenhouse conditions (Gutterman, 1996a). *S. diandra* black hairy seeds that developed and matured under day lengths of 8, 12 or 18 h also showed a quantitative long-day response for germination after 47 days of wetting (Gutterman, 1994b).

Carrichtera annua (*Brassicaceae*), an annual desert plant from the Saharo-Arabian geographical region (Zohary, 1966) has a day-length-independent response for flowering (Evenari and Gutterman, 1966). However, seeds matured on plants under 20 h days have much better germinability

(51.5%) in comparison with seeds from 8 h days (7% germination) when germinated at 25°C in light (Gutterman, 1973). Potted plants of this species were transferred from natural day length of 13 h to either 8 h or 20 h days, after the green fruit that had achieved the final size were covered with aluminium foil. The seeds that matured in the covered fruit at the three day lengths, 8, 13 and 20 h, were compared for their germination at 25°C in the light 144 h after wetting. Again, the longer the day length, the higher the percentage germination (Gutterman, 1978b). From these results, it is possible to speculate that *C. annua* seeds matured under long days in the late spring are the seeds that will germinate first. The seeds that are matured under short days in the early winter are the seeds that will remain in the seed bank for an extended period. Since the fruit was covered, the photoperiodic effect on seeds must be mediated via the leaves and green stems of the mother plants, as was shown in *T. arabica* (Gutterman, 1978c) and *L. esculentum* (Gutterman 1978a).

The critical time of day length during seed maturation

In *O. sicula*, *T. arabica* (Gutterman and Evenari, 1972; Gutterman, 1978c), *Lactuca sativa* (Table 3.6; Gutterman, 1973), *Portulaca oleracea* (Fig. 3.7; Gutterman, 1974) and *C. annua* (Gutterman, 1978b,

Table 3.5. The influence of different day lengths during growth and seed maturation, under greenhouse or outdoor conditions, on seed germinability of *Polypogon monspeliensis*. The photoperiodic treatments started from 20–24 December 1979 until the harvesting of the seeds in March 1980. The seeds were wetted at 25°C in light in October 1980 and the results were observed after 3 days of wetting. (From Gutterman, 1982a.)

Day length during growth of mother plant and seed maturation (h)	Seeds from greenhouse plants: germination (%)	Seeds from outdoor plants: germination (%)
9.0	0.0	1.5
11.0	0.0	9.5
12.0	17.5	64.0
13.5	38.0	98.5
15.0	60.5	97.0
18.0	90.5	98.0
Control (natural day length)	93.0	91.5

Table 3.6. Photoperiodic treatments given to the plants of *Lactuca sativa* 'Grand Rapids 517' and the germinability of their seeds (% ± SE), at 26°C in the dark with short (5 min) illumination of white light. There were 200 (4 × 50) seeds in each treatment. The germination experiment began immediately after harvest. (From Gutterman, 1973.)

Photoperiodic conditions during growth of mother plants	Germination (%) after 2 days	Germination (%) after 11 days
SD, then LD (80)[a]	0	4 ± 1.4
LD, then SD (80)	29.5 ± 2.6	32 ± 3.2
SD, then LD (12)	5 ± 1.2	8 ± 1.4
LD, then SD (12)	13.5 ± 3.4	18 ± 3.4
Continuous LD	5 ± 0.6	6 ± 0.8
Continuous SD	16.5 ± 2.2	24 ± 2.5

[a] Number of days under the photoperiodic conditions before harvest.
SD, short day, 8 h; LD, long day, 16 h.

1982a), the critical time for the day-length effects is during the last stages of seed maturation: that is, from the time when the fruit reaches its final size but is still green, to full maturation 7–14 days later (Gutterman, 1978c). In soft fruit, such as cucumbers and tomatoes, 5–15 days are also sufficient for the day-length effect (Gutterman and Porath, 1975; Gutterman, 1978a). The importance of the final period of seed maturation in determining germinability is seen in lettuce. *L. sativa* plants were transferred from long days to short days or vice versa 12 days before the harvest of the achenes. Controls were maintained at either constant long or constant short days. Seeds from plants grown under short or long days in the last 12 days of ripening (having been transferred from the other day length) behaved like those grown under continuous short or long days, respectively (Table 3.6). In *Chenopodium album*, the transfer from long to short days at flower-bud formation increased germination in comparison with that obtained from seeds of plants kept under continuous long days (Karssen, 1970). In *C. polyspermum*, the 8 days after flower-bud formation is the critical time (Pourrat and Jacques, 1975).

Influences of light quality during maturation on seed germination

Light quality during seed maturation can influence germinability. For example, in *Arabidopsis thaliana* (*Brassicaceae*), seeds matured under white light with a high red/far-red (R/FR) ratio have a higher dark germination than seeds from plants grown under light with a low R/FR ratio (McCullough and Shropshire, 1970). Seeds matured under incandescent light (high R-absorbing phytochrome (P_r)) require light for germination but not seeds matured under fluorescent light (high in FR-absorbing phytochrome (P_{fr})). Immature seeds are sensitive to light quality up to 1 day before full seed maturation (Hayes and Klein, 1974).

The quality of the light received at particular times in the 24 h cycle is crucial in determining seed germinability – for example, in *Portulaca oleracea*, which has a quantitative response to day length during maturation affecting germination (Fig. 3.7; Gutterman, 1974).

It seems that the light treatments during *P. oleracea* plant development and seed maturation have different influences on the number of leaves at the time of the appearance of the first flower-bud and the germination percentages of the seeds harvested from these plants. These different responses of flowering and seed germination are even more pronounced after treatment of 8 h R or FR light given before or after the 8 h dark (D) period, in comparison with 8 h of white light following the 8 h of daylight. The 8 h R or FR following the 8 h of daylight has a 'short-day effect' on the number of leaves at flower-bud appearance and the 8 h R or FR following the 8 h D has a pronounced 'long-

day effect' on the number of leaves at flower-bud appearance. But all of these four treatments have a 'short-day effect' as far as the germination percentages are concerned. This is different from the treatment of 8 h white light, which has a 'long-day effect' for both flowering and germination (Gutterman, 1974). It is interesting to note that the photoperiodic germination response was found in other plant species: *Carrichtera annua*, *Lycopersicum esculentum* and *Cucumis sativus*. In these species there is no photoperiodic effect on flowering but there is an influence on seed germinability. From all the above, it would seem that the mechanisms affecting flowering are different from the mechanisms affecting seed germinability, at least in the plant species mentioned.

If mature and turgid fruit of *Cucumis prophetarum* and *C. sativus* are stored in continuous FR light, the dark germination of their seeds will be reduced because most of their photoreversible phytochrome has been converted to the P_r form. At this stage, the seeds require light to germinate. If such fruit are kept under R light, germination is very high, due to the conversion of the photoreversible phytochrome to the P_{fr} form. The total photoreversible phytochrome has been shown to be much higher in seeds after the storage of the fruit under FR light in comparison with seeds that were separated from fruit stored under R light (Table 3.7). However, after the seeds were exposed to a period of dry storage, these differences in the dark germination completely disappeared (Gutterman and

Porath, 1975). In *Chenopodium album*, the R light effect during seed maturation disappears 4 months after maturation (Karssen, 1970).

Postharvested turgid fruit of *Cucumis prophetarum* were stored in the laboratory for 9 days under continuous R, FR or dark conditions. The seeds were separated and germinated at 20°C in continuous light. Seeds originating from fruits stored in FR light, which contained higher amounts of photoreversible phytochrome (Table 3.7), germinated to high percentages 7 days after wetting, in comparison with seeds from fruit stored under R light, which contained lower amounts of photoreversible phytochrome. The seeds from fruit stored in the dark, which contained high photoreversible phytochrome, reached the highest germination percentages (Gutterman, 1992b, 1993).

Leaf canopies have been found to inhibit germination of matured light-sensitive seeds (Black, 1969; Vander Veen, 1970; Gorski, 1975; King, 1975; Fenner 1980a, b). Only 1 h under leaf-transmitted light is required to inhibit germination in the dark of detached *Bidens pilosa* (*Asteraceae*) seeds (Fenner, 1980b). During seed maturation on the mother plant in different plant species, there is a relationship between the chlorophyll concentrations that surround the developing seeds during the different stages of seed maturation and dehydration. In seeds matured entirely surrounded by green maternal tissues, most of their phytochrome will be arrested in the inactive P_r

Table 3.7. Amounts of photoreversible phytochrome, the state of phytochrome in the seeds in the postharvested fruit and germination (% ± SE) (at 25°C) of *Cucumis prophetarum* (after 50 h) and *C. sativus* seeds (after 170 h), influenced by fruit storage under different light conditions (at 23–25°C) (adapted from Gutterman and Porath, 1975).

Species	Light conditions to the harvested fruits	Photoreversible phytochrome in the seeds (Δ OD) $\times 10^{-4}$	Far-red-absorbing phytochrome in seeds (% P_{fr})	Seed germination (%) in the dark
C. prophetarum	Red	8.6 ± 0.4	93.5	100.0
	Far red	20.0 ± 0.7	0.0	0.0
C. sativus	Red	24.0 ± 2.1	53.3	91.9 ± 4.3
	Far red	35.1 ± 2.0	0.0	27.5 ± 4.3
	Dark	36.4 ± 1.8	8.5	22.5 ± 2.5
	Sunlight	28.8 ± 2.0	47.2	100.0

OD, optical density.

form and therefore these seeds will require a light stimulus for germination in the dark (Cresswell and Grime, 1981).

Water stress during maturation affecting seed germination

Desiccation during maturation enhances germinability. For example, the green pre-mature seeds of *Hirschfeldia incana* (*Brassicaceae*) did not germinate when wetted 4–6 weeks after anthesis (WAA). However, when seeds were taken off the parent plant 4–6 WAA and dried for 2 weeks at room temperature, they remained green but germinated to 91% when wetted in the light at 26°C (Evenari, 1965). Similarly, immature developing seeds of soybean (*Glycine max*) will not germinate when wetted unless they are previously desiccated (Adams *et al.*, 1983). However, in soybean plants exposed to drought stress levels during seed fill, the greater the number of stress days, the lower the standard germination percentage (Dornbos *et al.*, 1989). Drought during seed maturation may affect seed germinability by changing the properties of the maternal tissue surrounding the seed. Benech Arnold *et al.* (1992) showed that the increased germination of seeds of *Sorghum halepense* subjected to drought during maturation was due to a modification of the glumes rather than of the caryopses themselves.

Immature developing seeds of castor bean (*Ricinus communis*) and *Phaseolus vulgaris* that were removed from the capsules and wetted did not germinate. When such seeds were removed and stored at relatively high humidity, their water content slightly declined and they germinated when immersed in water (Bewley *et al.*, 1989). Water stress during stages of seed maturation may cause it to switch from the seed-developing system to the seed-germinating system (Kermode *et al.*, 1986). This switch involves changes in protein patterns (Lalonde and Bewley, 1986) and messenger RNA (mRNA) (Bewley *et al.*, 1989). Desiccation also induces changes in mRNA population within the endosperm of *R.*

communis (*Euphorbiaceae*) (Kermode *et al.*, 1989).

Out of 13 plant species examined in the literature by Baskin and Baskin (1998), water stress during seed development decreased dormancy in seven species and increased it in six. There seems to be no consistent pattern distinguishing species with physiological dormancy from those with physical dormancy.

Temperatures during maturation affecting seed germination

In different plant species, sometimes even small differences in temperature during plant development and seed maturation can have an influence on the germinability of the seeds produced by these plants. For example, germination of *Amaranthus retroflexus* seeds was higher when matured under temperatures of 27/22°C than under 22/17°C. Similarly, in *Aegilops ovata* (*A. geniculata*), maturation temperatures of 28/22°C produced caryopses that were more germinative than those grown at 15/10°C (Datta *et al.*, 1972a; Table 3.1). In both these cases, the higher temperature resulted in seeds with higher germinability. The seeds produced under warmer conditions were lighter than those which developed at lower temperatures.

In some cases, there is an inverse relationship between maturation temperature and germinability. For example, in soybeans, Keigley and Mullen (1986) found that the more accumulated days of high temperatures (32/28°C) after flowering, the lower the germination in comparison with maturation and seed fill under temperatures of 27/22°C. The germination of *Chenopodium album* seed was lower after maturation at 22/22°C than at 22/12°C (Karssen, 1970). The question of the effect of temperatures during seed development on their subsequent germination needs more detailed study. In this connection, Plett and Larter (1986) show the importance of testing germination over a range of temperatures when investigating the effect of maturation temperature. The maturation

temperature resulting in the highest germination depended on the germination temperature at which the seeds were tested.

Baskin and Baskin (1998) have summarized the responses when mother plants produce seeds under different temperatures. They found that an increase in temperatures during the time of seed development has a preconditioning effect on at least four plant species to decrease seed dormancy. Under controlled temperatures, many plant species that grow under higher temperatures produce seeds with higher germinability. Fenner (1991) lists 15 cases where high temperatures during maturation result in lower dormancy. However, three plant species, grown in higher controlled temperatures produce seeds with increased dormancy. In still other plant species, the time of exposure to varying temperatures during seed development has an important effect on seed germination requirements.

Mineral nutrition

Baskin and Baskin (1998) have summarized 24 plant species in which different mineral nutrients affect seed germination as preconditioning during seed development. As a general rule, the addition of nutrient fertilizers (notably nitrogen) to parent plants decreases dormancy in the seeds. Fenner (1991) cites a number of such cases. The physiological mechanism involved is unknown.

Conclusions

From the examples given in this chapter, it seems that, in various plant species, seeds with different germinability develop on the same mother plant and on plants of the same species growing in different environments; maternal position and environmental factors cause these differences by their influence on plant development and seed maturation. At least in some species, it was shown that the last 5–15 days of seed maturation is the critical time.

The genotypic influences of a plant species ensure that the adaptation of the plant to its habitat conditions is such that germination is likely to occur in the right season and in the right place. The phenotypic influences, including environmental and maternal effects, during maturation on seed germination ensure that, even under optimal conditions, only a portion of the seed population will germinate in one rain event or in one season. It was observed in the Negev Desert highlands that only one, or at most two, seedlings appear in one season from a dispersal unit of the desert plant *Pteranthus dichotomus* containing seven pseudocarps (seeds). The same phenomenon was observed in the Mediterranean plant *Aegilops geniculata* (= *A. ovata*) in its natural habitat. Out of five or six caryopses of a dispersal unit, only one or two seedlings appear in one season. In *Ononis sicula* and *Trigonella arabica*, the brown seeds with the undeveloped seed-coats will swell and some of these will germinate in the following season, along with a small portion of the green seeds. The yellow seeds with the well-developed seed-coats will germinate much later.

The importance of this heteroblasty for the survival of species by dispersing the germination in time is obvious. The main question is whether there is 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? Whether the first or the second possibility is the correct one, the biochemical events that are involved in these phenomena are still not known. At this stage, we can only speculate, as has already been done in the past (Gutterman, 1980/81b, 1982b, 1985, 1993), that it is possible that during seed maturation the different factors affect the accumulation of different relative amounts of materials that are involved later on in the germinability of the seeds, which could react through three main pathways:

1. They could lead to the development of seed-coats with different degrees of impermeability, according to the day length and age effects, as was observed in some species of the *Fabaceae*: *O. sicula* (Gutterman, 1973) and *T. arabica* (Gutterman, 1978c).

2. These materials may result in an accumulation of germination inhibitors in the fruit, as was found in tomato, and/or in the embryos and hulls, as was found in *A. geniculata* (Datta *et al.*, 1972a, b). There could be an accumulation of germination inhibitors, such as polyphenols, in the seed-coats that increase with the higher altitude, as was found in *Chenopodium bonus-henricus* (Dorne, 1981). Is there an accumulation of different materials in the embryo, according to the day length during maturation, that are involved later on in the germination process and result in seed germinability, as was found in *Carrichtera annua*? Such materials could include germination inhibitors.

3. Are part of these materials hormones, such as ethylene? In tomatoes different rates of ethylene are released from maturing fruits, depending upon the length of even one night (Gutterman, 1978a, 1982a). In *Cucumis sativus*, an additional amount of ethylene changes the levels of germination of seeds matured under short days (SD) or long days (LD) to the opposite direction (Gutterman and Porath, 1975). It is possible that, at different elevations, enzymes are activated to produce polyphenols, such as those that accumulate in seed-coats of *Chenopodium bonus-henricus*, and inhibit the germination (Dorne, 1981). Enzymes and other materials that accumulate in the embryo in different relative amounts, according to the environmental conditions during seed maturation, possibly affect the germinability.

In some species of the *Papilionaceae*, the day length affects the water permeability of the seed-coat according to the day length during the last stage of seed maturation. It was also shown that the 'day-length effects' are transferred from the leaves and affect the development of the seed-coat in covered fruit. So far, the biochemistry of this process and the material or materials that are transferred from the leaves to the seeds and affect the process that leads to the degree of seed-coat development have not yet been identified.

Another very interesting point is the fact that, in some plant species, the effect of the environmental factors, such as day length, on flowering differs from the effect of the same treatment on seed germination. Therefore, it is possible that the regulation of flowering and the regulation of seed germination involve two different biochemical pathways. For instance, in *O. sicula* and *T. arabica*, the LD treatment accelerates flowering but the SD treatment increases the seed germinability. In some neutral-day plants for flowering, the germinability of the seeds is accelerated by SD, as in *Lycopersicum esculentum* and *Cucumis sativus*, or by LD, as in *Carrichtera annua.*

Are the observed responses by seeds to maternal environmental conditions necessarily adaptive or merely random in their action? At least in some of the plant species inhabiting the most extreme and unpredictable desert conditions, the heteroblasty contributes very strongly to the survival of the species. Heteroblasty prevents catastrophes of mass germination after a relatively heavy rain, followed by a long dry period, which would cause all the seedlings to die out. In some other plant species inhabiting deserts, there are also other mechanisms that regulate the dispersal and germination in time (Gutterman, 1993, 1994a, 1998a). In many plant species found in deserts, there are serotinous aerial seed banks (Baskin and Baskin, 1998; van Rheede van Oudtshoorn and van Rooyen, 1999). Another such mechanism is the seed dispersal by rain, as studied in *Blepharis* spp. (Gutterman *et al.*, 1967). The number of seeds that are released is regulated in such a way that in one rain event only a part of the seed bank stored on the dead mother plant will be released and germinate. A similar phenomenon is seen in *Asteriscus pygmaeus* (Fahn, 1947; Koller and Negbi, 1966; Gutterman and Ginott, 1994).

There are a number of major areas of research that need to be carried out on the effects of maternal position and environmental conditions during seed development on germination and dormancy, such as the following:

- Which material or materials are transferred from the leaves to the seeds and affect the germinability, and what are the physiological processes involved?
- What are the physiological processes involved in the accumulation of different materials by the seed during development, including possibly germination accelerators or inhibitors? For example, are there interrelations between the aerial and subterranean capitula, which affect the germinability of the seeds in the amphicarpic plants *Emex spinosa* (Evenari *et al.*, 1977) and *Gymnarrhena micrantha*? It is interesting to note that, under SD in the greenhouse or outdoors, *G. micrantha* plants developed both aerial and subterranean capitula, but under LD in the greenhouse only the aerials developed. Under LD outdoors, only the subterraneans developed (Evenari and Gutterman, 1966). Are there also some interactions between the individual seeds within dispersal units, e.g. in *Aegilops geniculata* and *Pteranthus dichotomus*? In spikelets a and b of *A. geniculata*, the terminal caryopses, a_2 and b_2, are inhibited in their germination in comparison with the lower caryopses, a_1 and b_1 (Datta *et al.*, 1970, 1972a, b). In *P. dichotomus*, the opposite was found: the terminals germinate the best and the lowest seeds germinate the poorest. The upper order changes the germinability of the seeds of the lower order (Evenari, 1963). Similarly, in the capsule of *Mesembryanthemum nodiflorum*, the terminal seeds germinate the best and the seeds from the lowest group germinate the poorest (Fig. 3.1; Gutterman, 1980/81a, 1993, 1994a).
- What are the materials involved in the different relative levels of germination of *Portulaca oleracea* (Gutterman, 1974), *Cheiridopsis* spp., *Juttadinteria* (Gutterman, 1990a) and *Lactuca serriola* seeds (Gutterman, 1992a) under different

temperatures during wetting? A detailed kinetic study is necessary for a better understanding of these changes in the levels of germination. For example, *P. oleracea* seeds matured under different environmental conditions and transferred during the germination process from low to high temperatures germinated to different percentages at different temperatures. In each temperature, the seed population reaches another level of germination and the relative amounts of germination of the different treatments differed from one temperature to another. The relative effect of parental light-quality treatments on germination depends on the temperature at which the seeds are tested (Gutterman, 1974).

- In some plant species the photoreversible phytochrome is arrested in the P_r form, which causes the seeds to require light for germination. Does this phenomenon depend on the chlorophyll content of the maternal tissue surrounding the developing seeds during dehydration (Cresswell and Grime, 1981)? In which other plants do the seeds that mature under red light and have a high percentage of P_{fr} also require light for germination after a short time of storage (Karssen, 1970; Gutterman and Porath, 1975)?

There are about 16 plant species in which it was found that the seeds that mature early in the growing season are heavier than seeds that mature late (Baskin and Baskin, 1998). The opposite was found in *Atriplex heterosperma* (Frankton and Bassett, 1968). Seed size is one of the results of the position effect on the mother plant during maturation.

As summarized in great detail by Baskin and Baskin (1998), there are 79 species in which seed size (and in many cases also germination) has been observed to be affected by maternal position and environmental factors to which the mother plant has been exposed during seed maturation. There is no doubt, that in most species, individual plants produce seeds that vary phenotypically in their germinability. The ecological effect is presumed to be catastrophe avoidance by spreading the risk of mass mortality among seedlings.

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