8
Life Cycles: Environmental Influences and Adaptations

1. Introduction

Previous chapters have emphasized the physiological responses of mature plants to their environment. The environmental stresses encountered and optimal physiological solutions, however, can change dramatically as plants develop from the seedling to vegetative and reproductive phases. Following germination, most species pass through several distinctive life phases: **seedling** (loosely defined as the stage during which cotyledons are still present), **vegetative** (sometimes with a juvenile phase preceding the adult phase), and **reproductive**. This chapter addresses the major ecophysiological changes that occur in the life cycles of plants. These involve changes in **development** (i.e., the initiation and occurrence of organs), **phenology** (i.e., the progress of plants through identifiable stages of development), and **allocation of resources** to different plant parts. The pattern and duration of developmental phases depend on environmental conditions and pattern of acclimation to specific conditions. The developmental pattern also varies genetically, which may reflect adaptations to specific abiotic or biotic environments. This chapter discusses plant development and processes associated with transition between developmental stages.

2. Seed Dormancy and Germination

Germination includes those events that commence with **imbibition** of water by the dormant, usually dry, seed and terminate with the elongation of the embryonic axis. It is the event that marks the transition between two developmental stages of a plant: **seed** and **seedling**. The seed has a package of food reserves that makes it largely independent of environmental resources for its survival. This changes dramatically in the photoautotrophic seedling, which depends on a supply of light, CO_2, water, and inorganic nutrients from its surroundings for autotrophic growth, i.e., the phase when the seedling has become independent of maternal reserves. In this section we discuss the mechanisms by which some seeds sense the suitability of the future seedling's environment. For example, how does a seed acquire information about the expected light, nutrient, and water availabilities?

Germination is the process when part of the embryo, usually the radicle, penetrates the seed coat and may proceed with adequate water and O_2 and at a suitable temperature. **Dormancy** is defined as a state of the seed that does not permit germination, although conditions for germination may be favorable (temperature, water, and O_2). Dormancy thus effectively delays germination. Conditions required to break dormancy and allow subsequent germination are often quite different from those that are favorable for growth or survival of the autotrophic life stage of a plant.

Timing of seed germination can be critical for the survival of natural plant populations, and dormancy mechanisms play a major role in such timing. These mechanisms are pronounced in many **ruderals** and other species from habitats that are subject to disturbance. Many trees, particularly temperate and tropical species from undisturbed forest, lack pronounced dormancy, and their large seeds often do not tolerate desiccation. The germination of these **recalcitrant** seeds typically occurs quickly after dispersal. Recalcitrant seeds rapidly lose viability when dried, and storage of such seeds is notoriously difficult. Some seeds that lack dormancy are **viviparous**; they germinate prior to, or coincident with, abscission from the maternal plant (e.g., seeds of many mangrove and seagrass species).

In a dormant seed, the chain of events that leads to germination of the seed is blocked. This block, and hence dormancy itself, can be relieved by a specific factor or combination of factors (e.g., light, temperature regime, and/or specific compounds).

In some cases environmental factors, such as the absence of light, NO_3^-, and/or a diurnally fluctuating temperature, may keep seeds in a dormant state (**enforced dormancy**). The term dormancy is used here because these environmental factors function as an environmental signal that removes a block leading to germination, rather than being involved in metabolism, as is the case for environmental factors such as water, O_2, and temperature (Bewley & Black 1994, Finch-Savage & Leubner-Metzger 2006). This form of dormancy is relieved as soon as the signal is present. Enforced dormancy is not always considered as a form of dormancy, but as a mechanism that prevents germination (Vleeshouwers et al. 1995, Baskin & Baskin 2004). Seeds are considered to be in a true (deeply) dormant state when they do not germinate even if given the stimuli for breaking enforced dormancy and favorable conditions for germination. Breaking of this type of dormancy occurs gradually over weeks, months, or even longer. Seeds may be dormant upon release from the mother plant (**primary** or **innate dormancy**), and dormancy can also be induced in seeds after they have become nondormant (**secondary** or **induced dormancy**), if conditions become unfavorable for germination. Transitions among the various forms of dormancy are illustrated in Fig. 8.1. As seeds gradually come out of primary dormancy, they pass through a phase of conditional dormancy when seeds germinate only over a narrow range of conditions. Similarly, induction of dormancy is accompanied by a gradual narrowing of the range of conditions that allow germination (Baskin & Baskin 2001).

Baskin & Baskin (2001, 2004) distinguish five classes of primary dormancy. **Physiological dormancy** (PD) refers to physiological mechanisms in the embryo and/or its surrounding structures (endosperm, seed coat) that prevent radicle emergence. Seeds with **morphological dormancy** (MD) have small underdeveloped or even undifferentiated embryos; germination will only occur until growth and development have proceeded till a predefined stage. Seeds with hard coats that are impermeable to water have **physical dormancy** (PY). Separate classes are reserved for combinations of physiological with morphological dormancy [**morphophysiological dormancy** (MPD)] and physiological with physical dormancy [**combinational dormancy** (PD + PY)]. The most extensive subdivision in levels (from deep to nondeep) and types is given for physiological dormancy (three levels and five types) and morphophysiological dormancy (eight levels but no types). Physical dormancy and combinational dormancy are not subdivided. Physiological dormancy at a nondeep level is the most common kind of dormancy in seed banks in temperate climates and occurs in gymnosperms and in all major clades of angiosperms.

2.1 Hard Seed Coats

The hard **seed coat** of many species (e.g., in Fabaceae, Malvaceae, and Geraniaceae) can prevent germination because it is largely impermeable to water (physical dormancy) (Baskin & Baskin 2001). Water uptake occurs only when the seed coat is sufficiently deteriorated; imbibition increases with the degree of damage to the seed coat, e.g., in *Coronilla varia* (purple crownvetch) seeds (Fig. 2). In *Pelargonium* species with hard seed coats, palisade cells effectively close the site where water will ultimately enter the seed, whereas soft seeds form a wide opening at this site (Meisert et al. 1999).

Hard seed coats that are permeable to water do not represent a real mechanical barrier for outgrowth of the embryo in nondormant seeds (Baskin & Baskin 2001), but merely protect it. In other seeds the seed coat is not hard, but the outer layers such as the endosperm and seed coat can represent a mechanical barrier in combination with the force exerted by the embryo (coat-imposed dormancy). The balance in strength of the two opposing forces
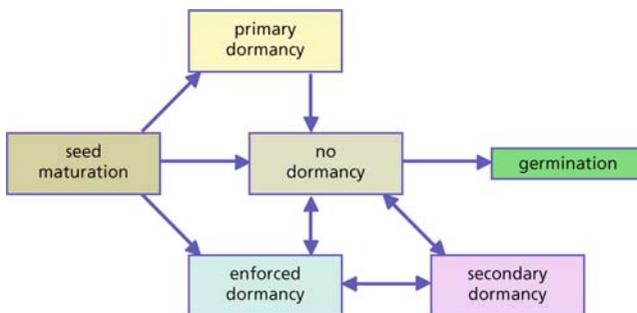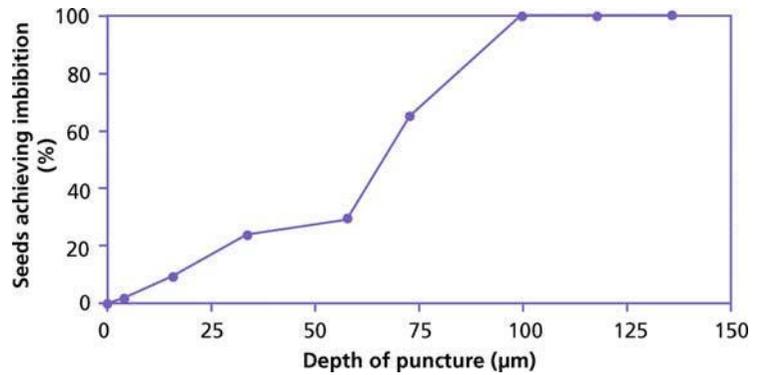

FIGURE 1. Schematic representation of changes in dormancy after seed maturation.

determines whether or not the radicle will break through. This balance is subject to regulation and an important mechanism involved in physiological dormancy (Sect. 2.7).

Deterioration of the seed coat may be due to microbial breakdown, when seeds are buried in soil. It may also be due to physical processes, such as exposure to strong temperature fluctuations at the soil surface, as occurs in a desert. In both conditions the breakdown of the seed coat is gradual and, consequently, germination is spread in time. Exposure to short periods of high temperatures, such as during a fire (approximately 100°C), may lead to synchronous breaking of dormancy as a result of increased water permeability or other changes in the seed. However, temperature can easily become lethal in intense fires or when seeds are at the soil surface. Another mechanism that stimulates germination after fire is related to specific chemicals in smoke (Sect. 2.4).

In the seed coat there is a preformed "weak site", e.g., the **strophiole** in Fabaceae, where tissue degradation first occurs and through which water uptake starts. Dormancy associated with constraining tissues often complicates germination for plant cultivation purposes. It can be relieved artificially in hard-coated seeds by boiling, mechanical (sanding or breaking the seed coat), or chemical (concentrated sulfuric acid) treatments.

2.2 Germination Inhibitors in the Seed

Arid climates are characterized by little precipitation, often concentrated in just a few unpredictable showers. After such a shower, massive seed germination of short-lived plants may occur. How can the seeds perceive that the environment has become more favorable for germination and growth? A common trait of many species germinating under such

conditions is the presence of **water-soluble inhibitors** in the pericarp (i.e., the matured ovulary wall, including seed coat and attached parts of the fruit). Light rain may not fully remove these inhibitors, so germination cannot take place (Fig. 3). Germination occurs only after a major rainfall event or prolonged rain that elutes the inhibitor; in this case the emerged seedling has access to sufficient water to enhance its chances to survive and complete its life cycle. The substance that inhibits germination may be either a specific organic compound or accumulated
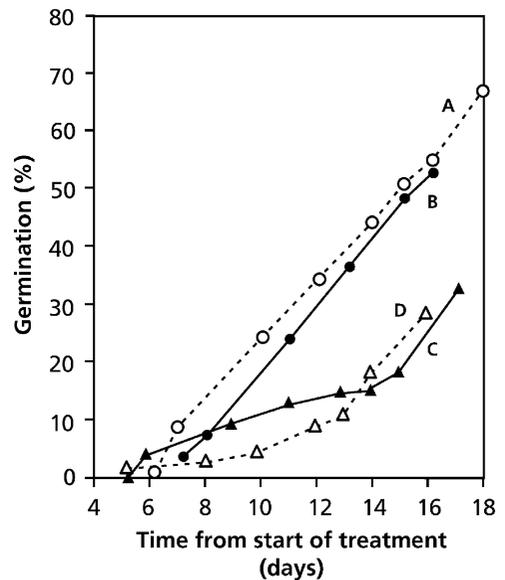

FIGURE 3. **Time course of germination of *Oryzopsis miliacea* (smilograss) as affected by duration of a drip treatment. The origin of the *x*-axis represents the start of the drip treatment. Curves *A*, *B*, *C*, and *D* refer to a duration of the treatment of 93, 72, 48, and 24 hours, respectively. Control seeds did not germinate (Koller & Negbi 1959). Copyright Ecological Society of America.**

salts. Following moderate rains, those seeds that fail to germinate synthesize additional inhibitors; therefore, subsequent rains must still be substantial to trigger germination.

Germination inhibitors also play an important role in preventing germination of seeds in fleshy fruits. These germination inhibitors can be general (e.g., high solute concentration of many fruits) or highly specific. For example, ABA inhibits the germination of the seeds of *Solanum lycopersicum* (tomato) in combination with osmotic strength, as illustrated by seed germination inside the fruit of ABA-deficient mutants (Karssen & Hilhorst 1992). In a comparison of a range of mangrove and non-mangrove species, ABA levels are consistently lower in embryos of **viviparous** mangrove species than in related nonmangrove, nonviviparous species (Farnsworth & Farrant 1998).

2.3 Effects of Nitrate

Germination of many seeds of **ruderal** species is stimulated by **nitrate** (Fig. 4). This role of NO_3^- as an environmental trigger is not associated with a need for NO_3^- for protein synthesis, because no nitrate reductase activity is detected in seeds (Hilhorst & Karssen 1989). Rather, NO_3^- functions as a **signaling compound** and thus as a factor breaking
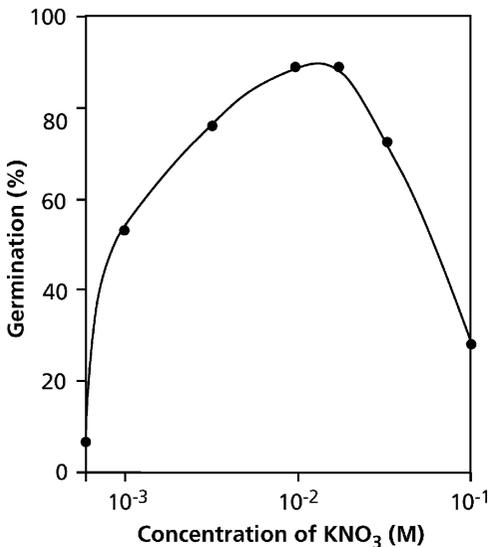
enforced dormancy, especially in many ruderal species. When the mother plant has grown at a NO_3^--rich site, seeds may accumulate NO_3^- and then lose the requirement for external NO_3^- to trigger germination. NO_3^- interacts with temperature and light in the regulation of dormancy and germination, and a mechanism has been proposed that accounts for this interaction at the level of a membrane-bound receptor protein (Karssen & Hillhorst 1992). Why would weedy and ruderal species use NO_3^- as an environmental cue?

A **NO_3^- requirement** may function as a mechanism to detect a **gap in the vegetation**, just like the perception of other environmental variables, e.g., light and diurnal temperature fluctuation, which are involved in enforced dormancy. Seeds in soil where a large plant biomass depletes soil NO_3^- experience a low-NO_3^- environment, which enforces dormancy. When the vegetation is destroyed, mineralization and nitrification continue, but absorption by plants is reduced. This increases soil NO_3^- concentrations to levels that can break dormancy as shown for *Plantago lanceolata* (snake plantain) seed buried in grassland in open patches and between the grass (Pons 1989).

2.4 Other External Chemical Signals

Various compounds in the natural environment of seeds may have stimulating or inhibiting effects on seed germination (Karssen & Hilhorst 1992). The inhibition of germination of buried seeds often cannot be explained by the absence of light or alternating temperatures alone. The gaseous environment may play a role (low O_2 and high CO_2), and in some cases specific organic compounds, such as leachates from living or decaying plant material containing **allelochemicals** (Sect. 2 of Chapter 9B), inhibit seed germination, e.g., in *Nicotiana attenuata* (Indian tobacco) in response to *Artemisia tridentata* (sagebush), which releases methyl jasmonate (Preston et al. 2002).

Germination can be stimulated by **smoke** derived from the combustion of plant material; this stimulates seed germination of *Audouinia capitata*, a fire-dependent South African fynbos species (De Lange & Boucher 1990). Exposure of dormant seeds to cold smoke derived from burnt vegetation also promotes seed germination of many species from the English moorlands (Legg et al. 1992), the California chaparral in United States (Keeley 1991), and Western Australian sandplains (Dixon et al. 1995). Chemicals in cold smoke also promote germination of seeds that are normally difficult to germinate, even of species that have not evolved in fire-prone

FIGURE 4. **The relation between germination percentage of seeds of *Epilobium montanum* (broad-leaved willowherb) and KNO$_3$ concentration. Germination took place in the dark for 14 days at 16–20°C (redrawn after Hesse 1924).**

FIGURE 5. Glasshouse germination studies with Western Australian species. (A) Species for which there is a significant difference in germination between control (*open bars*) and smoke treatment (*filled bars*). (B) Species that did not germinate in the absence of smoke but whose germination percentage was increased to as little as 3% and as much as 72% in the presence of smoke (Dixon et al. 1995).
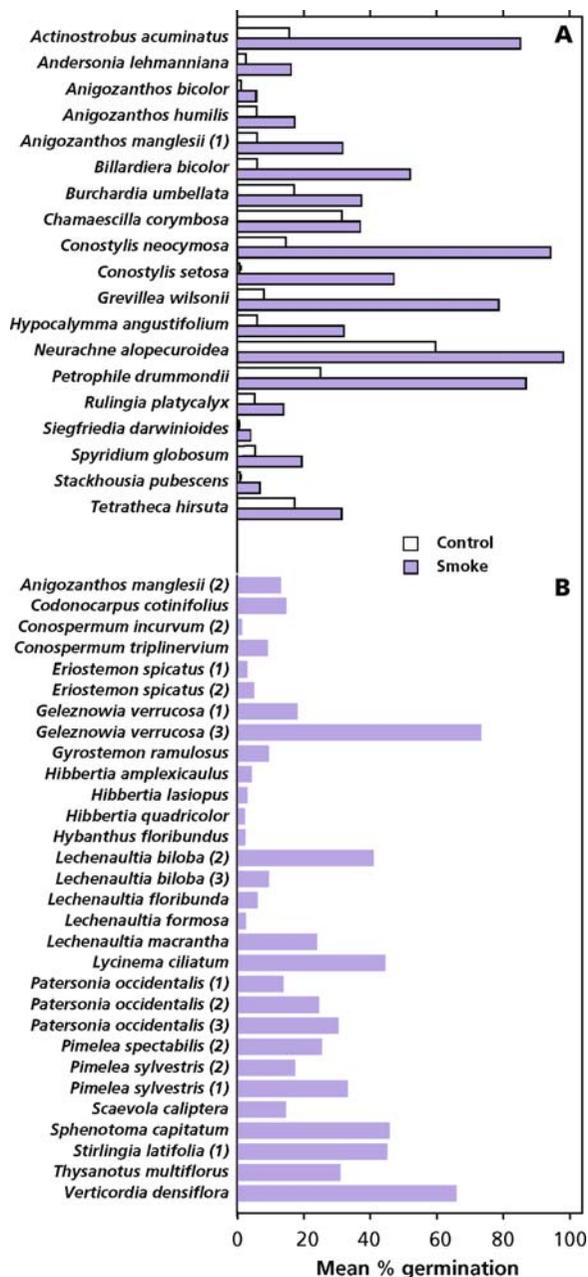
environments (Fig. 5). The main compound that triggers germination in smoke-sensitive seeds is a **butenolide** (Flematti et al. 2004b). However, triggering of germination by the butenolide, now known as karrikinolide, is not restricted to plants in fire-dominated ecosystems, but also includes several crop and weed species that have evolved in ecosystems where fire is not an ecological trigger; this suggests that karrikinolide may also occur in other types of disturbances (Sect. 2.3; Flematti et al. 2004a). Commercial "smoke" products are available to enhance the germination of seeds that are difficult to germinate and to promote seed germination for mine rehabilitation in Western Australia (Roche et al. 1997). However, any ecological advantage of the capacity to respond to compounds present in smoke for species that do not occur in a fire-dominated system remains to be demonstrated.

2.5 Effects of Light

Light is an important factor determining enforced dormancy in seeds (Pons 2000). A wide variety of light responses have been described. These depend strongly on other environmental conditions, such as temperature, water potential, and nitrate, and on prior conditions, such as temperature regime, and include conditions to which the parent plant was exposed.

The light climate under natural conditions has many components, some of which are used by seeds for regulation of dormancy. Three major types of light responses can be distinguished.

1. A **light requirement** prevents germination of seeds that are buried too deeply in soil. Such seeds germinate only when exposed to **light**, and thus do not germinate below a soil depth where no light penetrates. This prevents "fatal germination" of the predominantly small seeds in which this mechanism is most frequent. Germination occurs only when the soil is turned over or the seeds otherwise reach the soil surface where they are exposed to light. This often coincides with damage or the complete disappearance of the established vegetation. The emergent seedlings thus have a more favorable position with respect to established plants than they would have otherwise.

2. **Light intensity and duration of exposure** (photon dose, integrated over a period of time) determine whether dormancy enforced by darkness is broken. A steep light gradient exists near the soil surface. Seeds of some species [e.g., *Digitalis purpurea* (foxglove)] germinate at the extremely low intensity prevailing at 10 mm depth in sand ($0.026\ \mu mol\ m^{-2}\ s^{-1}$), whereas others [e.g., *Chenopodium album* (lambsquarters)] do not germinate below 2 mm (Bliss and Smith 1985). The very low photon dose required by buried weed seeds is also illustrated by their emergence after soil cultivation in light, but not in darkness, with an estimated exposure time of about 0.2 s (Scopel et al. 1994). Other species, e.g., *Plantago major* (common plantain), require much longer or repeated exposures (Pons 1991b). A high light sensitivity may provide more certainty of germination after a disturbance event, but increases the probability of fatal germination after reburial.

3. The **spectral composition** of daylight as modified by a leaf canopy also influences the **timing of germination after disturbance** of vegetation. Light under a leaf canopy is depleted in red compared with that above the canopy (Fig. 6)

resulting in a low red:far-red ratio. This enforces dormancy in many species (Fig. 7). This is particularly important shortly after seed shedding, when conditions might otherwise be suitable for
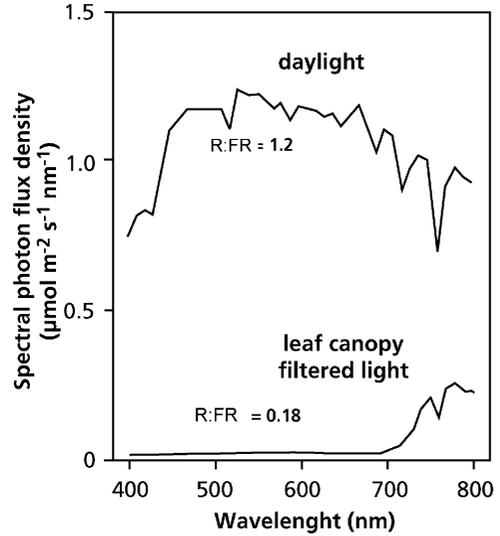
FIGURE 6. The spectral energy distribution of sunlight and light filtered through a leaf canopy. Red:far-red ratios (660:730) are also shown (after Pons 2000).

FIGURE 7. Germination of *Plantago major* (common plantain) in daylight under stands of *Sinapis alba* (white mustard) of different densities resulting in different red:far-red photon ratios of the transmitted light. Corresponding leaf area index (LAI) and phytochrome photoequilibria (P_{fr}:P_{total} ratios) are shown (after Pons 2000).

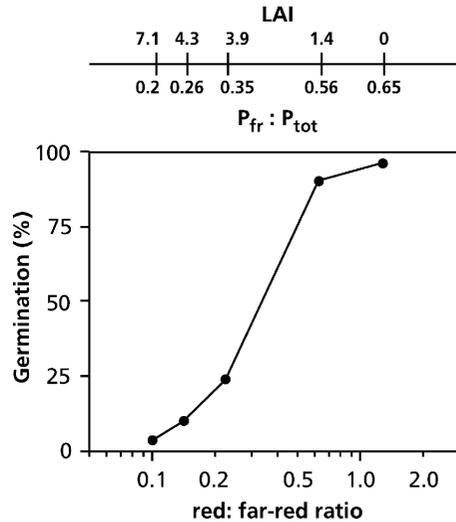germination. The seeds may subsequently get mixed into the soil, where a light requirement further enforces dormancy and where the risks of predation are smaller than at the soil surface. Litter, especially dry litter, also decreases the red:-far-red ratio, which further reduces the probability of germination (Vazquez-Yanes et al. 1990).

Perception of light per se as well as the response to the spectral composition of the light involves the **phytochrome** system (Box 7.2). Seeds with a dormancy mechanism involving phytochrome require a minimum amount of the far-red-absorbing form of phytochrome (P_{fr}) to break dormancy. Light with a high red:far-red ratio enhances the formation of P_{fr}. When the seeds are exposed to light with a low red:far-red ratio, less P_{fr} is formed. The amount of P_{fr} is also determined by photon dose in the non-saturating region. The amount of P_{fr} required for germination depends on environmental conditions and the level of other forms of dormancy; it also differs among species. Hence, a low red:far-red ratio does not enforce dormancy in all light-requiring species and not under all conditions.

If, after exposure to light of appropriate spectral composition, germination is subsequently impaired by some other environmental factor, then a new exposure to light is required to break dormancy. This is due to the decay of P_{fr} in the dark. This mechanism also explains why seeds that are initially not light-requiring upon ripening become so after burial in the soil (Pons 1991b). A requirement for light for breaking dormancy is clearly not a fixed

characteristic of a species. Seeds that are not obviously light-requiring may still have a dormancy mechanism that is regulated by phytochrome. In such seeds there may be sufficient P_{fr} in the ripe seeds, influenced by the chlorophyll content of covering structures during the ripening process, to allow germination in the dark (Cresswell & Grime 1981).

Many light responses of seeds are typically referred to as the **low fluence response** (LFR). That is, a rather low photon dose is required to give the response. Some seeds under certain conditions respond to much lower light doses (three to four orders of magnitude) with the breaking of dormancy. Such a response is called the **very low fluence response** (VLFR). The two responses can be found in the same seeds, depending on pretreatment, e.g., in *Lactuca sativa* (lettuce) (Fig. 8). Transition between LFR and VLFR also varies seasonally during burial of seeds in soil (Derkx & Karssen 1993). The VLFR under natural conditions is probably involved in the response to the short exposures to light that occur during soil disturbance as mentioned above (Scopel et al. 1994).

Studies with mutants of *Arabidopsis thaliana* (thale cress) have shown that different forms of phytochrome trigger VLFR and LFR responses. Phytochrome A is required for the VLFR and phytochrome B for the LFR (Casal & Sànchez 1998); both phytochrome A and B are involved in the far-red reversible stimulation of germination by red light (Hennig et al. 2002).

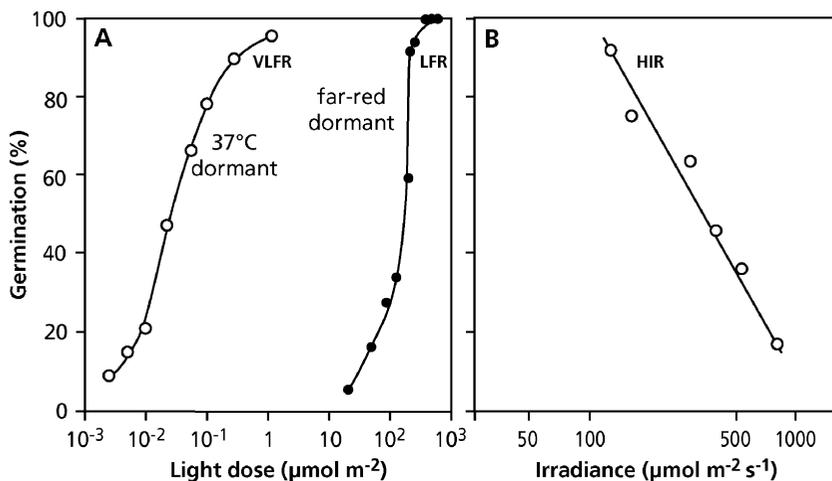**FIGURE 8. The three light responses of seed germination demonstrated in one species *Lactuca sativa* (lettuce). (A) Fluence response to red light of seeds pretreated at 37°C and with far-red showing the very low fluence response (VLFR) and the low fluence response (LFR), respectively (after Blaauw-Jansen & Blaauw 1975). (B) Irradiance response to daylight showing the high-irradiance response (HIR) (Gorski & Gorska 1979).**

Germination of many species [but not of *Arabidopsis thaliana* (thale cress)] can also be inhibited by exposure to light when exposure times are long. The inhibition increases with increasing irradiance (Fig. 8), and the maximum effective wavelength region is 710–720 nm. This response is called the **high-irradiance response** (HIR). The cycling between P_r and P_{fr} and their intermediates is somehow involved in the HIR, but the mechanism is not fully understood. Seeds that are negatively **photoblastic**, i.e., whose germination is prevented by light, have a strongly developed HIR. Short exposures and low irradiances are not inhibitory, and they sometimes even stimulate germination in such seeds. Experiments with mutants of *Solanum lycopersicum* (tomato) that are deficient in different forms of phytochrome show that phytochrome A is the principal form involved in the HIR (Appenroth et al. 2006).

Light responses of seeds have been extensively studied with short exposures to light (LFR and VLFR). Seeds, however, mostly experience long exposure times under natural conditions. For seeds under a leaf canopy, both the photoequilibrium of phytochrome and the HIR are important, because seeds experience many hours of exposure to wavelengths that are effective. Hence, the inhibiting effect of a leaf canopy can be stronger than expected from the spectral composition alone.

Seeds on the surface of bare soil may be inhibited by the HIR due to the prevailing high irradiances. In light-requiring seeds, this may restrict germination to the upper few millimeters of the soil profile where light penetrates, but does not reach a high intensity, and where both light and moisture are available.

2.6 Effects of Temperature

Temperature influences seed dormancy and germination in several ways

1. **Diurnal fluctuation** in temperature controls enforced dormancy of many seeds. The response is independent of the absolute temperature which illustrates that it is the amplitude that causes the response (Fig. 9). This mechanism prevents germination of seeds **buried deep** in the soil, where temperature fluctuations are damped. In addition, seeds in unvegetated soil experience larger temperature fluctuations than seeds under a canopy. Hence, the capacity to perceive temperature fluctuations allows the detection of soil depth and of gaps in the vegetation. Most small-seeded marsh plants also germinate in response to diurnally fluctuating temperature which indicates the absence of deep water over the seed. Hence, in these plants temperature fluctuation functions as a mechanism to detect **water depth** (Fig. 9).

2. The **temperature range** over which germination can occur is an indication of the degree of true dormancy of the seed. If this range is narrow, then the seed is strongly dormant. If it is wider, then the seed is less dormant or nondormant. Variation in this temperature range may occur as a result of a shift in the upper and/or lower critical temperature limits for germination (Baskin & Baskin 2001).

3. The **temperature** to which the seed is exposed when no germination takes place is a major factor in determining release and induction of
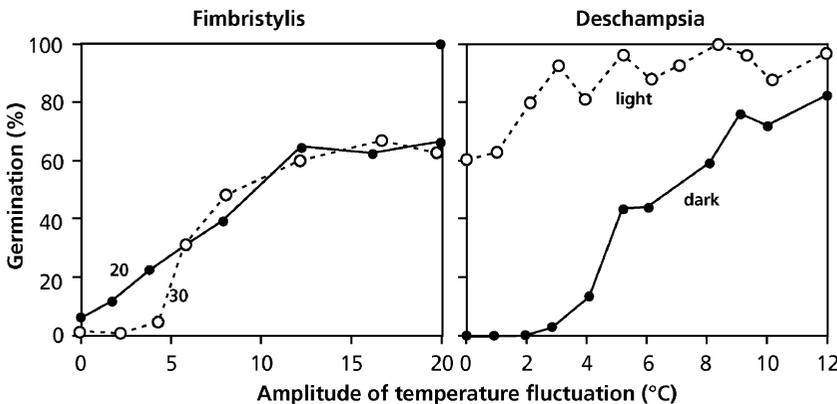
FIGURE 9. Germination responses to various amplitudes of diurnal temperature fluctuations. (*Left*) The light-requiring rice-field weed *Fimbristylis littoralis* (grass-like fimbry) at mean temperatures of 20 and 30°C (Pons & Schröder 1986). (*Right*) The grass species *Deschampsia caespitosa* (tufted hair-grass) in light and darkness (Thompson et al. 1977). Reprinted with permission from *Nature*, copyright 1995 Macmillan Magazines Ltd.
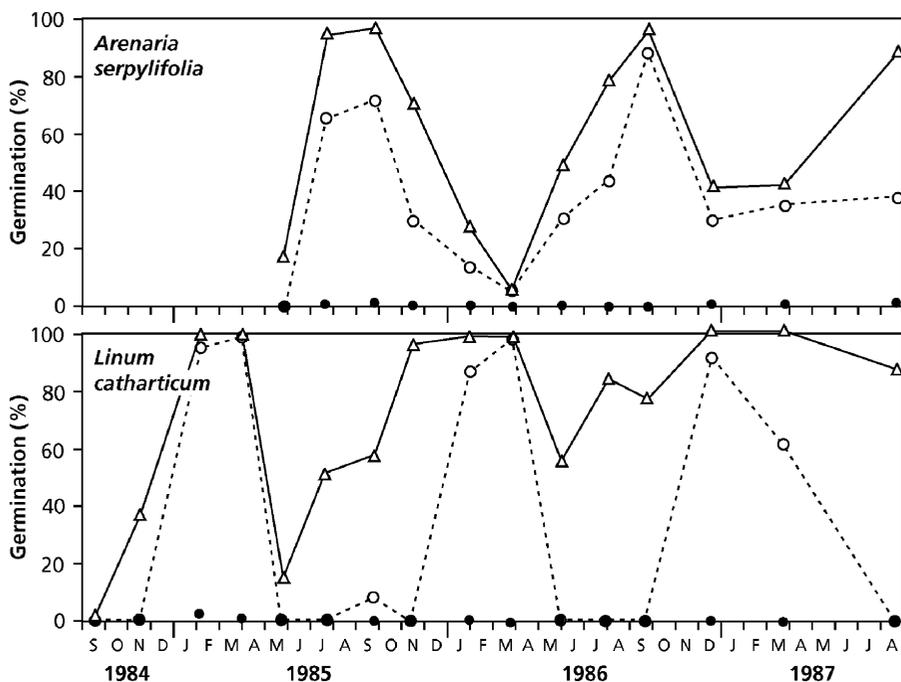
FIGURE 10. Germination of exhumed seeds under laboratory conditions after different burial times in a chalk grassland in South Limburg, the Netherlands: *Arenaria serpylifolia* (thyme-leaved sandwort), which is a winter annual, and *Linum catharticum* (fairy flax), which is a biennial that emerges in spring. Germination in darkness (*closed symbols*) and in light (*open symbols*), *solid line* final germination percentage, *dashed line* germination after 1 week at 22/12°C (Pons 1991a). Copyright Blackwell Science Ltd.

physiological dormancy, mostly at a nondeep level (Baskin & Baskin 2004). Two main types of responses are discerned in climates with seasonally changing temperatures:

a. **Summer annuals** and other species that produce seeds in autumn and germinate in the spring. A long exposure (1–4 months) of imbibed seeds to low temperature (approximately 4°C; **stratification** or chilling) relieves dormancy by gradually decreasing the minimum temperature for germination (Fig. 11). In many species with a persistent seed bank, secondary dormancy is subsequently induced by exposure to higher summer temperatures (e.g., 20°C) which causes large seasonal changes in the degree of dormancy (Fig. 10). This seasonal change in dormancy restricts germination to spring, the beginning of the most suitable season for growth in temperate climates (Fig. 11).

b. **Winter annuals** set seed in spring and early summer; they generally germinate in autumn. Exposure to relatively high summer temperatures gradually relieves the dormancy by increasing the maximum temperature that allows germination. This occurs even without imbibition. In this case, low temperatures induce dormancy (Fig. 10). This seasonal dormancy pattern causes the seeds to germinate in autumn (Fig. 11), which is the beginning of the most suitable season for many species from Mediterranean climates.

Seeds may go through several cycles of induction and release of dormancy if enforced dormancy prevents germination (e.g., by the light requirement of seeds buried in the soil) (Fig. 1).

Water supply is the factor that makes winter the most favorable season for growth of winter annuals and, thus, autumn the best period for germination; however, seed dormancy is controlled by **temperature**. In many seasonal climates, such as the Mediterranean climate, temperature and water supply are closely correlated, but temperature is a better predictor of the beginning of the wet season than is moisture itself. In summer annuals, it is the low temperature in winter that releases dormancy in the seeds and, hence, it is used as a signal; however, the subsequently occurring high temperatures in summer form the suitable conditions for growth of the autotrophic plant.
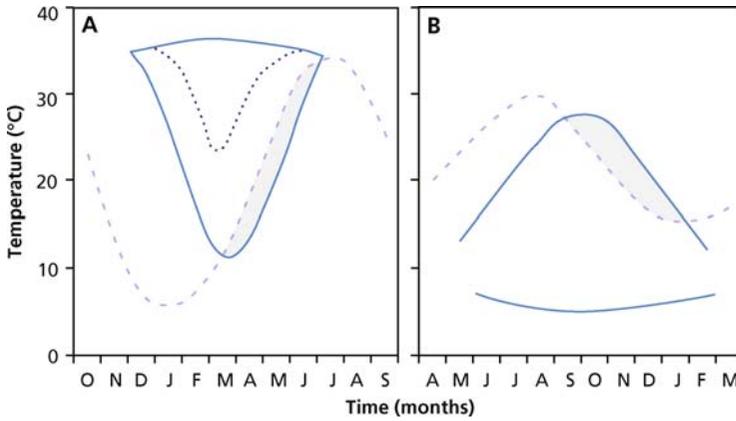
FIGURE 11. Widening and narrowing of the temperature range of germination in relation to the temperature in the natural habitat during the season. The *broken line* gives the mean daily maximum temperature in the field; the *continuous line* gives the temperature range for germination in light; the *dotted line* represents the minimum temperature for germination in darkness. In the *hatched area*, the actual and the required temperatures in light overlap. (A) Summer annual; (B) winter annual (after Karssen 1982).

2.7 Physiological Aspects of Dormancy

Many studies have examined the mechanisms of physiological dormancy, particularly the role of **phytohormones** (Box 7.2). Little progress was made, however, until mutants that are deficient in the synthesis of a phytohormone or that have a reduced sensitivity to a phytohormone [e.g., *Arabidopsis thaliana* (thale cress) and *Solanum lycopersicum* (tomato)] became available. More recently, molecular work using the large variation in accessions of *Arabidopsis thaliana* has further contributed to the understanding of the complex nature of this form of dormancy. On the basis of these studies, a fascinating view has emerged that probably applies to many species where the structures surrounding the embryo restrict radicle outgrowth (Koornneef et al. 2002, Finch-Savage & Leubner-Metzger 2006).

During seed development on the mother plant, there is an increase in **abscisic acid** (ABA) in the embryo. This phytohormone is involved in the prevention of precocious germination, synthesis of reserve proteins, development of desiccation tolerance, and induction of primary dormancy. External ABA is not very effective in inducing dormancy. Induction of and release from primary dormancy involves changes in both the concentration of ABA and the sensitivity to this phytohormone. **Gibberellic acid** (GA) has an effect opposite to that of ABA, and the ABA:GA ratio resulting from synthesis and catabolism and the sensitivities to these hormones regulate the release and induction of physiological dormancy. Release from dormancy is typically accompanied by an increase in sensitivity to GA (Fig. 12), whereas, with release from enforced dormancy, GA is synthesized de novo. ABA reduces the growth potential of the embryo, whereas GA can stimulate it. GA is further involved in the induction

of enzymatic hydrolysis of carbohydrates, especially of galactomannan-rich endosperm cell walls. Cell-wall hydrolysis weakens the endosperm layer, so that the radicle of the embryo can penetrate the seed coat, when its growth potential is sufficiently large, leading to the germination event.

Induction of secondary dormancy, as occurs in buried seeds, is accompanied by a decrease in the sensitivity to GA. Phytohormone receptors in the plasma membrane could be affected by the temperature-dependent state of membranes, thus at least partly explaining the effect of temperature on dormancy. The change in sensitivity to GA is reflected in the sensitivity for environmental stimuli that break enforced dormancy, such as light that stimulates GA synthesis, causing the above-mentioned endosperm weakening.
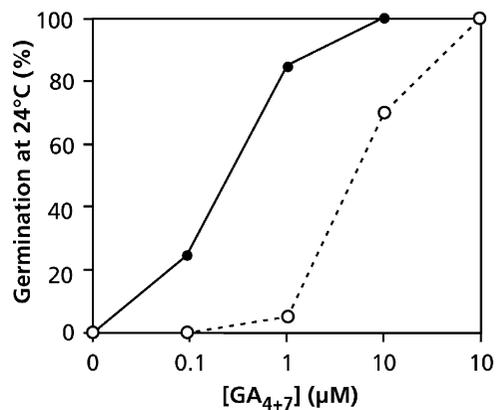

FIGURE 12. The effect of gibberellin concentration on the germination of a GA-deficient mutant of *Arabidopsis thaliana* (thale cress) in darkness at 24°C. Seeds directly sown (*open symbols*) or preincubated at 2°C for 7 days (*filled symbols*) (Hilhorst & Karssen 1992).

<Table>

TABLE 1. A summary of the possible ecological significance of environmental factors involved in breaking seed dormancy.

Environmental factor	Ecological role
Light	Gap detection
	Sensing depth in soil
Diurnal temperature fluctuation	Increasing longevity in seed bank
	Gap detection
	Sensing depth in soil and water
Nitrate	Gap detection
	Nutrient availability
Rain event in desert	Detection of water availability
Smoke	Response to fire
High temperature	Response to fire
Seasonal temperature regime	Detection of suitable season
	Increasing longevity in soil
Time	Avoidance of unsuitable season
	Spreading risks in time

</Table>

2.8 Summary of Ecological Aspects of Seed Germination and Dormancy

Section 2 discussed how environmental factors control dormancy. These environmental cues lead to a **timing** of germination which maximizes the chances of seedling survival and subsequent reproductive success. Table 1 summarizes these germination cues. The cues that indicate presence of disturbance (light, diurnal temperature fluctuation, nitrate, and other chemicals) are typically best developed in early-successional species. In the absence of these cues, these species enter long-lasting seed reserves ("seed banks") in the soil, where they can remain for tens or even hundreds of years until the next disturbance occurs. By contrast, late-successional species have short-lived seeds that are produced regularly and have poorly developed seed dormancy mechanisms. As a result, these species are poorly represented in the seed bank. The viability of seeds in the seed bank declines with time, but it is quite common for the seed bank to be a major source of germinants, even when disturbance occurs more than a century after the previous disturbance that gave rise to the seed bank.

3. Developmental Phases

Most species pass through several distinct life phases after germination. Plants grow most rapidly, but are most vulnerable to environmental stress and to the effects of competition, during the seedling phase.

There is then a gradual transition from the seedling to the juvenile phase, where many species allocate significant resources to defense and storage. Finally, there is an abrupt hormonally triggered shift to the reproductive phase, where some shoot meristems produce reproductive rather than vegetative organs. The response of plants to the environment often differs among these developmental phases, and species differ substantially in the timing and triggers for phase shifts. For example, **annuals** rapidly switch to their reproductive phase, whereas **perennials** may remain vegetative for a longer time, sometimes many years. **Biennials** are programmed to complete their life cycle within 2 years, but this may take longer if environmental conditions are less favorable. What are the physiological differences between plants with these contrasting strategies, and how is the program in biennials modified by the environment?

3.1 Seedling Phase

Seedlings are susceptible to many abiotic and biotic stresses after germination. During germination of a dicotyledonous plant, such as *Pisum sativum* (pea), the shoot emerges from the seed with a hook-shaped structure that protects the apical meristem and first leaves while the seedling pushes through the soil. When the seedling reaches the light as perceived by **phytochrome**, the leaves expand, and the photosynthetic apparatus differentiates, a process called **de-etiolation**. Until that time the apical hook is maintained by an inhibition of cell elongation of the inner portion of the hook which is mediated by **ethylene**. Cells on the inner, concave, side of the hook accumulate more mRNA that encodes 1-aminocyclopropane-1-carboxylate oxidase, which is the terminal enzyme in the biosynthesis of ethylene (Box 7.1), than do cells on the outer, convex, side. The cells at the concave side are also more responsive to ethylene. To form a straight stem below the hook, ethylene inhibition is released, and the cells on the inner side expand rapidly to match the length at the outer side (Peck et al. 1998).

Due to their small root systems seedlings are vulnerable to desiccation from minor soil drying events, so there is strong selection for rapid root extension. Where seedling densities are high, there is also strong competition for light, and an advantage of even 1 or 2 days in time of germination is a strong determinant of competitive success (Harper 1977). Most plant mortality occurs in the seedling phase through the interactive effects of environmental stress, competition, pathogens, and herbivory, so there is strong selection for rapid growth at this vulnerable phase to acquire resources (leaves and
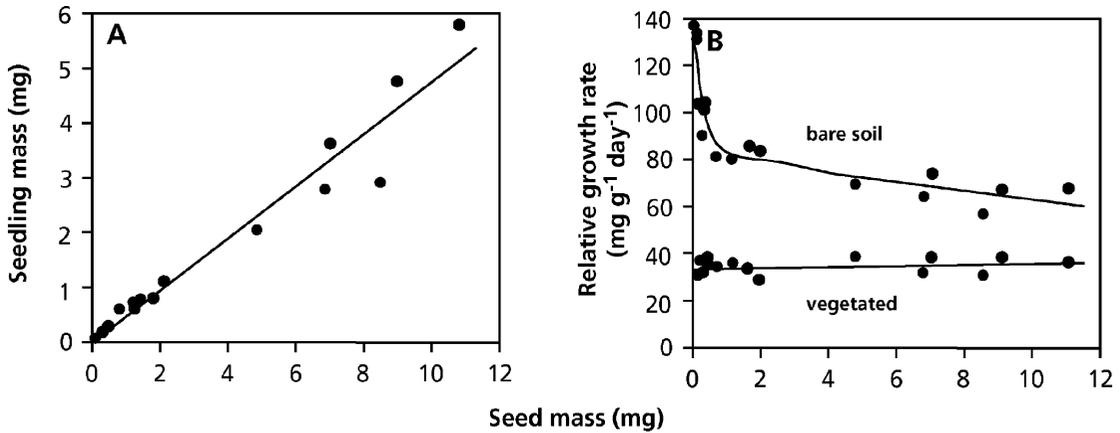
FIGURE 13. Relationship between seed mass of prairie perennials and (A) mass of newly emerged seedlings (<12 hours) or (B) relative growth rate of seedlings on bare soil and in a mat of *Poa pratensis* (Kentucky bluegrasses) in the glasshouse. Absolute plant size increases with increasing seed mass. Relative growth rate decreases with increasing seed size in the absence of competition, but it increases with increasing seed size in the presence of competition. Species are *Verbascus thapsus* (mullein), *Oenothera biennis* (evening primrose), *Daucus carota* (carrot), *Dipsacus sylvestris* (common teasel), *Tragopogon dubius* (yellow salsify), and *Arctium minus* (lesser burdock) (after Gross 1984).

roots) and to grow above neighbors (stem) (Cook 1979). In most species, this can be achieved only through minimal allocation to storage or defense.

Seed size is a major determinant of initial size and absolute growth rate of seedlings (Leishman et al. 1995) (Fig. 13). Species that colonize disturbed open sites with minimal competition typically produce abundant, small seeds which maximize the probability of a seed encountering a disturbed patch, but minimizes the reserves available to support initial growth and survivorship (Fig. 14; Leishman & Westoby 1994). Trees, shrubs, and woodland herbs, which confront stronger competition at the seedling stage, however, often produce a few large seeds (Fenner 1985, Shipley & Dion 1992). Thus, for a given reproductive allocation, there is a clear **trade-off** between seed size and seed number, with seed size generally favored in species that establish in closed vegetation. It is interesting that small seed size is one of the few traits that differentiate rare from common species of grass (Rabinowitz 1978), perhaps because of the longer dispersal distance associated with rare species.

Many tropical trees and some temperate trees produce extremely large nondormant seeds that germinate, grow to a small size, and then cease growth until a branch or tree-fall opens a gap in the canopy. This **seedling bank** is analogous to the seed bank of ruderal species in that it allows new recruits to persist in the environment until disturbance creates an environment favorable for seedling establishment. Large seed reserves to support maintenance respiration are essential to species that form a seedling bank. There is a strong negative relationship between seed size and death rate in shade (Fig. 15). In contrast to the situation in rapidly growing seedlings, the leaves of seedlings in the seedling bank are extremely well defended against herbivores and pathogens. These seedlings quickly resume growth following disturbance and have a strong initial competitive advantage over species that persist as a seed bank in the soil.

3.2 Juvenile Phase

There is a gradual transition from a seedling phase with minimal storage reserves to a juvenile phase with accumulation of some reserves to buffer the plant against unfavorable environmental conditions. There are striking differences among plants in the length of the juvenile phase and the extent of reserve accumulation, however. At one extreme, *Chenopodium album* (pigweed) can be induced to flower at the cotyledon stage immediately after germination, whereas some trees may grow for decades before switching to reproduction [e.g., 40 years in *Fagus sylvaticus* (beech)]. The switch to reproduction is typically hormonally mediated.

Annuals allocate relatively little of their acquired resources (carbon and nutrients) to storage, whereas perennials are characterized by storage of both nutrients and carbohydrates. The greater resource allocation to storage, rather than to leaf area, partly accounts for the lower growth rate of perennials. The stored reserves, however, allow perennials to start growth early in a seasonal climate and to survive

FIGURE 14. **Frequency distribution of seed size in different ecological groups of plants (after Salisbury 1942). Species that establish in closed habitats tend to have larger seeds than open-habitat plants.**
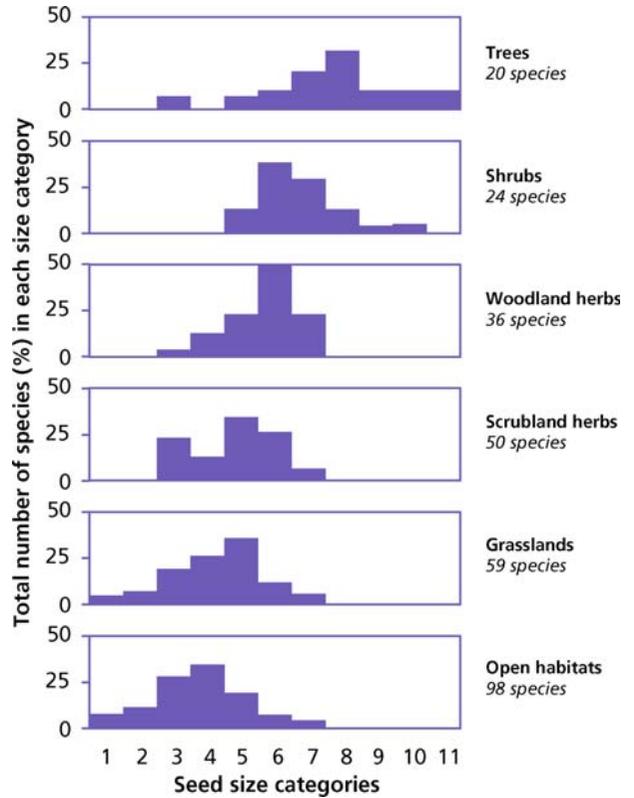
conditions that are unfavorable for photosynthesis or nutrient acquisition.

3.2.1 Delayed Flowering in Biennials

Biennial species typically grow as vegetative rosettes until the storage pools are sufficiently filled to allow a

FIGURE 15. **Relationship between death rate (mean number of fatalities per container in 12 weeks in shade) and log mean mass of seed reserve in nine North American tree species (after Grime & Jeffrey 1965).**

switch to the reproductive phase; this transition commonly requires **vernalization** (Sect. 3.3.3). Compared with an annual, biennials are able to grow and accumulate nutrients throughout a larger part of the year and are therefore able to produce more seeds (De Jong et al. 1987). Biennials may grow longer than 2 years at a low irradiance (Pons & During 1987) or low nutrient supply if their stores are not filled sufficiently to induce a switch to flowering (Table 2). In general, shifts from one developmental phase to another correlate more closely with plant size than with plant age. Hence, the term **biennial** is

TABLE 2. **Probability of flowering in *Cirsium vulgare* (spear thistle) of small rosettes after transfer from the field to a long-day regime in a growth room in February.**

Treatment	Probability of flowering (%)	Average time before bolting (days)
Without nutrients	25	45
With nutrients	80	40

Source: Klinkhamer et al. (1986).
Note: A control group in the field showed 13% flowering.

less appropriate than **monocarpic perennial,** which indicates that the plant terminates its life cycle once the transition to the reproductive stage has been made. Vegetative growth in some monocarpic perennials [e.g., in *Cycas revoluta* (sago palm) and *Agave americana* (century plant) species] can be very long.

3.2.2 Juvenile and Adult Traits

In woody plants there is a distinctive suite of morphological and chemical traits that disappear when the plant becomes reproductively mature. Juvenile plants are typically more strongly defended against herbivores, either by producing spines (e.g., apple or orange trees) or by a variety of chemical defenses (Bryant & Kuropat 1980). Many woody species exhibit a difference in morphology between their **juvenile** and **adult foliage**. For example, the young foliage of many *Acacia* (wattle) species in Australia is characterized by bipinnate leaves, whereas older individuals produce "phyllodes" (i.e., compressed petioles) (New 1984). Phyllodinous species in which the juvenile foliage persists longest are generally native to moist regions, whereas phyllodes that are reduced to small whorled spines are common in *Acacia* species from many (semi)arid zones. *Acacia* species commonly show a mosaic of bipinnate leaves and phyllodes, with the highest frequency of bipinnate leaves under more favorable conditions. In *Acacia pycnantha*, a shade-tolerant forest species, seedlings produce predominantly juvenile foliage for more than 9 months if growing in the shade, and they show a high survival rate and high leaf area ratio (LAR). When grown in full sun, they become entirely phyllodinous after a few months. Treatment with GA favors production of the bipinnate leaves.

Acacia melanoxylon (blackwood) is another Australian forest species with a mosaic of leaves, like the Hawaiian shade-intolerant *Acacia koa* (koa) that grows at sites characterized by unpredictable drought periods. It has been suggested that the bipinnate *Acacia* leaves function as shade leaves, whereas the phyllodes may be sun leaves. To test this hypothesis, gas-exchange characteristics of the contrasting leaves have been determined (Table 3). The juvenile *Acacia* leaves have higher rates of photosynthesis (on a leaf mass and leaf N basis) and transpiration (leaf area basis), but a lower water-use efficiency and leaf water potential when compared with the adult phyllodes. The traits of the juvenile leaves promote establishment (rapid growth), whereas the phyllodes are more like the leaves of slow-growing stress-tolerant species.

3.2.3 Vegetative Reproduction

Many plants such as grasses or root-sprouting trees have a modular structure composed of units, each of which has a shoot and root system. This "vegetative reproduction" can be viewed simply as a form of growth, as described in the Chapter 7 on growth and allocation, or as a mechanism of producing physiologically independent individuals without going through the bottleneck of reproduction and establishment (Jonsdottir et al. 1996).

Vegetative reproduction is best developed in environments where flowering is infrequent and seedling establishment is a rare event. For example,

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TABLE 3. Gas-exchange characteristics, water relations, and aspects of leaf chemical composition and morphology of juvenile bipinnate leaves and adult phyllodes of *Acacia koa* (koa), a shade-intolerant endemic tree from Hawaii.

Parameter	Juvenile bipinnate leaves	Adult phyllodes
Light-saturated rate of CO_2 assimilation ($\mu mol\ m^{-2}\ s^{-1}$)	11.1	12.1
Light-saturated rate of CO_2 assimilation ($nmol\ g^{-1}\ s^{-1}$)	0.8	0.5
Stomatal conductance (daily mean) ($mol\ m^{-2}\ s^{-1}$)	0.4	0.3
Transpiration (daily mean) ($mmol\ m^{-2}\ s^{-1}$)	7.5	6.9
Water-use efficiency (daily mean) [$mmol\ CO_2\ (mol\ H_2O)^{-1}$]	1.3	1.5
Internal CO_2 concentration ($\mu mol\ mol^{-1}$)	282	274
Carbon-isotope fractionation (‰)	19.7	18.0
Leaf water potential (MPa)	−1.2	−0.9
Leaf N concentration ($mmol\ g^{-1}$)	2.1	1.7
Photosynthetic nitrogen-use efficiency [$mmol\ CO_2\ (mol\ N)^{-1}\ s^{-1}$]	0.24	0.20
C/N ($mol\ mol^{-1}$)	19.3	24.6
Leaf mass per unit area (LMA) ($kg\ m^{-2}$)	0.14/0.10[*]	0.24/0.51[*]

Source: Hansen (1986, 1996).

[*] The values are for open and understory habitats, respectively.

clones of *Carex aquatilis* (water sedge) are estimated to be thousands of years old as a result of continual production of new tillers by vegetative reproduction (Shaver et al. 1979); similarly *Larrea tridentata* (creosote bush) across the Chihuahuan, Sonoran, and Mohave Deserts of western North America is thousands of years old (McAuliffe et al. 2007). In this situation, the carbon cost of producing a new tiller by sexual reproduction is estimated to be 10000-fold greater than the cost of a new tiller by vegetative reproduction, because of very low rates of seedling establishment (Chapin et al. 1980). Aspen (*Populus tremuloides*) clones in the Rocky Mountains of the central United States are similarly estimated to be of Pleistocene age as a result of root sprouting. This is an effective mechanism of maintaining a given genotype under conditions where sexual reproduction is a rare event. The trade-off is that vegetative clones often lack the genetic diversity for long-term evolutionary change.

Clonal growth is one mechanism by which plants can explore **patchy habitats**. For example, daughter ramets (i.e., a unit composed of a shoot and root) of *Fragaria chiloensis* (beach strawberry) draw on reserves of the parental ramet to grow vegetatively. If the daughter ramet encounters a resource-rich patch, it produces additional ramets, whereas ramets that move into resource-poor patches fail to reproduce vegetatively. Resource translocation can also occur between established ramets of clonal plants, supporting damaged or stressed ramets growing under relatively unfavorable conditions (Chapman et al. 1992, Jonsdottir et al. 1996). When the roots of one ramet of *Trifolium repens* (white clover) are in a dry patch, whereas those of another are well supplied with water, relatively more roots are produced in the wet patch. Similarly, when leaves of one ramet are exposed to high irradiance, whereas those of another are in the shade, the ramet exposed to high irradiance produces relatively more leaf mass (Fig. 16). Note that these environmental responses are opposite to the changes in allocation that occur when an entire plant is exposed to these conditions (Chapter 7, Sect. 5).

The data on *Trifolium repens* (Fig. 16) suggest that ramets can exchange captured resources. To test this in another clonal plant, *Potentilla anserina* (silverweed), phloem transport was interrupted by "steam girdling" which leaves the xylem intact. Under these conditions the shaded ramet produces less shoot and root biomass than does the control, with its phloem connection still intact. This experiment confirms that carbohydrates can be exported from the sun-exposed ramet to the shaded one (Stuefer 1995).

The developmental process by which vegetative reproduction occurs differs among taxonomic groups. These mechanisms include production of new tillers (a new shoot and associated roots) in grasses and sedges, initiation of new shoots from the root system (root suckering) in some shrubs and trees, production of new shoots at the base of the
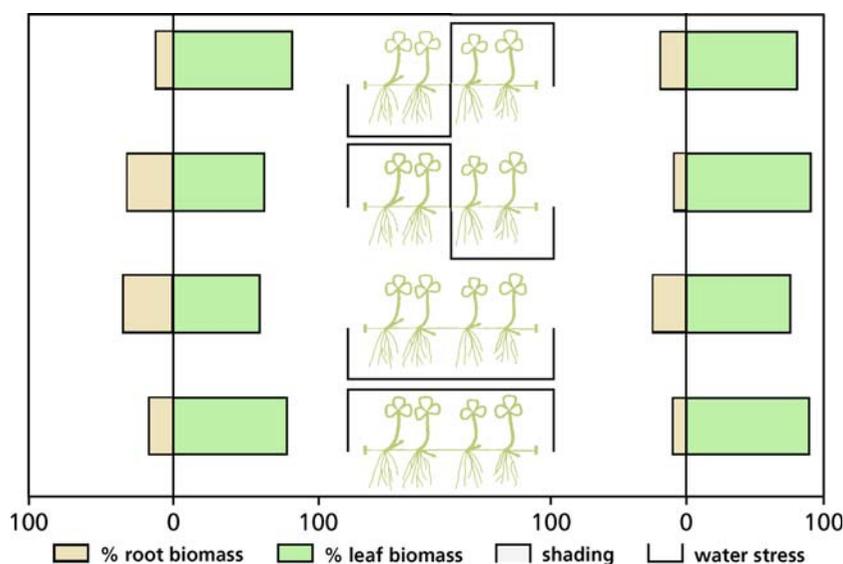

FIGURE 16. Percentage biomass allocation to leaves and roots of two interconnected ramets of *Trifolium repens* (white clover) (after Stuefer et al. 1996).

parental shoot (stump sprouting) in other shrubs and trees, initiation of new shoots from below-ground stems or burls, as in many Mediterranean shrubs, and rooting of lower limbs of trees that become covered by soil organic matter (layering) in many conifers.

3.2.4 Delayed Greening During Leaf Development in Tropical Trees

Many tropical, shade-tolerant rain forest species initiate leaves that are white, red, blue, or light-green, during the stage of leaf expansion which indicates their low chlorophyll concentration. This pattern of **delayed greening** is typical of shade-tolerant species and is less common in gap specialists (Table 4). The pattern of delayed greening is distinctly different from the shift from juvenile to adult foliage, because it is typical of all young leaves, even those on mature plants. Leaves show delayed greening function below the light-compensation point for photosynthesis at saturating light until fully expanded. After full expansion, their rate of dark respiration is very high, presumably due to high rates of metabolism associated with the development of chloroplasts. The completion of this development may take as long as 30 days after the leaves have fully expanded. In contrast, normally greening leaves achieve maximum photosynthetic capacity at the end of leaf expansion (Kursar & Coley 1992b, Woodall et al. 1998).

There is obviously a cost involved in delayed greening: during leaf expansion species showing this pattern of chloroplast development exhibit only 18–25% of the maximum possible photosynthetic rate, compared with 80% for leaves that show a normal developmental pattern. At the irradiance level that is typical of the forest understory,

TABLE 5. Rates of herbivory of young leaves, measured during the 3 days prior to full expansion (when they lack toughness) and 4–6 days after full expansion (when their toughness has increased substantially).[*]

Species	Number of leaves	During expansion	After expansion
Ouratea lucens	274	3.08	1.63
Connarus panamensis	179	0.22	0.03
Xylopia micrantha	90	0.57	0.01
Desmopsis panamensis	262	0.75	0.27
Annona spragueii	204	0.37	0.08

Source: Kursar & Coley (1991).
[*] **Values are expressed as the percentage of the leaves which were eaten per day; they were all significant at $p < 0.01$.**

the quantum yield of photosynthesis is also less than half that of green leaves, largely due to their low photon absorption (Kursar & Coley 1992a). What might be the advantages of delayed greening?

Delayed greening may be a strategy to reduce herbivory of young leaves. All young leaves lack toughness, which is provided by cell-wall thickening and lignification, which are processes that tend to be incompatible with cell expansion and leaf growth. Because toughness provides protection against both biotic and abiotic factors, young leaves are poorly protected (Table 5). The accumulation of proteins and other nutrients associated with chloroplast development in species without delayed greening presumably makes young unprotected leaves even more attractive to herbivores. Hence, although delayed greening may represent a loss of potential carbon gain, it also reduces carbon losses associated with **herbivory**. In a high-irradiance environment losses incurred by delayed greening could be substantial. In the low-light environment of shade-adapted species, where the irradiance is only about 1% of full sunlight, losses by herbivory could be relatively more important (Table 6).

We have so far discussed the delayed greening in terms of lack of chlorophyll; however, the red or blue appearance also reflects the presence of specific pigments: **anthocyanins**. Early hypotheses that these anthocyanins raise leaf temperature have been rejected. The suggestion that these anthocyanins protect against damage by ultraviolet light (Sect. 2.2.2 of Chapter 4B on effects of radiation and temperature) also seems unlikely, considering the very low irradiance level in understory habitats. Bioassays using leaf-cutter ants, however, suggest that

TABLE 4. The color of young leaves of 175 species, common in a tropical rain forest in Panama.

Leaf color	Gap specialist (%)	Shade tolerant (%)
White	0	8
Red	3	33
Light-green	3	41
Delayed greening	7	82
Green	93	18

Source: Kursar & Coley (1991).
Note: Values are the number of species and families in each category. Percentages are calculated for gap-specialist and shade-tolerant species separately.

TABLE 6. **Hypothetical carbon budgets for white and green young leaves in sun and shade environments.**

Habitat	Leaf color	CO$_2$ assimilation (carbon gain)	Herbivory (carbon loss)	Net carbon gain/loss
Sun	Green	High	High	+++
	White	Low	Low	−
Shade	Green	Low	High	− −
	White	Low	Low	−

Source: **Kursar & Coley (1991).**

these anthocyanins may protect the leaves because of their **antifungal** properties. These leaf-cutter ants collect leaves, store them underground as substrate for fungi, which are fed on by ants. Leaves that contain anthocyanins, either naturally or experimentally added, are collected to a lesser extent than leaves with lower anthocyanin concentrations (Coley & Aide 1989).

3.3 Reproductive Phase

We know that some plants **flower** in spring, when days are getting warmer and longer, whereas others flower in autumn, when temperatures are getting lower and days are shortening. Similarly, **tuber formation** also typically occurs either in spring or in autumn. How do plants sense that it is spring or autumn? Depending on the species, plants may use either the **daylength** or the **temperature** as environmental cues. Many plants from temperate regions use a combination of both cues and are thus able to distinguish between spring and autumn (Garner & Allard 1920, Samach & Coupland 2000). Our

understanding of the timing mechanisms of plants has led to greater insight into how plants time their switch from the vegetative to the reproductive phase, as well as to important applications in the glasshouse industry.

3.3.1 Timing by Sensing Daylength: Long-Day and Short-Day Plants

In Chapter 7 on growth and allocation (Sect. 5.1.2) we discuss how vegetative growth can be affected by daylength. This environmental cue is pivotal in triggering **flowering** (Mouradov et al. 2002) and **tuberization** (Martinez-Garcia et al. 2002) in many species. Daylength does not play a role in the so-called **day-neutral plants**, like *Cucumis sativus* (cucumber), *Ilex aquifolium* (sparked holly), *Solanum lycopersicum* (tomato), *Impatiens balsamina* (touch-me-not), and *Poa annua* (annual meadow-grass). It is most important, however, in plants whose flowering is triggered by the short days in autumn (**short-day plants**, which require a photoperiod less than about 10–12 hours) or the long days in spring (**long-day plants**, which require a photoperiod longer than about 12–14 hours).

Examples of short-day plants include *Chrysanthemum* species, *Eupatorium rugosa* (snakeroot), *Euphorbia pulcherrima* (poinsettia), some *Fragaria* species (strawberry), *Glycine max* (soybean), *Nicotiana tabacum* (tobacco), *Oryza sativa* (rice), and *Xanthium strumarium* (cocklebur), which is one of the best-studied short-day species (Fig. 17). Long-day plants include *Arabidopsis thaliana* (thale cress), *Avena sativa* (oat), *Coreopsis verticillata* (tickseed), *Hordeum vulgare* (barley), *Lolium perenne* (perennial ryegrass), *Rudbeckia fulgida* (black-eyed Susan), *Trifolium pratense* (strawberry clover), *Triticum aestivum* (wheat), and

FIGURE 17. **Induction of flowering by exposure to short days (= long nights) in *Eupatorium rugosa* (snakeroot). No flowering is observed above a critical daylength of 16 hours. Courtesy B. Fausey and A. Cameron, Department of Horticulture, Michigan State University, USA.**
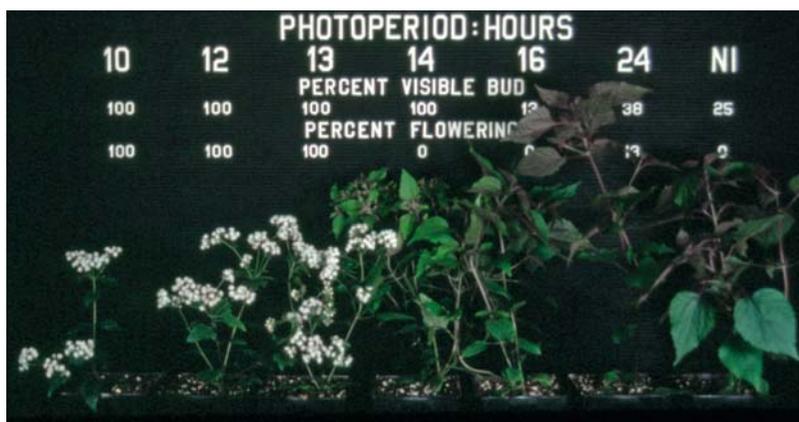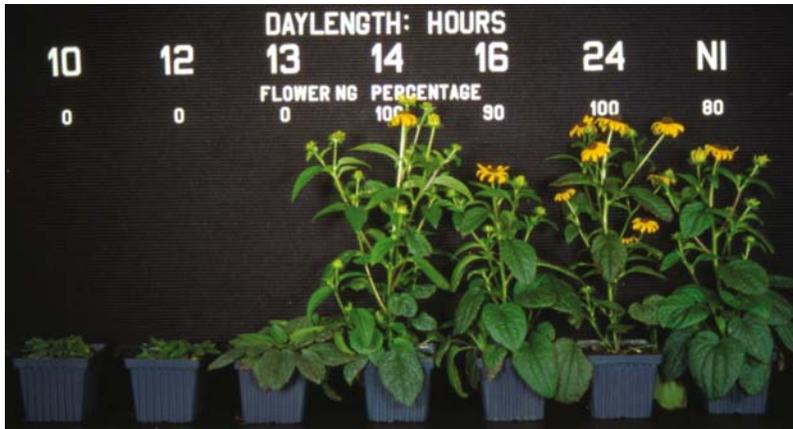
FIGURE 18. Induction of flowering by exposure to long days (= short nights) in *Rudbeckia fulgida* (black-eyed Susan). No flowering is observed below a critical daylength of 14 hours. Courtesy E. Runkle, Royal Heins, and A. Cameron, Department of Horticulture, Michigan State University, USA.

Hyoscyamus niger (black henbane), which is a much-researched long-day species (Fig. 18). Some species [e.g., *Bouteloua curtipendula* (side-oats grama)] have short-day ecotypes at the southern end of their distribution and long-day ecotypes at the northern end (Olmsted 1944). The requirement for a certain daylength may be **qualitative** [e.g., in *Perilla nankinensis* (shiso)] meaning that plants will not flower at all without exposure to at least 1 day of the appropriate photoperiod. It may also be **quantitative** or **facultative** [e.g., in *Arabidopsis thaliana* (thale cress)], which means that flowering will occur more quickly when exposed to the appropriate photoperiod. Do plants really sense the daylength, or is it the duration of the night period that is perceived?

The answer to this question has come from experiments in which the night was interrupted with either **white** or **red light**. A short interruption of the dark period prevents or delays flowering in a short-day plant, whereas the same treatment promotes flowering in long-day plants. Interrupting the light period has no effect on either short-day or long-day plants. The period between two light periods, normally the **night**, clearly must be the **critical time** that is perceived by the plant. *How* do plants perceive the duration of the night?

The answer again has come from experiments in which the night was interrupted, now using light of a specific wavelength: **red** (660 nm) or **far-red** (730 nm). A short flash is generally sufficient to obtain the effect: red light has the same effect as white light, and this effect is reversed by exposure to far-red light. This points to **phytochrome** as the photoreceptor involved in perception of the photoperiod (Box 7.2). In fact, phytochrome was discovered in the first place through these sorts of experiments (Bernier et al. 1981).

Classic grafting experiments have shown that daylength is detected in the leaves that have just matured and that a signal is transmitted from there to the shoot apex where flowering is induced (Piñeiro & Coupland 1998). Exposure of just one leaf to the inducing photoperiod may be enough. Experiments with the short-day plant *Zea mays* (corn) have shown that four to six leaves are required for the shoot meristem to become committed to form flowers. The daylength signal is transmitted to the shoot apical meristem, both in the long-day plant *Arabidopsis thaliana* (thale cress) (Corbesier et al. 2007) and in the short-day plant *Oryza sativa* (rice) (Tamaki et al. 2007).

In *Arabidopsis thaliana* (thale cress) the shoot apical meristem of plants that have been grown for 30 days under short days ceases producing leaf primordia and starts producing flower primordia within a few hours of being shifted. This suggests that the signal from the leaves acts directly on existing primordia to alter their identity (Koornneef et al. 1998). The signal may be a chemical compound or compounds, but the exact nature remains unclear. Gibberellins and ethylene can induce flowering in some long-days plants, whereas ABA inhibits the process. In the short-day plant *Pharbitis nil* (Japanese morning glory) ABA both promotes and inhibits flowering, depending on addition before or after the 14-hour inductive dark period (Takeno & Maeda 1996). Cytokinin levels in the short-day plant *Chenopodium rubrum* (lambsquarters) are also affected by exposure to a photoperiod inductive for flowering (Machackova et al. 1996). The signals may therefore involve the classical phytohormones, although it is not yet possible to account for all the observed effects (Koornneef 1997).

Because interruption of the photoperiod at different times of the night has different effects on

induction or prevention of flowering, a biological clock with a rhythm of about 24 hours (a **circadian clock**) has been postulated in plants. Such a circadian clock also plays a role in plants that fold their leaves at night and in many other processes. The biological clock presumably controls the sensitivity for P_{fr}. If the ability of plants from temperate climates to sense the length of the night is impressive, that of some tropical species is truly astounding. Here the variation in daylength may be very short and a change of 20–30 min may suffice to trigger flowering (Mouradov et al. 2002).

3.3.2 Do Plants Sense the Difference Between a Certain Daylength in Spring and Autumn?

Daylength is a tricky environmental cue, because days of the same length occur in both spring and autumn. How do plants sense the difference between the two seasons? Many long-day and short-day plants from cold climates may never perceive daylength in spring, since there is no appreciable metabolic activity. This would be the case for, e.g., *Eupatorium rugosum* (white snakeroot) and various *Helianthus* (sunflower) species in Michigan, USA. However, that situation is different in warmer environments. It was once thought that plants could sense the **lengthening** or the **shortening** of days; however, experiments have not confirmed the existence of such a mechanism. How, then, do they do it?

In addition to daylength, plants need a second environmental cue (e.g., temperature) (Sect. 3.3.3). Such a combination is required to induce flowering in *Fragaria ananassa* (strawberry) and *Beta vulgaris* (sugar beet). Flower primordia are induced in autumn, when daylength is reduced to a critical level. Further development of the primordia is stopped by low temperature in winter and only continues when the temperature increases in spring (Bernier et al. 1981).

3.3.3 Timing by Sensing Temperature: Vernalization

In temperate climates, changes in daylength coincide with changes in temperature. Many species that flower in spring are not long-day plants; rather, they use **temperature** as an environmental cue (Fig. 18). Exposure of the entire plant or of the moist seed induces flowering. We owe much of the information on effects of temperature on flower induction to the Russian botanist **Lysenko**. He showed that exposure of moist seeds of winter wheat (*Triticum aestivum*) to low temperatures allowed the plants to flower, without exposure of the seedlings to the harsh Russian winter. The physiological changes triggered by exposure to low temperature are called **vernalization** (from the Latin word for spring, *ver*) (Atkinson & Porter 1996).

Lysenko unfortunately did not place his important findings in the right scientific perspective. Rather than concluding that phenotypic changes in the seeds exposed to low temperature accounted for the flowering of the mature wheat plants, he insisted that the changes were genetic. Inspired and supported by the political flavor of the 1930s in his country, he stuck to his genetic explanation, much to the detriment of genetics and geneticists in the Soviet Union.

Vernalization is essential, both for crop species such as *Triticum aestivum* (winter wheat) and for winter annuals in general which survive during winter as seedlings. Vernalization also triggers flowering in biennials that overwinter as a rosette, such as *Digitalis purpurea* (fox glove), *Lunaria annua* (honesty), *Daucus carota* (carrot), *Beta vulgaris* (beet), and in perennials such as *Primula* (primrose) and *Aster* species, and plants that overwinter as a bulb, tuber, or rhizome. Figure 19 shows the effect of exposure to low temperature for 3–12 weeks on flowering of *Campanula* (harebell).

Vernalization is believed to require perception of low temperature in the vegetative apex. In *Arabidopsis thaliana* (thale cress), the vernalization requirement of late-flowering genotypes is due to up-regulation of a specific gene. In *Triticum aestivum* (wheat) the difference between winter wheat and spring wheat is controlled by a single gene (Yan et al. 2003). After cold treatment, the transcripts of this gene are down-regulated and remain so for the remainder of the plant's life (Michaels & Amasino 2000). Cold treatment supposedly induces the breakdown of a compound that accumulated during exposure to short days in autumn and which inhibits flower induction. At the same time, a chemical compound is produced that promotes flower induction, most likely GA (Mouradov et al. 2002).

The practical applications of our ecophysiological knowledge on environmental cues that trigger flowering are enormous. Many flowers that used to be available during specific seasons only can now be produced all year round. Building on fundamental ecophysiological experiments, in the Netherlands the flower industry has become a flourishing branch of horticulture.
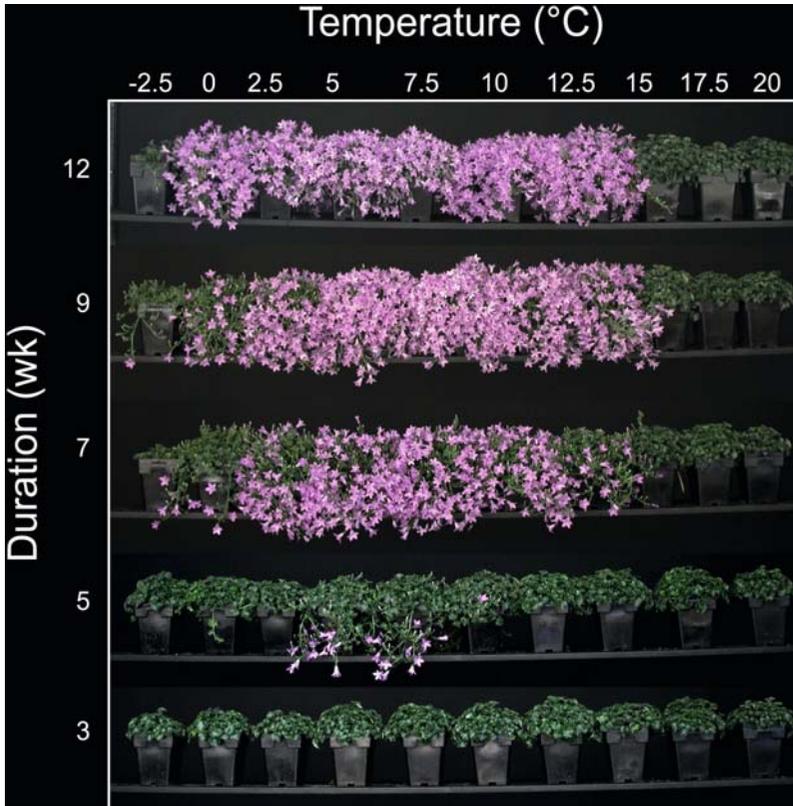
Figure 19. The effect of vernalization temperature and duration of flowering of *Campanula* birch hybrid (harebell). No flowering is observed if the vernalization period is less than 5 weeks. Courtesy S. Padhye and A. Cameron, Department of Horticulture, Michigan State University, USA.

3.3.4 Effects of Temperature on Plant Development

Low temperature is a **trigger** for flower induction of biennials (Sect. 3.3.3) and also affects plant **development** (Atkinson & Porter 1996). Reaumur (1735) introduced the concept of a **thermal unit** to predict plant development. This concept assumes that plants need a fixed temperature sum to fulfill a developmental phase. This assumption implies that the rate of development, expressed as the inverse of the duration in days for a given phase, is a linear function of temperature. Although the concept of thermal unit is widely applied, it has no physiological basis (Horie 1994).

3.3.5 Attracting Pollinators

Pollination of flowers by insects, birds, lizards, or bats requires attraction of pollinators. Attraction may occur through secondary phenolic compounds (flavonoids) in the petals (Shirley 1996). These **UV-absorbing compounds** are invisible to the human eye, but they are perceived by pollinating bees. The flowers of many species change color with pollination, thus guiding potential pollinators to those flowers that are still unpollinated, and provide a nectar reward (Weiss 1991). The change in color may be due to a change of the pH in the vacuole, in which the phenolics compounds are located [e.g., in *Ipomoea caerulea* (morning glory)]. Following pollination, most flowers cease nectar production. Pollinators quickly learn which colors provide a nectar reward.

The quantity of nectar provided by a flower depends on the number of flowers in an inflorescence and the type of pollinator that a flower is "designed" to attract. For example, long-tubed red flowers pollinated by hummingbirds typically produce more nectar than short-tubed flowers pollinated by small insects; this makes sense in view of the 140-fold greater energy requirement of hummingbirds (Heinrich & Raven 1972). Those species that produce many flowers in an inflorescence typically produce less nectar per flower than do species that produce a single flower. In general, plants produce enough nectar to attract pollinators, but not to satiate them, thus forcing pollinators to visit additional flowers to meet their energetic requirements and increasing the probability of effective pollen transfer (Heinrich 1975).

Secondary compounds play a role as **visual** cues for insects. Others, with specific **scents**, are often released only at a specific time of the day or night, associated with thermogenic respiration. These scents may be faint smells or an olfactory delight for humans, e.g., terpenoids released by **thermogenic** cones of *Macrozamia* (cycad) species (Terry et al. 2004). On the other hand, *Helicodiceros muscivorus* (dead horse arum) produces an inflorescence that resembles the anal area of a dead mammal and produces a foetid scent during the few hours after sunrise. Flies enter the floral chamber, pollinate the female florets, and become trapped until the next morning, when pollen is shed from the male florets and the flies are released (Seymour et al. 2003). The cyanide-resistant **alternative path** increases in activity prior to heat production and is partly responsible for it (Sect. 3.1 of Chapter 2B on plant respiration). Although this is not the only reason for thermogenesis (high respiration rates per se are also important), it definitely contributes to the **heat production** because the lack of proton extrusion coupled to electron flow allows a large fraction of the energy in the substrate to be released as heat.

The temperature of the flower, compared with that of the ambient air, can also be enhanced by **solar tracking**, which is a common phenomenon in alpine and arctic species that belong to the Asteraceae, Papaveraceae, Ranunculaceae, and Rosaceae and involves the perception of blue light (Stanton & Galen 1993). This may raise flower temperature by several degrees above the ambient temperature, as long as the wind speed is not too high (Sect. 2.2 of Chapter 4A on the plant's energy balance). Solar tracking might therefore affect fitness in many ways. When solar tracking is prevented in *Dryas octopetala* (mountain avens), by tethering the plants, lighter seeds are produced, but the seed set is not affected (Kjellberg et al. 1982). A similar treatment decreases both seed set and seed mass in *Ranunculus adoneus* (snow buttercup) (Stanton & Galen 1989). The flowers of the solar-tracking Norwegian alpine buttercup (*Ranunculus acris*) traverse an arc of about $50°$, with speed of movement and solar tracking accuracy being highest at midday (between 11 am and 5 pm). This solar tracking enhances flower temperature by about $3.5°C$. Solar tracking decreases with flower aging and stops completely as the petals wither, so that it cannot have effects on post-anthesis events. Tethering the flowers does not affect the attractiveness to pollinating insects, seed:ovule ratio, seed mass, or seed abortion rate (Totland 1996). If solar tracking has any selective advantage in this species, then it is probably only under special weather conditions (e.g., when pollinator activity is limited by low temperatures).

Orchids more than any other plant family have engaged in complex pollination systems, with species adopting the full spectrum of pollination syndromes from autogamy (a means of self-pollinating), food rewarding, food deception, nest-site deception, to sexual deception (Cozzolino & Widmer 2005). Whereas food-deceptive systems are the most common in orchids, it is sexual-deceptive systems that have attracted most interest where orchid flowers produce insectiform flowers and pheromones (known as **allomones**) that match the calling hormone of female insects, usually wasps and bees. The most extreme cases of sexual deception are found in Australian orchids, where hammer orchids (*Drakaea* and *Chiloglottis*) have almost exclusive one-to-one relationships between male wasps and orchid species. In the case of *Chiloglottis*, the hormone has been characterized and is known as chiloglottine (Schiestl et al. 2003); it precisely matches the pheromone chemistry produced by the female wasp. Such levels of evolutionary specialization present important consequences for conservation management where managing the orchid requires careful consideration of the wasp.

3.3.6 The Cost of Flowering

Some of the most important tropical–subtropical fruit trees produce extremely large numbers of flowers, for unknown reasons. Their respiratory demands are high (Sect. 5.1.2 of Chapter 2B on plant respiration) and the overall daily demand for carbohydrates during bloom may often exceed the daily photosynthate production. Flowering in *Citrus paradisi* (grapefruit) for a tree that bears 20000–50000 flowers requires 166–400 mol C $tree^{-1}$. In comparison, the amount of carbon required for the growth of the ovaries, the only floral organs that persist after flowering, is only 33–38 mol C $tree^{-1}$. Together with the abscission of fruitlets, the amount of carbon that is lost at early stages of the reproductive cycle is about 27% of the annual photosynthate production (Bustan & Goldschmidt 1998).

From an evolutionary perspective the advantages that are associated with the production of large numbers of reproductive units must justify the apparent waste of resources. Uncertainties concerning pollination and improvement of fruit/seed quality by selective abscission have been suggested as factors influencing the excessive production of reproductive units. From the grower's point of view the heavy bloom of *Citrus* may seem to be a

waste of resources; preventing it might lead to an increase in yield or fruit quality.

3.4 Fruiting

Allocation to reproduction varies substantially among plants and with environmental conditions, ranging from 1 to 30% of net primary production, with median values of perhaps 10%. This modest allocation to reproduction (the process that most directly governs plant fitness) is less than typical allocation to root exudation under nutrient stress or nutrient uptake under favorable conditions (Table 2 in Chapter 2B on plant respiration) which suggests that the processes of resource acquisition under conditions of environmental stress and competition with neighboring plants often leave relatively few resources for reproduction.

Wild plants generally produce fewer fruits than flowers. Low allocation to reproduction sometimes reflects poor pollination, when weather conditions are bad for pollinators or for appropriate pollen-producing plants. Even when the flowers are artificially pollinated, however, the ratio between fruits and flowers, commonly referred to as **fruit set**, may still be substantially below 1. In addition, increased pollination may have more seeds setting, but at the expense of seed size, which indicates that seed production may be both "pollen-limited" and "resource-limited" (Stanton et al. 1987).

Allocation to reproduction differs substantially among species. In general, annuals and other short-lived species allocate a larger proportion of annual production to reproduction than do long-lived perennials, which suggests a **trade-off** between reproduction and traits that promote survival or growth (Bazzaz et al. 1987). For example, many conifers and other tree species reproduce prolifically once in several years. These "mast years" are correlated with years of low wood production and are often synchronized among individuals in a population. Mast reproduction may be possible only after several years of reserve accumulation. This pattern of reproduction serves to "swamp" seed predators in years of abundant seed production and to limit the population growth of seed predators in intervening years (Eis et al. 1965).

Allocation to female function is generally considered the most costly component of reproduction, because of the large investments of carbon and nutrient required to produce seeds. This may explain why female individuals of dioecious species are generally underrepresented in sites of low water availability (Bazzaz et al. 1987); however, male

function also entails substantial costs. For example, *Phacelia linearis* (threadleaf phacelia) has both female and hermaphroditic individuals. Those individuals that have both male and female function (hermaphrodites) grow more slowly than do females, particularly at low nutrient supply which suggests that it is the nutrient investment in male function that accounts for the slower growth of hermaphrodites (Eckhart 1992a,b). During the vegetative phase, hermaphroditic genotypes of *Plantago lanceolata* (snake plantain) have exactly the same growth rate and photosynthetic characteristics as the ones with only female function. When grown at a nutrient supply that resembles that in their natural environment, however, the female plants have a three- to fivefold higher reproductive output. Female genotypes invest three times more biomass in each flower, with an even greater difference in terms of N investment, because the stamens contain relatively more N than do the female components of flowers (sepals and petals). The female plants use the N saved by not producing pollen for additional vegetative as well as reproductive growth, showing that resource compensation is a primary mechanism that accounts for the persistence of genotypes that are exclusively female (Poot 1997).

Allocation to reproduction is difficult to quantify because the inflorescence can often meet much of its own carbon requirement and because some structures serve both reproductive and nonreproductive roles. A substantial proportion of the energetic costs of reproduction are met by photosynthesis in the inflorescence and associated leaves. For example, photosynthesis by the inflorescence accounts for 2–65% (median 22%) of the carbon required for reproduction of temperate trees (Bazzaz et al. 1979). In cereals, the ear accounts for up to 75% of the photosynthate required for grain production, and the inflorescence plus the closest leaf (the flag leaf) provide all of the photosynthate required for reproduction (Evans & Rawson 1970). When vegetative leaves are removed by herbivores, an increased proportion of flag-leaf photosynthate goes to vegetative organs, whereas damage to the flag leaf increases carbon transport from other leaves to the inflorescence. Thus, the role of each leaf in supporting reproduction depends on the integrated carbon supply and demand of the entire plant. Stem growth often increases during reproduction of herbaceous plants which increases the probability of pollen exchange and the dispersal distance of wind-dispersed fruits. The greatest gains in yield of crop (e.g., cereals, peanuts, sugar beet) have come from breeding for a higher **harvest index** [i.e., the ratio between harvestable biomass and total

(above-ground) biomass]. In cereals this has been achieved by selection for varieties with reduced stem allocation, which is due to a low production of or sensitivity to GA. There has been no increase in photosynthetic capacity during crop breeding for higher grain yield (Evans 1980, Gifford et al. 1984). However, actual yields are now approaching potential crop yields in many areas. Further increases in yield may be possible only by increasing photosynthetic capacity (Mitchell & Sheeny 2006).

3.5 Senescence

After flowering, phloem-mobile nutrients are exported from the senescing leaves and roots to the developing fruits (Sect. 4.3.2 of Chapter 6 on mineral nutrition). Unlike "getting old and wearing out", senescence in plants is a carefully programmed, hormonally controlled developmental process: **programmed cell death** (Jones & Dangl 1996). It is an integral part of plant development that is affected by environmental factors (e.g., irradiance level, photoperiod, and nutrient supply). It is promoted by **ethylene** and **ABA**, and slowed down or reversed by **cytokinins** and/or **GA**. A number of specific genes are up-regulated during leaf senescence (Smart 1994). An early visible symptom of leaf senescence is leaf yellowing, due to loss of chlorophyll. Rubisco and other chloroplast proteins are hydrolyzed by proteolytic enzymes, and free amino acids are exported via the phloem. Mitochondrial proteins tend to be hydrolyzed in a later phase, and tissues around the vascular system which are required for nutrient export are the last to senesce. The breakdown of the nucleus, whose activity is essential for senescence to proceed, is a relatively late event in the developmental process (Gan & Amasino 1997). Nitrogenous compounds are remobilized, as are most other compounds that can move in the phloem. Unlike phloem-mobile elements, Ca concentrations in phloem sap are very low (Sect. 2 of Chapter 2C on long-distance transport).

Considering the driving force for phloem transport (i.e., a gradient in hydrostatic pressure between source and sink; Sect. 3 of Chapter 2C on long-distance transport), it is not surprising that some of the compounds remobilized from senescing leaves are transported to roots, even though these may show a net export of nutrients (Simpson et al. 1983). The pattern is somewhat similar to that in vegetative plants, which show a continuous cycling of N between leaves and roots, via both phloem and xylem (Sect. 5.4.1 of Chapter 7 on growth and allocation). The rather indirect manner in which N moves

from senescing leaves to developing kernels probably reflects the way the systems for long-distance transport (i.e., xylem and phloem) operate. That is, phloem sap will move in the sieve tubes from a site where the phloem is loaded, thus creating a high pressure, to a site where phloem unloading takes place, thus decreasing the pressure. Xylem sap will move in the xylem conduits, down a gradient in hydrostatic pressure. There is some exchange between the transport pathways, especially in the stem (Fig. 19), but this is obviously not sufficient to stop the need for a continuous cycling process in plants.

4. Seed Dispersal

Seeds are often well protected, either physically, by a hard seed coat (Sect. 2.1), or chemically, due to poisonous compounds, e.g., cyanogenic glycosides or specific inhibitors of digestive enzymes (Sects. 3.1 and 3.2 of Chapter 9B on ecological biochemistry).

Numerous plant attributes are associated with seed dispersal [e.g., floating designs in aquatics, sticky seed parts in mistletoes that ensure deposition on a host branch (Mitich 1991, Amico & Aizen 2000), hooks that facilitate attachment to animal furs, structures that attract animals, "ballistic" structures, plumes and wings that allow transfer through air (Murray 1986)]. Some of these mechanisms involve aspects of the plant's physiology, of which a few examples will be presented in this section.

4.1 Dispersal Mechanisms

Explosive or **ballistic** seed dispersal occurs in many plant species. Such dispersal mechanisms are highly undesirable in crop plants because they cause "shattering" and loss of seed during harvest [e.g., in *Brassica* (cabbage) species]. In the tropical rain forest legume tree, *Tetrabelinia moreliana*, such a mechanism allows seeds to be launched and transferred over as much as 50 m (Van der Burgt 1997). It is a consequence of drying of the pod walls which creates tension that builds up between the two valves of the pod. Once the tension exceeds a threshold value, the pod explodes and the seed is launched.

Tension in the tissue may also occur without drying of the reproductive structure [e.g., in *Impatiens* (touch-me-not)]. In this case the tissue tension reflects an aspect of tissue water relations, which we alluded to in Sect. 4 of Chapter 3 on plant water relations. That is, within the reproductive tissue,

the water relations of individual cells must differ widely, creating **tissue tension**. Touch or wind may cause a threshold to be exceeded which causes rupture in the reproductive structure and launching of the seeds.

4.2 Life-History Correlates

Plants have an ancient and uneasy relationship with vertebrate animals that eat their fruits and either digest or disperse their seeds. As early as 300 million years ago, Carboniferous progenitors of modern cycads bore fleshy fruits, which were apparently adapted for consumption by primitive reptiles that then dispersed the seeds (Howe 1986).

Many species [e.g., *Acacia* (wattle) species in Australia] produce a lipid-rich morphological structure, termed **aril** or **elaiosome**. Such a structure allows dispersal via ants (Hughes et al. 1994), which transport the seeds to their nest, thus burying the *Acacia* seeds, safe from fire (O'Dowd & Gill 1985). *Cabralea canjerana* (cancharana), on the other hand, is a typical bird-dispersed tree in Atlantic forests in south-east Brazil. Ants treat their seeds in different ways, depending on the species. Some ants remove the arillate seeds to their nest, thus reducing seed predation by insects and rodents. Other ants remove the aril on the spot or cover the seeds before removing the aril. Aril removal greatly facilitates seed germination in some species (Pizo & Oliviera 1998).

5. The Message to Disperse: Perception, Transduction, and Response

Plants continuously **sense** their environment, both as adults and as seeds, before germination starts. Seeds acquire information about the suitability of their environment for seedling growth, and they use this information to germinate or to remain dormant. There are numerous environmental cues, with plants from different environments using different cues. At a later stage plants similarly sense their environment to change from the vegetative to the reproductive stage and to time their flowering. Daylength and low temperature are major cues, with irradiance level and nutrient supply occasionally playing an additional role in the switch to the reproductive phase in biennials.

There are also changes during development that are programmed, with environmental factors playing at most a moderating role. For example, leaf senescence is part of a scenario of programmed cell death that can be hastened by low irradiance and limiting N supply. The switch from juvenile to adult foliage is also programmed, but it can be affected by irradiance, nutrient availability, and plant water status.

Once flowering has started, the plant may require pollinating animals to produce seeds. Olfactory and visual cues are produced to attract these pollinators. The seeds that are subsequently produced may end up close to the mother plant, but there are also numerous mechanisms that ensure dispersal of the seeds over relatively great distances. One of the mechanisms of ecophysiological interest is that of plants that "launch" their seeds. Other dispersal mechanisms require allocation of reserves to elaiosomes (i.e., producing food for dispersing ants). Ants both disperse and bury the seeds; therefore, it is assumed that the seeds are safe during a fire, but this remains to be established. Surviving seeds remain dormant until the right environmental (chemical) cues have been perceived, and the life cycle continues.

Plants sense their environment during their entire life, and the acquired information determines what is going to happen in several steps of the plant's life cycle. We now have a reasonable understanding of important environmental cues and plant responses. Right now, our knowledge of signal-transduction pathways that connect the environmental cue and the plant's response is expanding rapidly.

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