Chapter 7
Environmental Regulation of Dormancy and Germination

Abstract The seed stage of the higher plant life cycle allows for the survival of individual species, as well as populations, over long periods of time. Emergence of seedlings from the soil seed bank depends on a range of environmental factors of which water and temperature are the most important. The existence of germination response thresholds for (soil) water and temperature has allowed for the development of hydrothermal time models to predict germination and emergence. Additional environmental cues that determine germination are light (through phytochrome), nitrate, and smoke components. These factors are pivotal in sensing competitors and vegetation gaps. Seeds in the soil seed bank undergo dormancy cycling in synchrony with the seasons. In this way precise timing of emergence in the correct season and location are ensured. The survival of a population of annual species predominantly depends on flowering time and dormancy.

Keywords Dormancy cycling • Germination • Hydrothermal time model • Seedling establishment • Secondary dormancy • Seed dispersal • Soil seed bank

The biological importance of dormancy must be seen in relation to the ecology of germination—when and where a seed germinates. Interactions between seasonal dormancy-breaking agents, such as chilling and after-ripening, and the sensitivity of seeds in the soil to such dormancy-relieving factors as light and nitrate, in combination with sufficient amounts of oxygen and water, are responsible for determining whether a seed will germinate in a particular situation and season. The germination and dormancy mechanisms are therefore of great adaptive importance in ensuring that seedling emergence occurs at the most advantageous time and place. This chapter will consider some examples to illustrate the ecological significance of the control processes.

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7.1 Seed Dispersal and Burial

After seeds become detached from the parent plant they may travel short to long distances before they are buried in the soil and are subjected to the ambient environment for variable periods of time before they germinate and emerge, if at all. Even then, seeds may relocate because of soil disturbance, for example by flooding, predation, and cultivation. Seeds, or rather "dispersules" that may include fruits or other structures along with the seed, may have morphological adaptations to aid to their dispersal. These are usually modifications of the seed/fruit coat, such as "wings" and "hairs" (Fig. 7.1).

Seeds may be dispersed in several ways. Gravity is a simple dispersal mechanism, e.g., of apples, coconuts, and other larger fruits. They may become detached because of their weight and then roll away. Wind dispersal has two primary forms: seeds can float on the breeze or they can flutter to the ground. A well-known example is the dandelion, which has a feathery pappus attached to the seeds that allows them to float on the wind for dispersal over long distances. Maples have winged seeds (samara) that flutter to the ground over much shorter distances.

Many aquatic and some terrestrial species use hydrochory, or seed dispersal through water; examples are water lily, palm, and mangrove seeds. Some species disperse their seeds using autochory, which is the physical and sometimes explosive discharge of seeds from the fruit, as in Impatiens and some legumes.

Seeds can also be dispersed in several ways by animals. They can be transported on the outside of vertebrate animals, which is a process known as epizoochory. Epizoochorous seeds can have a variety of morphological adaptations, including an assortment of hooks, spines and barbs to attach to the skin or hair of animals. (As a side note, the tiny hooks on burdock fruits were the inspiration for the development of Velcro™ fasteners.) Many representatives of this mode of dispersal can be found in the Apiaceae and Asteraceae families. Seeds may also be dispersed via ingestion by vertebrate animals or endozoochory, which is the dispersal mechanism for many tree species. Finally, seeds can be dispersed by ants (myrmecochory), which is a dispersal mechanism of many shrubs and herbs. Myrmecochorous seeds have a lipid-rich attachment (elaiosome), which is a food source for ants. Ants carry these seeds into their colonies, feed the elaiosome to their larvae and discard the still viable seed in an underground chamber, thus adding it to the soil seed bank.

7.1.1 The Soil Seed Bank

After dispersal, a great quantity of seeds ends up on or in the soil, forming the soil seed bank. Germination may then take place instantly or may be delayed for an indeterminate period of time. Buried seed densities are highly variable. Lowest densities are found in tropical and temperate woodlands and alpine and arctic areas. Counts of over 100,000 seeds m^{-2} have been reported in wetlands. The highest density recorded for any species is 488,708 seeds m^{-2} for *Spergula marina*, a species with very tiny seeds (seed weight 0.05 mg). However, buried seed densities can be extremely patchy.

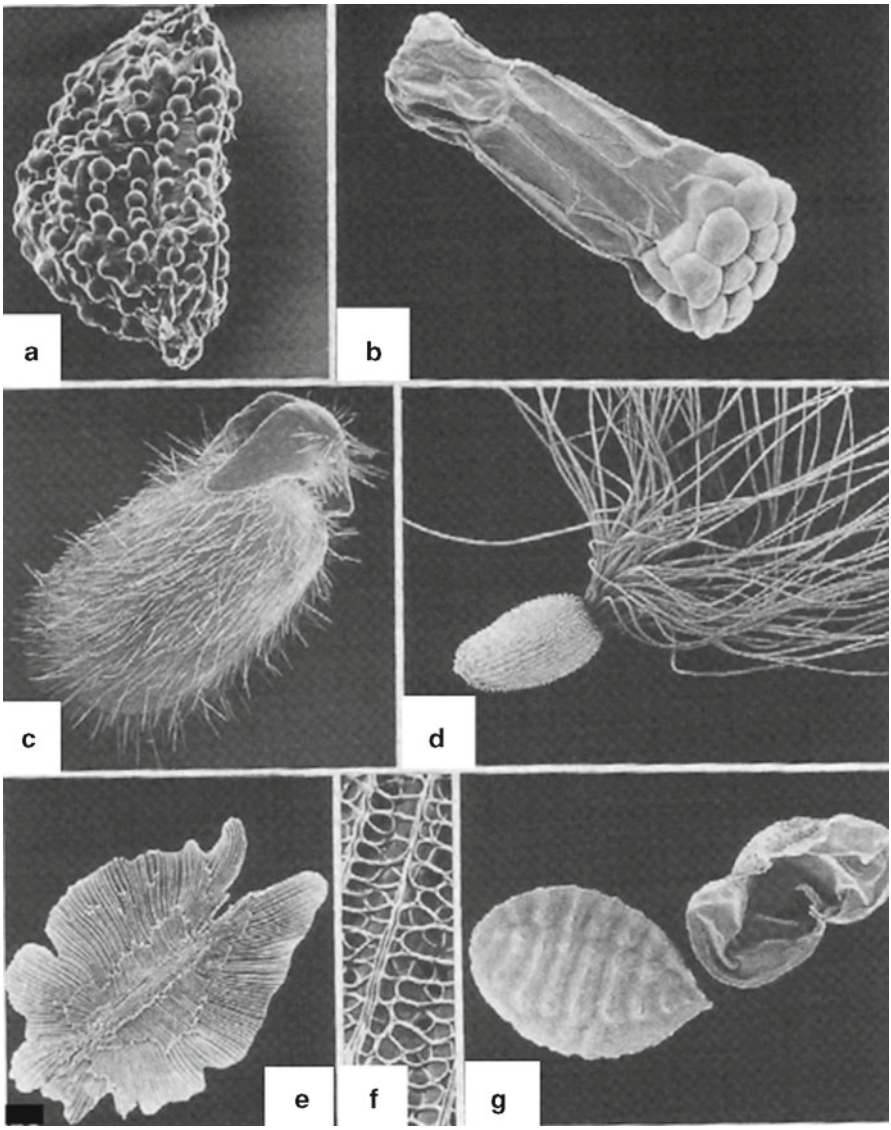

Fig. 7.1 Scanning electron micrographs of seeds showing different dispersal types. (**a**) *Voyria spruceana*, dust seed. (**b**) *Begonia glabra*, balloon seed with inflated seed ends. (**c**) *Polygala vulgaris*, hairy seed with elaiasome. (**d**) *Epilobium hirsutum*, seed with hair tuft. (**e**, **f**) *Paulownia tomentosa*, winged seed and detail of wing. (**g**) *Oxalis europeae*, dispersed seed with reversed outer part of outer integument. From Boesewinkel and Bouman (1995). Photograph courtesy of F. Bouman, Univ. Amsterdam

The distinction has been drawn between transient and persistent seed banks, the former consisting of seeds that mostly are viable in the soil for no more than 1 year, and the latter having a significant proportion of the seeds remaining viable for many years. The different types of seed banks exhibit varying seasonal acquisition of

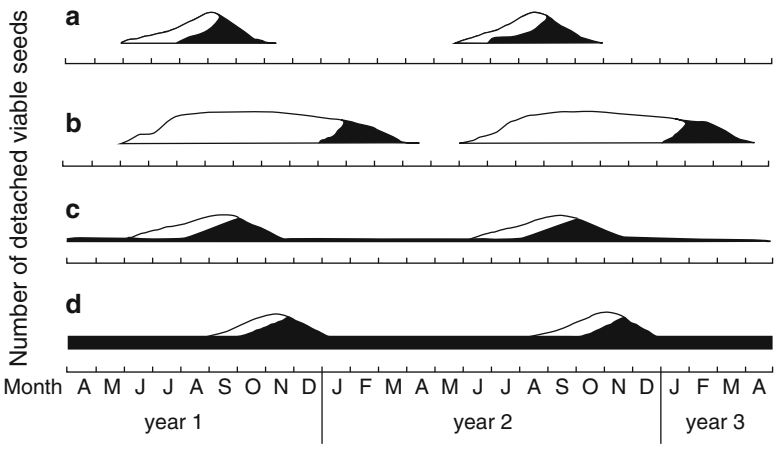

Fig. 7.2 Seed banks common in soils of temperate regions. Shaded areas indicate seeds that can germinate immediately when tested in the laboratory (i.e., nondormant seeds) and unshaded areas represent viable seeds that are dormant. (**a**) Seeds of annual and perennial grasses of dry or disturbed habitats (e.g., *Lolium perenne*). (**b**) Seeds that germinate in early spring, colonizing gaps in the vegetation. They include annual and perennial herbs, trees, and shrubs (e.g., *Impatiens glandulifera, Acer pseudoplatanus*). (**c**) Seeds of winter annuals, which germinate mainly in the fall. A small, persistent seed bank of nondormant seeds is maintained (e.g., *Erophila verna*). (**d**) Seeds of annual and perennial herbs and shrubs, which have large, persistent seed banks (e.g., *Stellaria media*). After Grime (1979)

germinability (or loss of dormancy), which gives each group of plants its characteristic emergence pattern (Fig. 7.2). These seasonal patterns are largely controlled by the seeds' responses to prevailing environmental factors, such as moisture, temperature, light and various chemicals in conjunction with seasonal environmental factors (e.g., chilling, after-ripening) that sensitize the seeds to the environment. The emergence of seedlings depends on more factors than those required for the breaking of dormancy and the induction of germination. During their prolonged stay in the soil, seeds and young seedlings may be victim to predation by animals or degradation by microorganisms. Also, successful seedling emergence depends on the depth at which germination occurs, as well as on soil properties such as physical impedance or crusting.

7.2 Environmental Control of Germination

The interactions of seed dormancy mechanisms with both the accumulated and current environmental conditions determine whether and what fraction of seeds in a seed bank will germinate at a given time (Fig. 7.3). The weather and soil physical characteristics establish the microclimate perceived by the seed. Depending upon whether the seeds are dry or wet, different mechanisms may be involved in alleviating dormancy, e.g., after-ripening or chilling. Once dormancy has been alleviated by the seed's response to cues from the microenvironment, sensitivity to the current environment, particularly to water, temperature, light, and nutrients, determine the rate

and extent of germination of nondormant seeds. Following germination, seedlings may fail to emerge or survive due to physical factors (soil crusting, burial depth) or to predation or disease. All of these factors constitute an interacting network of environmental signals and biological responses determining the entry and release of seeds from the soil seed bank (Fig. 7.3). This section considers these various factors and their interactions in relation to seed dormancy and germination in an ecological context.

7.2.1 Water

The most essential environmental factor required for seed germination is water. Seeds imbibe water from their surroundings, and the ψ of the soil water determines the maximum ψ that the seed can attain (Sect. 4.3). In dry environments, seeds in the seed bank may persist primarily in the dry state, then imbibe quickly and achieve germination when water is available following rainfall. Flushes of seedlings emerge following rain episodes, but otherwise germination is limited by lack of water. In humid regions, seeds in the seed bank persist largely in a hydrated state, and dormancy mechanisms rather than water availability prevent untimely germination.

7.2.1.1 Hydrotime Model of Germination

Water availability (i.e., water potential or ψ) affects both the rate of germination and the fraction of seeds in the population that will germinate. If the ψ is too low (e.g., at −1.2 MPa), germination is prevented (Fig. 4.10), as was described for the case of seed priming (Sect. 4.7). At higher ψ, both the speed and percentage of germination increase in a characteristic manner (Fig. 7.4a). The water relations of germination have been described by the hydrotime model, which is a unifying approach to describe the patterns of germination that occur in response to ψ of the seed's environment. It is based on the concept that the time to completion of germination (here called germination for simplicity) is proportional to the magnitude of the difference between the seed ψ and the water potential threshold for radicle emergence (termed "base water potential" or ψ_b). The ψ_b is the minimum ψ at which germination will occur for a given seed, and the time from the start of imbibition to completion of germination varies in proportion to the extent that the seed ψ exceeds this threshold ψ_b. In addition, individual seeds in a population vary in their ψ_b values; seeds with the lowest (most negative) ψ_b values germinate quickest in a population, followed in order by seeds with increasing ψ_b values. The distribution of ψ_b values in a seed population is generally normal or Gaussian, and can be defined by the median ($\psi_b(50)$) and standard deviation ($\sigma_{\psi b}$) (Fig. 7.4b), but other distributions are possible depending upon the characteristics of the seed population. Seed banks, for example, may be composed of seeds from different years of production that have experienced different after-ripening or dormancy-breaking regimes, resulting in multiple subpopulations with different dormancy characteristics; the relative proportions of

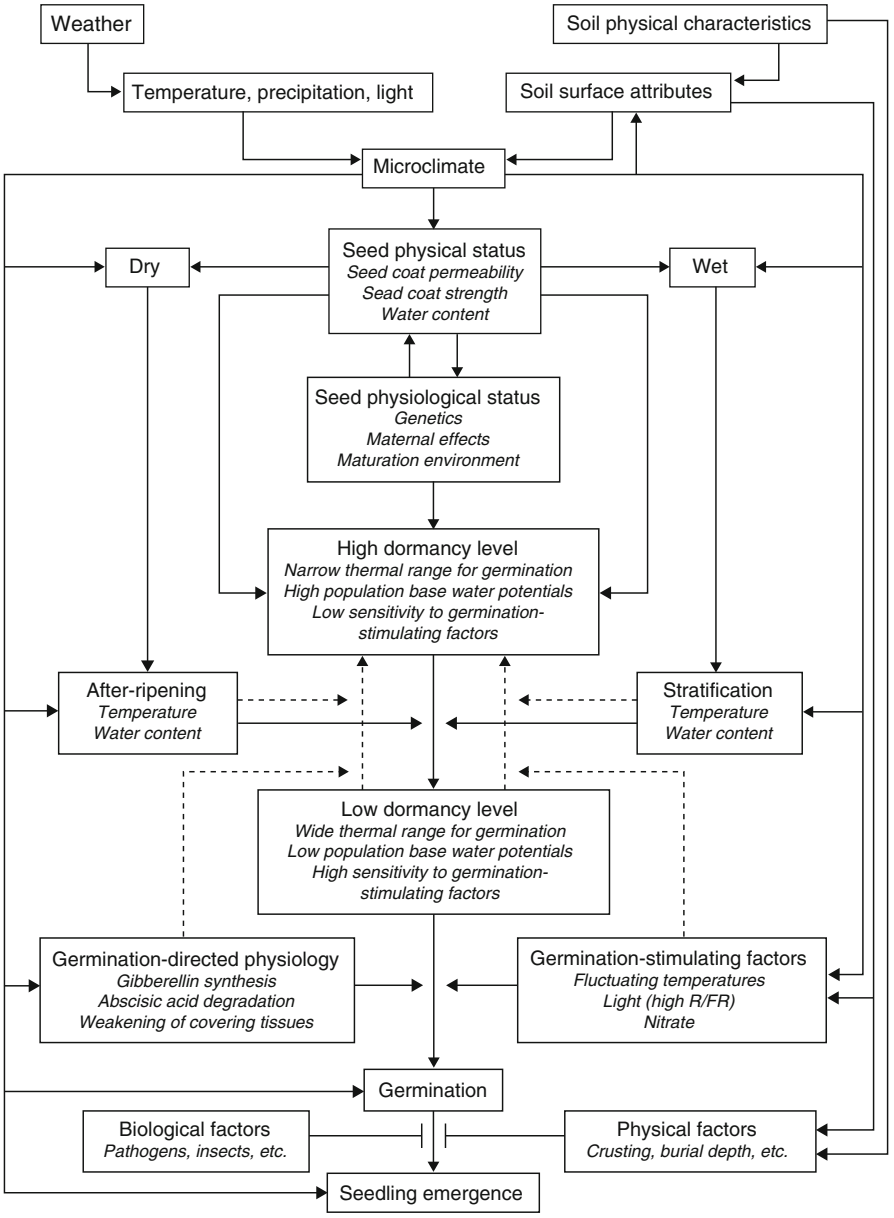

Fig. 7.3 Physical and biological factors associated with environmental control of seed dormancy and germination. Weather, soil physical characteristics and soil surface attributes (e.g., presence or absence of litter layer, topography) determine the seed zone microclimate. Microclimate controls seed dormancy status and germination primarily through moisture content and temperature. Physical attributes of the seed, such as seed coat permeability, can mitigate these microclimate effects. The physiological state of the seed, including its genetic background and maternal and environmental effects during development and maturation, influences the initial dormancy level.

different subpopulations in the total population can skew the distribution toward higher or lower ψ_b values.

The following equation describes the hydrotime model:

$$\theta_H = (\psi - \psi_b(g))t_g \tag{7.1}$$

where θ_H is the hydrotime constant (MPa-days or MPa-hours), ψ is the seed water potential, $\psi_b(g)$ is the base or threshold water potential defined for a specific germination fraction g, and t_g is the time to radicle emergence of fraction g of the population. The hydrotime model proposes that θ_H is a constant for a given seed population, implying that t_g must increase proportionately as the difference between ψ and $\psi_b(g)$ is reduced and approaches zero. This is illustrated for the 16th, 50th, and 84th germination fractions in Fig. 7.4c. These fractions are chosen because they represent the median (50%) and one standard deviation below and above the median in the $\psi_b(g)$ distribution (Fig. 7.4b). In a normal distribution, one standard deviation on either side of the median encompasses from 16 to 84% of the entire population. The times to germination of these fractions of the seed population in relation to ψ illustrate the threshold nature of the hydrotime model, with all seeds having similar times to germination when ψ is high, but as ψ decreases, the times to germination sharply increase. Due to the differences in their threshold ($\psi_b(g)$) values (Fig. 7.4b), the ψ at which germination times increase sharply varies among the different fractions. This corresponds to the skewness in the germination time courses (Fig. 7.4a), where the slower seeds to germinate are affected more by reduced ψ. In this way, the hydrotime model simultaneously accounts for both the timing and the final germination percentages of seed populations in response to changes in ψ.

Fig. 7.3 (continued) Dormancy-breaking processes occur in dry seeds (after-ripening) and in imbibed seeds (e.g., chilling or stratification). A high dormancy level (whether primary or secondary) is associated with a narrow thermal range permissive for germination, relatively high (more positive) population base water potentials, and a low sensitivity to germination-stimulating factors. Conversely, a low dormancy level is associated with a wider temperature range permissive for germination, lower (more negative) population base water potentials and increased sensitivity to germination-stimulating factors. Seeds can shift back and forth between low and high dormancy states through the imposition and release of secondary dormancy in response to environmental cues. Even for seeds in a low dormancy state, germination may still be dependent upon stimulation by factors such as light, nitrate or fluctuating temperatures. After germination has occurred, additional biotic and abiotic stresses can reduce the number of seedlings that successfully emerge from the soil. Interactions between environmental factors and seed dormancy status are shown via arrows; bars indicate repressive interactions. Dashed arrows indicate that when environmental conditions are not conducive to dormancy-breakage or germination, seeds can revert to a higher dormancy level (secondary dormancy). From Allen et al. (2007). Courtesy of Wiley

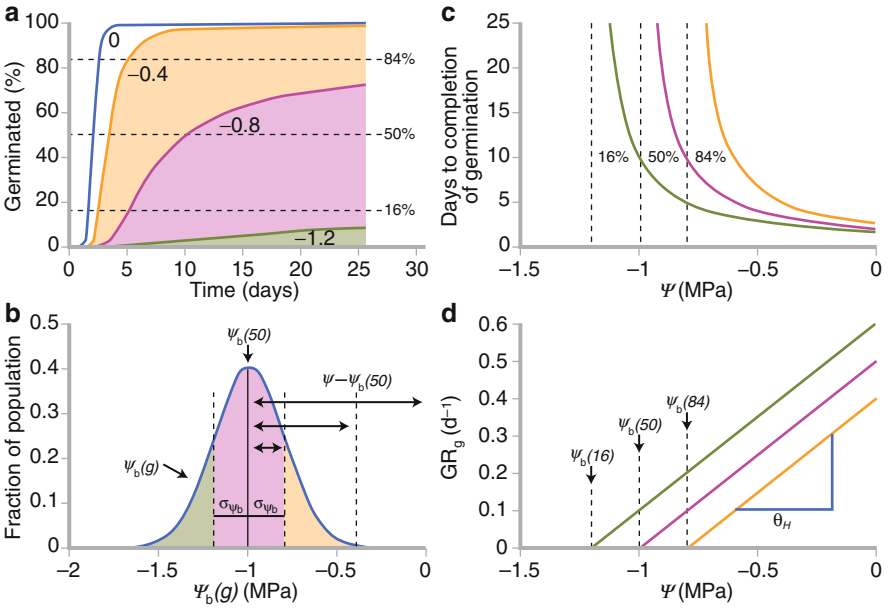

Fig. 7.4 Seed germination patterns in relation to water availability. (**a**) Germination time courses of seeds imbibed in 0, −0.4, −0.8 or −1.2 MPa, based upon the hydrotime model with values of $\theta_H = 2$ MPa d, $\psi_b(50) = -1.0$ MPa, and $\sigma_{\psi b} = 0.2$ MPa, all reasonable values for nondormant seeds. The colored regions refer to *panel b*, and germination percentages of 84, 50 and 16 are indicated by the horizontal dashed lines; these values represent ±1 $\sigma_{\psi b}$ around the mean. (**b**) The $\psi_b(g)$ distribution of threshold water potentials for the seed population. The normal distribution is indicated by the bell-shaped curve, which corresponds to the fractions of seeds in the population with the indicated $\psi_b(g)$ values. One standard deviation ($\sigma_{\psi b}$) on each side of the median ($\psi_b(50)$) is indicated. The difference between the seed ψ and the $\psi_b(50)$ is indicated for different values of ψ by the double arrows. At 0 and −0.4 MPa, essentially all seeds will complete germination. Between −0.4 and −0.8 MPa (*orange* region), a fraction of the population will not be able to germinate because the ψ is below their respective thresholds. This is shown by the reduction in germination percentage (and slower rate) of the *orange* shaded region in *panel a*. Similarly, reducing the ψ to −1.2 MPa prevents the germination of 84% of the seed population (*purple area* in *panel a*), and the remaining 16% germinate slowly as the ψ is close to their ψ_b (*green area* in *panel a*). (**c**) The times to germination of different fractions of the seed population imbibed at different ψ. At high water potentials, times to germination are similar, but increasingly diverge as ψ decreases. As the ψ approaches the ψ_b for a given seed fraction, times to germination increase very rapidly and asymptotically approach the ψ_b lines (*vertical dashed lines*). (**d**) Germination rates (GR_g), or $1/t_g$, for the curves illustrated in *panel c*. Plotting the inverse of t_g versus ψ results in lines with slopes of $1/\theta_H$ and intercepts on the *x*-axis of the ψ_b values for the specific germination fraction. For the fractions chosen, the intercepts differ by the value of $\sigma_{\psi b}$

The relationship between the $\psi_b(g)$ distribution and times to germination is determined by the difference between ψ and $\psi_b(g)$. If we consider the median seed of the population with a threshold of $\psi_b(50)$, then the difference between the threshold and the actual ψ is shown by the arrows in Fig. 7.4b. As ψ is reduced from 0 to −0.4 to −0.8 MPa, the difference $\psi - \psi_b(50)$ also decreases, which, according to

(7.1), means that the time to germination t_g must increase proportionately. When $\psi = \psi_b(50)$, t_g equals infinity for that fraction, which is the definition of the threshold, i.e., the ψ at which germination cannot be completed. For the example in Figure 7.4b, $\psi_b(50) = -1$ MPa with a standard deviation ($\sigma_{\psi b}$) of 0.2 MPa. Thus, at −0.8 MPa, a final germination percentage of 84 is expected, and at −1.2 MPa a germination percentage of 16. As shown in Fig. 7.4a, the respective germination time courses are approaching those values, but it will take a very long time for the asymptote to reach those percentages (~350 d), because the time to germination increases sharply as $\psi - \psi_b(g)$ gets very small (Fig. 7.4c).

Equation (7.1) can be rearranged in the following way to illustrate the relationship between ψ and germination rates (GR), or the inverse of time to radicle emergence for fraction g ($GR_g = 1/t_g$).

$$GR_g = 1/t_g = (\psi - \psi_b(g))/\theta_H \tag{7.2}$$

Thus, a plot of GR_g versus ψ gives straight lines with common slopes of $1/\theta_H$ and intercepts on the ψ axis equal to $\psi_b(g)$ (Fig. 7.4d). This is one way to determine the values of θ_H and of $\psi_b(g)$ for specific germination fractions. A more convenient method is to fit the original germination time courses at different ψ using regression models that allow the values of θ_H, $\psi_b(50)$ and $\sigma_{\psi b}$ to be determined. An alternative approach termed the "Virtual Osmotic Potential" (VOP) model shares the concept of a population distribution of $\psi_b(g)$, but assumes that progress toward germination is due to either accumulation of osmotic solutes to increase embryonic growth potential or a reduction in the restraint by enclosing tissues over time following imbibition (see also Sect. 4.6).

7.2.1.2 Hydrotime and Dormancy

The hydrotime model can reproduce the patterns of germination time courses that occur in response to reduced ψ. Interestingly, these same patterns are also encountered as seeds enter or leave dormancy, even when germinating on water. That is, there is generally an increase in both final germination percentage and speed of germination as a seed population loses dormancy. This is illustrated by the loss of dormancy due to after-ripening of botanical (true) potato seeds (Fig. 7.5). Initially, the seeds are partially dormant; germination is slow and the maximum, even in water, is only about 50% (Fig. 7.5a). After 7 or 30 days of after-ripening, germination increases to near 100% and is much more rapid and uniform (Fig. 7.5b, c). This is particularly evident when the seeds are germinated at reduced ψ, because −0.4 MPa almost completely prevents germination initially, but after 30 days of after-ripening, the same ψ only slightly delays germination. This change in sensitivity to ψ indicates that the $\psi_b(g)$ distributions of the seed population have shifted to lower values due to after-ripening. The $\psi_b(50)$ values go from −0.18 MPa initially to −1.89 in 30-day after-ripened seeds (Fig. 7.5d, f). Note that as far as the hydrotime model is concerned, there is no distinction between a constant threshold distribution and a

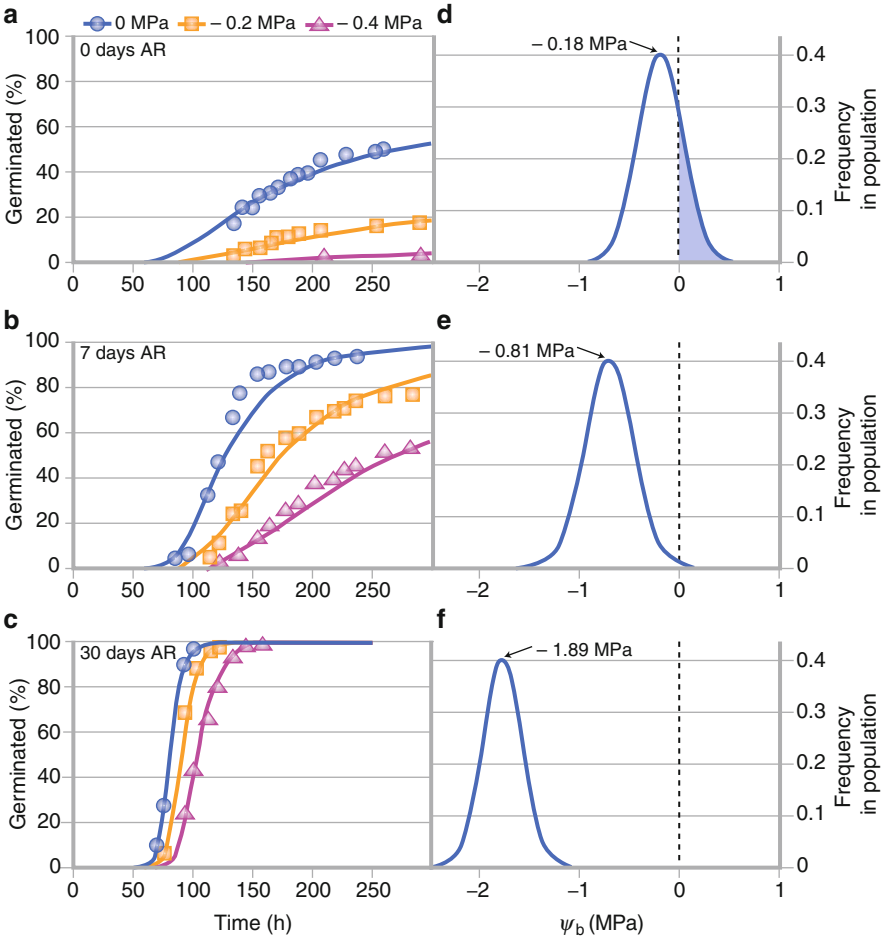

Fig. 7.5 Germination of botanical potato seeds at 14–15°C and different ψ (0, −0.2, −0.4 MPa) as affected by after-ripening (AR) for (**a**) 0, (**b**) 7 or (**c**) 30 days at 4% seed moisture content and 37°C. The symbols are the experimental data, and the curves are predicted from the hydrotime model based upon the $\psi_b(g)$ distributions shown in **d**, **e**, and **f**. Initially, the ψ_b distribution was high ($\psi_b(50) = -0.18$ MPa) and a fraction of the seed population was unable to germinate even in water (represented by shaded area under curve to the right of the dashed 0 MPa line in *panel d*). During after-ripening, the $\psi_b(g)$ distributions shifted to lower values ($\psi_b(50) = -0.81$ MPa, −1.89 MPa; *panels e* and *f*), corresponding to the more rapid germination and decreased sensitivity to inhibition by low ψ (*panels b* and *c*). Modified from Alvarado and Bradford (2005) and Allen et al. (2007)

change in ψ, or a constant ψ with an opposite direction change in the threshold distribution, because germination kinetics depend solely on the difference $\psi - \psi_b(g)$. Thus, a negative shift in the $\psi_b(g)$ distribution results in an identical effect on germination as an equivalent increase in ψ. Dormancy, the inability to germinate in

water, is equivalent functionally to a seed having a ψ_b threshold greater than 0 MPa, as indicated by the blue shaded fraction of the distribution in Fig. 7.5d.

Examples of both dry after-ripening and of moist chilling (stratification) affecting $\psi_b(g)$ threshold distributions have been reported. Thus, it may be a general phenomenon that the potential for germination (or alternatively, the depth of dormancy) is determined physiologically by shifts in the $\psi_b(g)$ distributions to higher or lower values, depending upon the environmental signals received by the seeds. As discussed previously (Sect. 6.6), hormones, particularly ABA and GA, are likely to be involved in regulating these transitions. It is consistent, therefore, that these hormones shift $\psi_b(g)$ distributions to more negative values when germination is promoted (i.e., in the presence of GA or absence of ABA) and to more positive values when germination is inhibited (in the presence of ABA or absence of GA). In fact, the sensitivity of seeds to hormones, oxygen, light and other factors can also be quantified by population-based threshold models based upon the hydrotime equation (7.1).

7.2.1.3 Ecological Applications of the Hydrotime Model

If the hydrotime model provides an accurate description of germination responses to dormancy-inducing and dormancy-breaking factors, what are the implications for seed ecology? In drier environments, seasonal or erratic rainfall is the primary determinant of seedling survival, and seeds from these environments often require dry after-ripening and are sensitive to inhibition of germination by high temperatures. These responses are illustrated by the germination and after-ripening of cheatgrass seeds in the dry Great Basin region of the western United States. Seeds are initially shed in early summer, and require several months of after-ripening to alleviate dormancy. Thus, at the time of shedding, their mean ψ_b thresholds are near 0 MPa, and are higher when set to germinate at warm temperatures (20/30°C) compared to cooler temperatures (10/20°C), indicating also the occurrence of thermoinhibition (Fig. 7.6). Values of $\psi_b(50) > 0$ MPa indicate dormant seeds. Over the summer months, the values of $\psi_b(50)$ for these populations after-ripening in soil under field conditions decline, indicating that the seeds are increasingly likely to germinate rapidly when water becomes available. The rate at which this decrease in $\psi_b(g)$ occurs is dependent upon the seed ψ. At high ψ (e.g., imbibed seeds), after-ripening does not occur and seeds either deteriorate or remain dormant. Between about −40 and −400 MPa, after-ripening proceeds, but at a decreasing rate as the ψ declines. At very low ψ (below −400 MPa), after-ripening does not occur. Thus, water availability (and temperature) influence the rate of after-ripening, and the consequence of after-ripening is a decrease in $\psi_b(g)$ such that germination rates and percentages will be higher the later that rainfall occurs in the fall. It has been noted that from an ecological perspective, slow germination is as effective as dormancy at unfavorable times in a fluctuating environment, because seeds are generally capable of tolerating dehydration if radicle emergence has not occurred. Maintaining a wide distribution of $\psi_b(g)$ values within the seed population assures that while some seeds will capi-

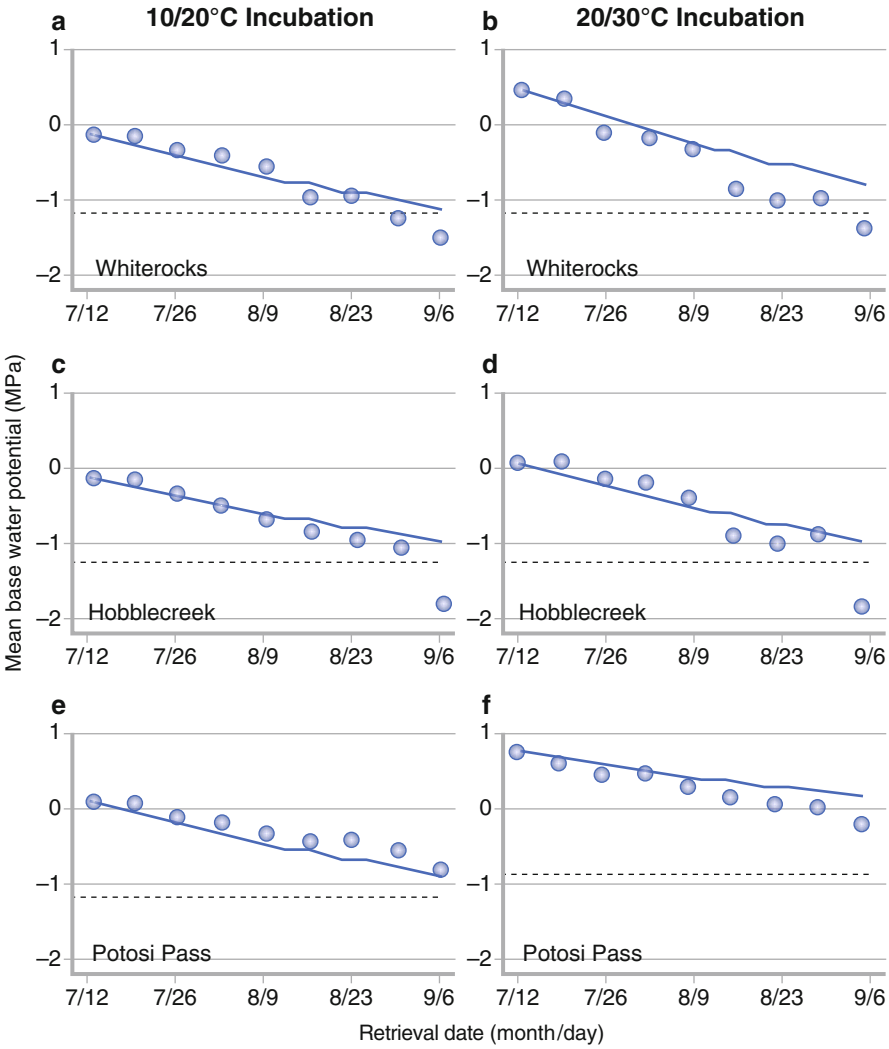

Fig. 7.6 Predicted and observed changes in $\psi_b(50)$ during field after-ripening of seeds of three populations of *Bromus tectorum* (Whiterocks, Hobblecreek and Potosi Pass) when measured at two incubation temperatures (10/20 or 20/30°C). Symbols represent values measured in the laboratory for seeds retrieved from the field, solid lines show values predicted from a simulation model of after-ripening rates for the environmental conditions (primarily affected by temperature), and the dotted horizontal lines represent the $\psi_b(50)$ values of seeds for each population when fully after-ripened and tested at the indicated temperature. Note that $\psi_b(50)$ values were generally higher when tested at higher temperatures, indicating that thermoinhibition of germination influences ψ_b distributions (see also Fig. 7.11). From Bauer et al. (1998). With permission of Oxford Univ. Press

talize rapidly on favorable conditions, others will be more conservative, committing to radicle emergence only after a much longer period of hydration or not at all. This "bet-hedging" strategy may be critical for survival of species in relatively unpredictable environments. In other cases, avoiding low temperatures and the danger of frost may be more important, requiring seeds to delay germination until after experiencing a cold period. This has also been associated with shifts in $\psi_b(g)$ distributions to more negative values after moist chilling.

There is an ecological rationality to having various environmental signals influence germination capacity via effects on $\psi_b(g)$. As seasonal and environmental requirements are met that indicate to the seed that an opportune time to germinate is approaching (e.g., after-ripening, stratification, light, nutrients, etc.), a negative shift in $\psi_b(g)$ will result in an increase in the fraction of seeds capable of germinating and in the overall speed of germination. However, since this increased capability is based upon the $\psi_b(g)$ threshold distributions, the seed population will still remain highly sensitive to the current local water availability. Even if the $\psi_b(g)$ distribution shifts to quite low values in a physiological sense (−1 to −2 MPa), a relatively small decline in soil ψ can still have a dramatic effect in delaying or preventing germination (c.f., Fig. 7.4). Thus, seasonal or environmental effects on the capacity for germination may act through physiological shifts in the $\psi_b(g)$ distribution, with the variation in $\psi_b(g)$ among individual seeds providing differential sensitivity to local conditions to ensure that there are both opportunistic and conservative individuals within the population. By responding to environmental factors via modification of their sensitivity to ψ, seed populations can achieve both long-term integration of their environmental history and regulation of their progress toward germination based upon current water availability.

7.2.2 Temperature

After water, temperature is the most important environmental determinant of seed germination. Temperature acts to regulate germination in the field in three ways: (a) by determining the capacity and rate of germination of nondormant seeds, (b) by removing primary and/or secondary dormancy, and (c) by inducing secondary dormancy. The latter two effects of temperature on dormancy release and induction largely determine the fraction of seeds that are potentially germinable in a given location at a specific time. The role of temperature in the induction and release of dormancy is discussed in Sects. 6.5, 6.6, and thus, attention here is focused primarily on the effects of temperature on germination rates and percentages of nondormant seeds.

7.2.2.1 Cardinal Temperatures for Seed Germination

It has been recognized since the mid-1800s that three "cardinal" temperatures (minimum, optimum and maximum) describe the range of temperatures (T) over which seeds of a particular species can germinate. The cardinal temperatures for

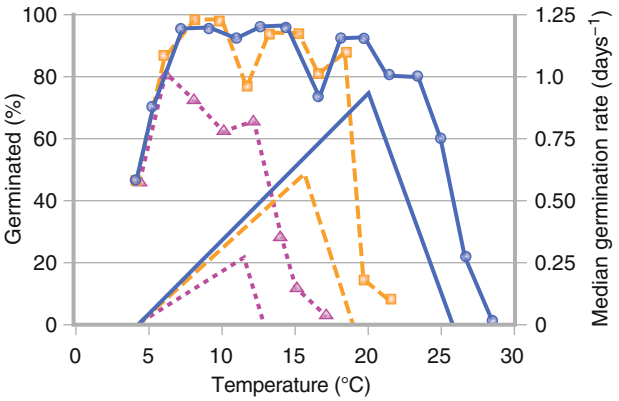

Fig. 7.7 Final germination percentages (*left y*-axis) of *Phleum arenarium* seeds in response to after-ripening at 15°C and 15% RH for 1 (*triangles*), 6 (squares) or 13 months (*circles*), illustrating the widening of the temperature window for germination as dormancy is alleviated. Superimposed are predicted median germination rates (*right y*-axis), which would increase linearly with temperature to a maximum, then decrease at inhibitory temperatures. Final germination percentage data from Probert (1992)

germination are generally related to the environmental range of adaptation of a given species and serve to match germination timing to favorable conditions for subsequent seedling growth and development. The minimum or base temperature (T_b) is the lowest T at which germination can occur, the optimum temperature (T_o) is the T at which germination is most rapid, and the maximum or ceiling temperature (T_c) is the highest T at which the seeds can germinate. The temperature range between T_b and T_c can vary with the dormancy status of the seeds, generally being more narrow in fresh or dormant seeds and widening as dormancy is lost. This is illustrated by *Phelum arenarium* seeds: fresh seeds germinated well only between about 5 and 13°C, but the upper temperature limit increased to 25°C following 13 months of dry after-ripening while the T_b remained constant (Fig. 7.7). Similar data are available illustrating reductions in the low temperature limit for germination following dormancy breaking (e.g., moist chilling), as in *Polygonum aviculare*. Since these relative temperature limits can vary with dormancy status, some consider that T_b and T_c should be defined as the minimum and maximum temperatures for germination of nondormant seeds of a species, with germination capacity approaching these minimum and maximum temperature limits as dormancy is alleviated.

7.2.2.2 Thermal Time Models

Germination rates (i.e., the inverse of times to germination for specific germination percentages) are also very sensitive to temperature, generally increasing with temperature to an optimum and then decreasing sharply at temperatures above the

optimum. Although total germination percentages tend to show a broad maximal range, germination rates more narrowly identify the optimum temperature for germination (Fig. 7.7). Germination rates of more dormant seed populations may also be slower compared to less dormant seeds at the same temperature. As the temperature window widens, germination rates will be similar at lower temperatures but continue to increase at higher temperatures as the T_o increases. Germination rates and percentages fall sharply as temperature increases above T_o.

Mathematical models have been developed to describe germination patterns in response to T. For suboptimal temperatures (from T_b to T_o), germination timing can be described on the basis of thermal time or heat units (i.e., degree-days). The basis of thermal time for suboptimal temperatures is that the T in excess of T_b multiplied by the time to a given germination percentage g (or t_g), is a constant for that percentage (the thermal time constant, $\theta_T(g)$):

$$\theta_T(g) = (T - T_b)t_g \tag{7.3}$$

or

$$GR_g = 1/t_g = (T - T_b)/\theta_T(g) \tag{7.4}$$

Since $\theta_T(g)$ is a constant for a given germination percentage, the closer T is to T_b, the correspondingly longer the time to germination, or the smaller the germination rate. As shown in (7.4), this model predicts that GR_g will increase linearly with temperature above T_b, as illustrated in Fig. 7.7. Although not always the case, T_b is often the same or similar for all seeds in the population, such that GR_g plots versus temperature all intersect the x-axis at the same point (Fig. 7.8). However, it is evident that the rate of germination is faster for lower percentages than for higher percentages, resulting in different slopes of the GR_g lines above T_b (Fig. 7.8). The inverse of the slopes equals the thermal time constants $\theta_T(g)$ for each fraction of the population (Fig. 7.8). As was noted previously for water potential thresholds (Sect. 7.2.1.1), the values of $\theta_T(g)$ are often normally distributed among seeds in the population, so they can be represented by a bell-shaped curve characterized by a mean ($\theta_T(50)$) and standard deviation ($\sigma_{\theta T}$) (Fig. 7.8 inset a). Thus, while all seeds in a population may have the same T_b value, they exhibit a distribution of times to germination ($\theta_T(g)$ values) that result in the familiar sigmoid germination time courses (Fig. 7.9a). When these time courses are plotted on a thermal (degree-hours) time scale (i.e., $[T - T_b]\ t_g$), they all fall on the same sigmoid curve (Fig. 7.9b). For most nondormant seeds, once the T_b, $\theta_T(50)$ and $\sigma_{\theta T}$ values have been determined, germination times for any fraction of the population at suboptimal temperatures can be estimated. T_b and $\theta_T(50)$ values characteristic of crop species are often used in conjunction with soil temperature data to estimate the days to seedling emergence after planting in the field. In many locations, weather data are available online already converted into degree-days units for various T_b values, making it easy to calculate accumulated thermal time since planting. Similarly, germination models

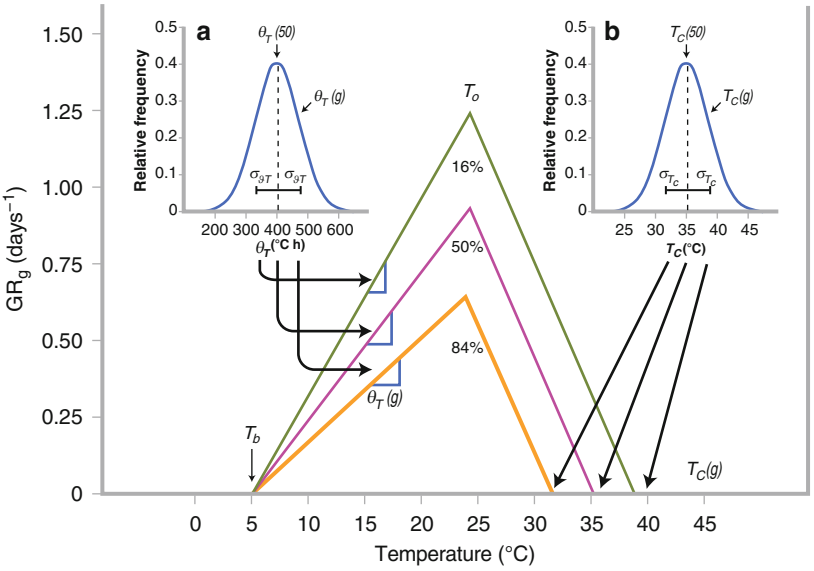

Fig. 7.8 Relationships between germination rates and temperature. At low temperatures, germination rates ($GR_g = 1/t_g$) for different percentages (g) of the seed population increase linearly with temperature above a common base temperature (T_b). The slopes of the lines are equal to the inverses of the thermal times to germination ($1/\theta_T(g)$), which vary among individual seeds in a normal distribution (*inset a*). The maximum GR_g occurs at the optimum temperature (T_o), and above this temperature GR_g decreases linearly. The ceiling temperatures for germination ($T_c(g)$) vary in a normal distribution among seeds within the population (*inset b*). Germination rates are shown for 16, 50 and 84%, which represent the median and ±1 standard deviation of the respective distributions. Modified from Bradford (2002)

based on thermal time are used for predicting weed seedling emergence in both cropping systems and non-crop landscapes.

Similar models have been developed to describe germination rates at supraoptimal temperatures (from T_o to T_c). In many cases, GR_g declines linearly with increasing T between T_o and T_c (Fig. 7.8). However, in contrast to a common T_b for all seeds in the population, it is generally observed that different fractions of the seed population have different T_c values. The following model accounts for this variation in T_c values:

$$\theta_2 = (T_c(g) - T)t_g \tag{7.5}$$

or

$$GR_g = 1/t_g = (T_c(g) - T)/\theta_2 \tag{7.6}$$

where θ_2 is a thermal time constant at supraoptimal T and $T_c(g)$ indicates that T_c values vary among fractions (g) in the seed population (Fig. 7.8 inset b). At supraoptimal temperatures, the differences in GR_g among seed fractions are a consequence of variation among seeds in their ceiling temperatures ($T_c(g)$), and the total thermal time is constant in the supraoptimal range of T for all seeds in the population.

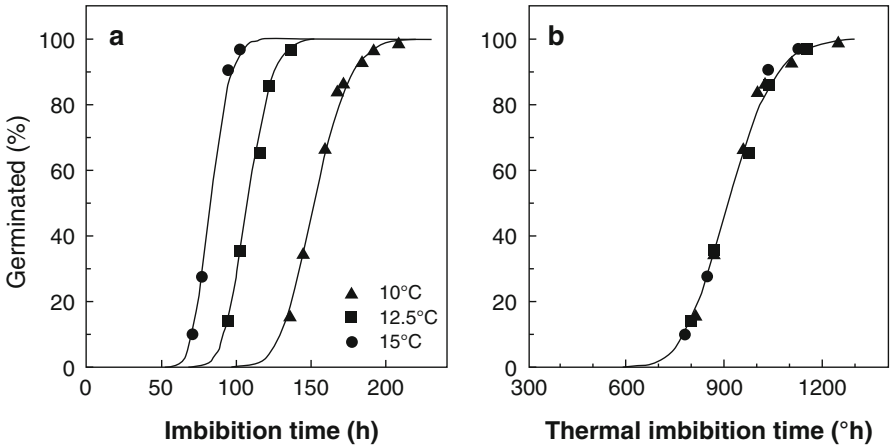

Fig. 7.9 Normalization of germination time courses across temperatures by thermal time. (**a**) Germination time courses of potato seeds at 10 (*triangles*), 12.5 (*squares*) and 15°C (*circles*). Symbols are data points, and curves are predicted from the thermal time model (7.3). (**b**) The same data as in *panel a* plotted on a thermal time scale, or $(T-T_b)\,t$ using a base temperature of 4°C. Thermal time or heat units accumulation (degree-hours) completely accounts for the differences in germination rates at these suboptimal temperatures. Original data of V. Alvarado and K.J. Bradford

7.2.2.3 Temperature and Water Interactions: Hydrothermal Time Models

As both T and ψ are critical environmental regulators of seed germination, it is convenient to combine their effects into a single "hydrothermal time" model. This can be done as follows for the suboptimal temperature range:

$$\theta_{HT} = (\psi - \psi_b(g))(T - T_b)t_g \tag{7.7}$$

Simply by multiplying the time to germination by $(T-T_b)$ the hydrotime model (equation 7.1) can be converted to a thermal time basis, with a new hydrothermal time constant (θ_{HT}). The conversion to thermal time largely accounts for the effect of suboptimal temperatures, while a normalization equation can also account for the effects of reduced ψ on germination. This equation converts germination time courses at any ψ into equivalent time courses in water (ψ=0 MPa) by normalizing for the delay in germination caused by reduced ψ:

$$t_g(0) = [1 - (\psi / \psi_b(g))]t_g(\psi) \tag{7.8}$$

where $t_g(0)$ is the time to germination of fraction g in water and $t_g(\psi)$ is the time to germination of fraction g at a lower ψ. The combination of this normalization function for ψ and thermal time can describe germination time courses at combinations of suboptimal temperatures and reduced ψ (Fig. 7.10). It is important to note that the normalization of time courses at different ψ to their equivalent in water is not a "hydrotime" scale in the same way that developmental events at different temperatures

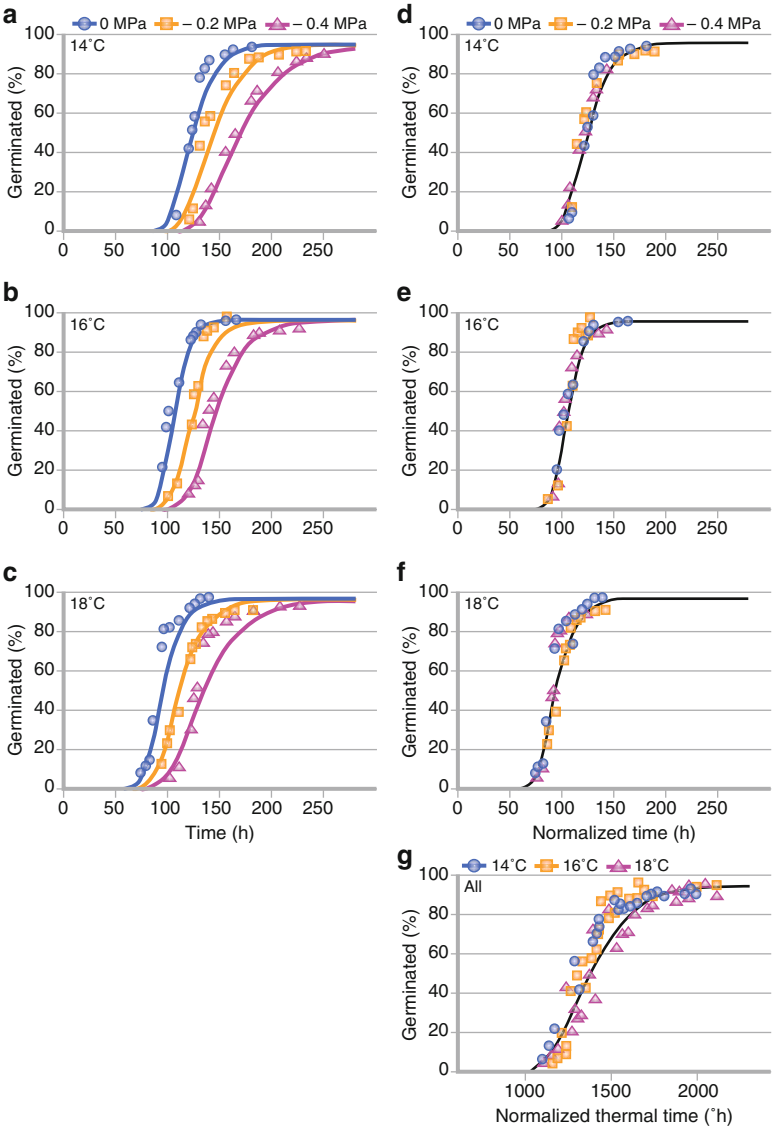

Fig. 7.10 Normalization of germination time courses across a range of suboptimal temperatures and reduced water potentials. **a**, **b** and **c** show germination time courses of potato seeds at 14, 16, and 18°C and at 0 (*circles*), −0.2 (*squares*) and −0.4 MPa (*triangles*) at each temperature. The curves are fit using the hydrotime model at each temperature (7.1). **d**, **e**, and **f** show the same data normalized to account for the delaying effect of reduced ψ according to (7.8). This function normalizes the time courses to match the germination rates in water (0 MPa). When these normalized curves are plotted on a thermal time scale (**g**), all of the germination time courses across both temperatures and water potentials fall on a common curve. Based on Alvarado and Bradford (2002)

can be plotted on a single thermal time scale (e.g., Fig. 7.9b). This is because the hydrotime to germination is the same for all seeds in the population; it is their ψ_b thresholds that vary among individual seeds.

As was discussed for changes in seed dormancy (Fig. 7.5), shifts in $\psi_b(g)$ distributions also contribute to temperature responses of seed germination. Recall that different fractions of seed populations exhibited different maximum temperatures for germination, or $T_c(g)$ values (Fig. 7.8). This can now be understood to be due to a shift of $\psi_b(g)$ to more positive values when T exceeds T_o. Different fractions of the seed population have different ψ_b values, so as the entire distribution shifts upward, those with the highest ψ_b values will reach 0 MPa, or be unable to germinate in water, at a lower temperature than seeds with more negative ψ_b values. For potato seeds, $\psi_b(g)$ values increase sharply at temperatures above T_o, intersecting the 0 MPa axis at the point where $GR(g)$ values also intersect the x-axis for the same fraction of the population (Fig. 7.11). Thus, the effect of temperature on $\psi_b(g)$ distributions appears to underlie the decrease in germination rates and inhibition of germination that occurs between T_o and T_c.

7.2.3 *Light*

Seeds may remain in the soil seed bank for many years, apparently unaltered, because germination of buried seeds is suppressed. If the soil is cultivated or natural disturbance takes place, as in a river bank, many of the seeds may germinate and a flush of seedlings results. This only occurs if seeds in the seed bank are nondormant, i.e., if they are sensitized by the previous seasonal conditions (Sect. 7.3). One investigation reported that weeds such as *Sinapis arvensis, Polygonum aviculare, Veronica persicaria,* and others increase from about 35 to 780 seedlings per square meter after the soil is turned over. Another study compared the occurrence of seedling flushes in two adjacent plots within a cultivated oats field. One plot was harrowed, as usual, during the daytime, whereas the other plot was cultivated in the same way but during the night. The difference in weed emergence was dramatic, with almost no emergence in the dark-cultivated plot and approximately 80% coverage by some 30 different arable weeds in the light-cultivated plot (Fig. 7.12). Light is primarily responsible for this effect. As little as 1 millisecond of exposure to full sunlight can cause many seeds to germinate and produce seedlings. This principle may be utilized to reduce the use of herbicides in weed management programs.

Since light controls dormancy and germination of seed banks, how effective is the soil as a light filter and how deep must seeds be buried to escape from its effects? Less than 2% of the light passes through 2 mm of sand, and the light that is transmitted consists only of wavelengths longer than about 700 nm (Fig. 7.13). A wide part of the spectrum can pass through clay loams, but if the soil particle size is small (when they will be closely packed), a layer 1.1 mm thick is virtually opaque. Inhibition of germination by other soils may require greater depths, however. About 8 mm of loam are needed to completely suppress germination of *Plantago major*, whereas light-promoted

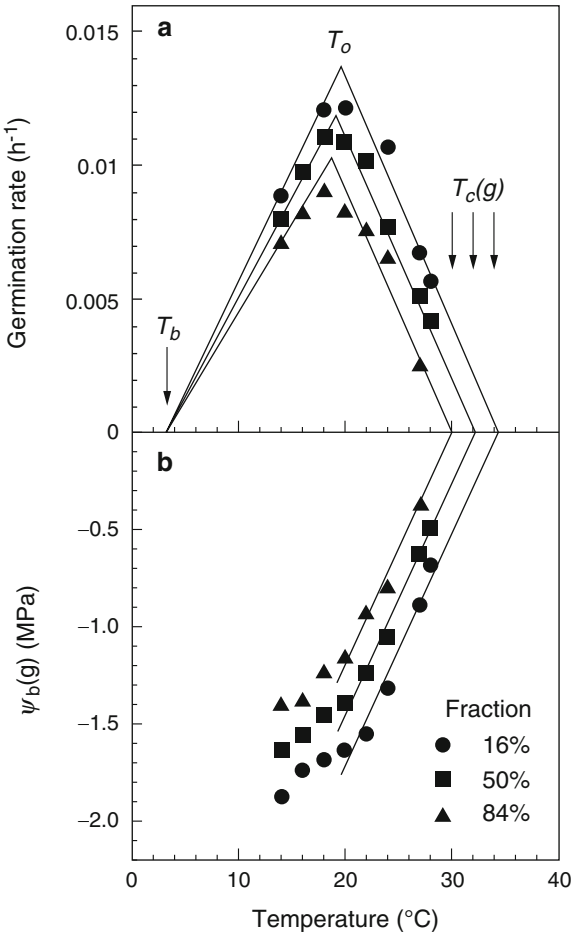

Fig. 7.11 The cardinal temperatures for germination of potato seeds. (**a**) Germination rates at different temperatures define the minimum or base temperature (T_b), optimal temperature (T_o), and maximum or ceiling temperatures (T_c). For this seed lot, T_b is 3.2°C, T_o is 19.3°C, and T_c varies with the seed fraction, being 34, 32, and 30°C for the 16th, 50th, and 84th percentiles, respectively. The symbols are the experimental data and the lines are germination rates determined by fitting the hydrotime model (equation 7.1) at sub- and supraoptimal T. (**b**) $\psi_b(g)$ increases linearly as T increases in the supraoptimal range. The $\psi_b(g)$ values calculated from the hydrotime model are plotted (*symbols*) along with the linear increases (*lines*) predicted by the model. The projected lines for different seed fractions (16, 50, and 84%) intercept the $\psi_b(g)=0$ MPa axis (where germination is prevented even in water) at the T_c values for these fractions. From Alvarado and Bradford (2002). Courtesy of Wiley

germination of *Digitalis purpurea* still occurs under 10 mm of sand, demonstrating differing sensitivities to light (Fig. 7.14). These examples also make clear that soil disturbance is of high ecological relevance, for without it the effective soil seed bank would be confined to the top soil layer of less than 1 cm.

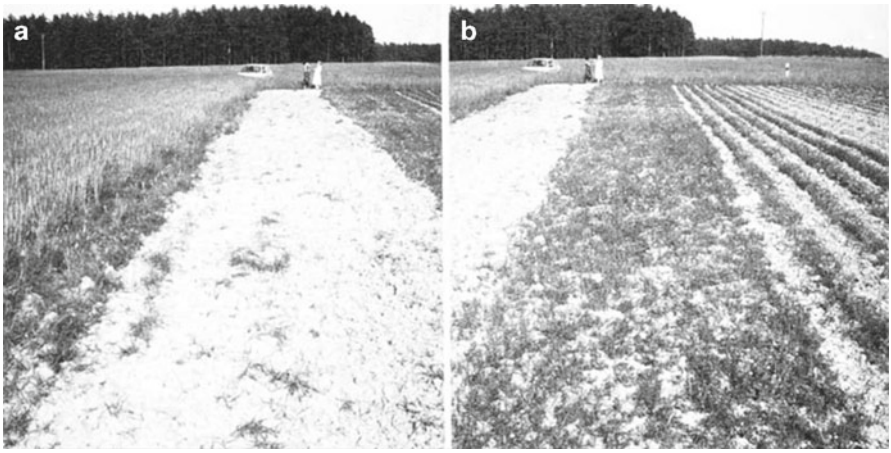

Fig. 7.12 Adjacent plots of about 55×3 m within an oat field in Germany. (**a**) All tillage was accomplished in the time span from 1 h after sunset until midnight. It was plowed in September, chopped in March and harrowed in April. The total coverage by weeds is about 2%. (**b**) All tillage was performed at noon, on the same days. The total area covered by weeds is about 80%. From Nezadal and Hartmann (1990)

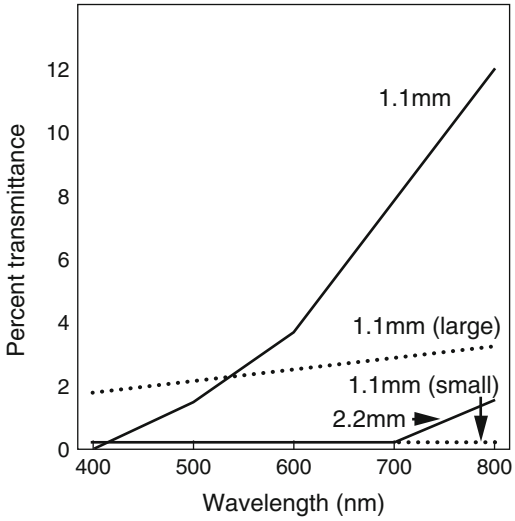

Fig. 7.13 Transmission of light through soils. Two soils were used, sand (——) and a clay loam (·····), at thicknesses indicated on the curves and, in the case of clay, at large (approximately 0.9 mm) and small (approximately 0.45 mm) particle size. Adapted from Woolley and Stoller (1978)

The quality of transmitted light is as important as the quantity. Since the longer wavelengths of light penetrate soil more easily, a buried seed experiences a relatively high proportion of far-red light (i.e., >700 nm), which affects the phytochrome photoequilibrium (ϕ) (Sect. 6.6.5.2). Light passing through 1 mm of dry, sandy soil results in a photoequilibrium of about 0.45, which should be sufficient to break

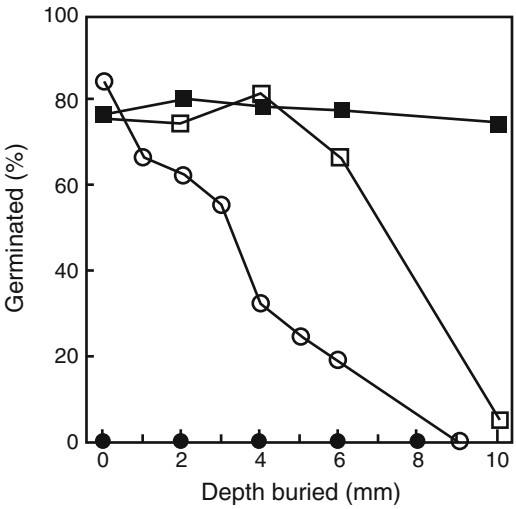

Fig. 7.14 Effect of burial on germination. *Plantago major* seeds were buried at different depths in wet loam held in the light (○) or dark (●). Seeds of *Digitalis purpurea* (■) and *Cecropia obtusifolia* (□) were buried at different depths in wet sand exposed to light. Germination of the last two species in darkness was almost zero. Adapted from Frankland and Poo (1980) and Bliss and Smith (1985)

dormancy in a high percentage of light-requiring seeds. That it does not necessarily do so may be because the very low fluence rates in the soil result in very low rates of Pfr formation. The germination of light-requiring seeds of some species is therefore restricted to the uppermost layers of soil where the light stimulus for dormancy breakage can operate. This is extremely important for small seeds with limited food reserves, because if germination is completed at too great a depth the seedling's reserves may be exhausted before it is able to reach daylight and begin to photosynthesize. Most species of light-requiring seeds are, in fact, small (<1 mg seed weight). This also implies that soil disturbance may lead to seedling death when the light-induced seed is reburied too deeply after the disturbance event. In addition, light requirements of seeds are modified strongly by other environmental factors, such as temperature and nitrate, which clearly will affect seed behavior in the field.

7.2.3.1 Phytochrome Responses

The role and mechanism of phytochrome in the breaking of dormancy and induction of germination were discussed in Chap. 6. In this section, phytochrome responses are viewed in an ecological context.

Light-induced germination often displays a biphasic response to the amount of photons or "fluence" of red (R) light (Fig. 7.15). The first phase is called the very-low fluence response (VLFR) and is present in seeds with extreme sensitivity to light. The VLFR is mediated by phytochrome A and is saturated by Pfr/Ptot ratios lower than 0.1%. This value of ϕ is also established by a pulse of far-red light (FR) because the absorption spectra of the active and inactive forms of phytochrome

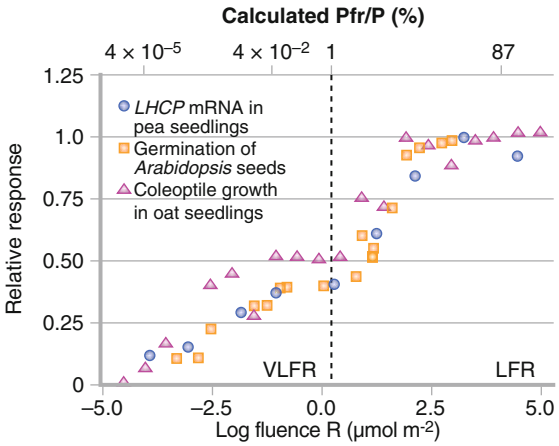

Fig. 7.15 VLFR and LFR influences on different physiological changes. Responses of seed germination in *Arabidopsis thaliana*, coleoptile growth in etiolated oat seedlings, and LHCP (light harvesting chlorophyll a/b-binding protein) mRNA expression in etiolated peas to the fluence of a R pulse and the proportion of Pfr established by these pulses. The commonality of the effects of VLFR (below 0.1% Pfr/P) and LFR (above 1% Pfr/P) are evident. From Casal et al. (1998). With permission of Oxford Univ. Press

overlap slightly (Sect. 6.6.5.2). Thus, these seeds do not show the classic R–FR reversibility. In the field, the VLFR may occur when the seeds have remained in the soil for a prolonged period of time. The second phase or low-fluence response (LFR) is saturated by moderate to high Pfr/Ptot ratios induced by R light. The LFR can be reversed when R is followed by a FR treatment. The main photoreceptor involved in LFR responses is phytochrome B. A third response to light is inhibitory to germination and is caused by the so-called high-irradiance response (HIR). The HIR can be induced by a prolonged irradiation with FR and may antagonize both the VLFR and LFR.

What is the ecological relevance of these different responses? The VLFR is thought to be involved in the promotion of germination by brief exposures to light during soil disturbances, as described above. The VLFR will also be the inducer of germination of seeds in the 1-cm top layer of the soil where very limited light penetrates. The LFR distinguishes itself from the VLFR by its R/FR reversibility. This has been established mainly under laboratory conditions and surprisingly little is known about the ecological relevance of the LFR.

Germination in many species is inhibited when seeds are on the soil surface. Often, the relative dryness of the soil accounts for this. Seeds of a large number of species, however, are affected by high fluence rates of light on the soil surface, which inhibit germination through the HIR. It has been argued that such sensitivity is a mechanism for discouraging germination under high solar radiation when the seedling would be subjected to harsh, drying conditions.

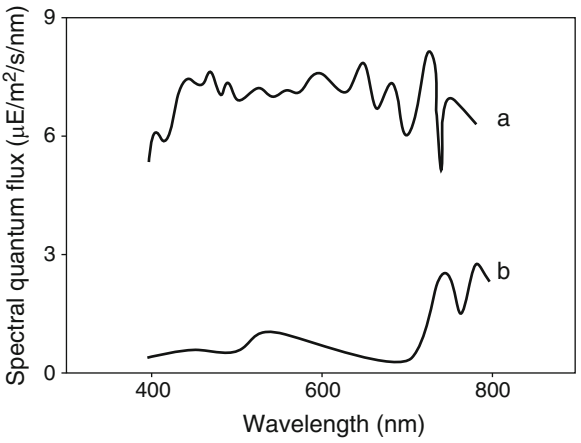

Fig. 7.16 Spectral energy distribution of sunlight and vegetational shade light. (a) Direct sunlight at 11:00 h., and (b) shade light (under sugar beet plants). The ratio of R to FR light (660/730 nm) in (a) is 1.18 and in (b) is 0.12. After Holmes and McCartney (1975)

Chloroplasts absorb light most strongly at approximately 675 nm and allow wavelengths >720 nm to be transmitted completely. Because of this, sunlight passing through green leaves has a very low R/FR ratio (Fig. 7.16). The phytochrome photoequilibrium (ϕ) established by such light can be as low as 0.15, depending on the thickness of the canopy. Most light-requiring seeds will not germinate under such conditions. Indeed, if they are exposed to this light for many hours over several days they will probably be induced into secondary dormancy. These seeds, therefore, become dormant as a result of irradiation with FR-rich canopy light and will germinate later only when a dormancy-releasing factor, such as chilling or light, has been experienced. Seeds of *Bidens pilosa*, for example, when forced into dormancy by canopy light, become light-requiring and subsequently germinate only when exposed to light of suitable quality to establish a relatively high photoequilibrium value of phytochrome; direct sunlight would, of course, suffice. This mechanism may account, for example, for the paucity of seedlings on forest floors and the flush that follows the appearance of a gap in the leaf canopy, brought about when individual trees die and fall or when tree clearance occurs. Thus, the seed bank in forest soils may be rich but germination is held in check, to a large extent by the canopy filtered FR light environment. In the field, vegetational shade is provided by grasses and herbs, of course, as well as by trees. For example, plants of *Arenaria* spp., *Veronica* spp., and *Cerastium* spp. establish themselves on vegetation-free ant mounds but not in the surrounding pasture. Seeds of these species are inhibited by light filtered through green leaves, but germinate in sites where the seedlings will face less competition with other plants for light for photosynthesis. Some species that are able to colonize shaded sites, e.g., *Centaurium erythrea*, are less sensitive to FR canopy light.

As the spectral energy distribution of canopy light is determined by the thickness of the canopy through which the light passes, the germination response of seeds under the canopy will vary according to the density of leaf cover.

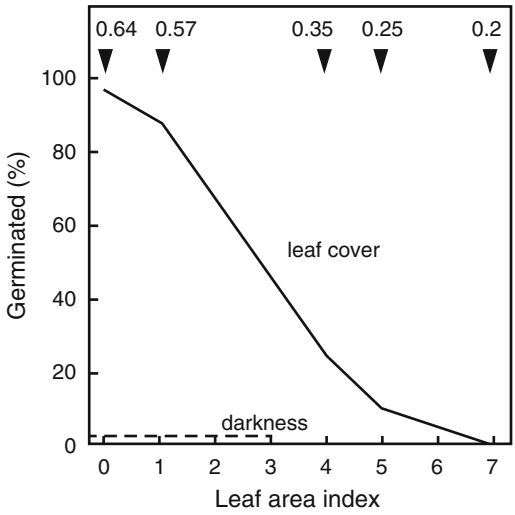

Fig. 7.17 Germination of light-requiring seeds under leaf cover. Seeds of *Plantago major* were sown beneath plants of *Sinapis alba* (*white mustard*) at different densities, as indicated by the leaf area index (i.e., unit leaf area per unit land area). Pfr/Ptot (ϕ) values (at soil level) at different densities are indicated at the top of the graph. (----) Germination in darkness. From data in Frankland and Poo (1980)

This has been simulated under experimental conditions using seeds of *Plantago major*. When placed under increasing leaf cover, provided by *Sinapis alba* plants, germination of these light-requiring seeds is increasingly inhibited as the cover becomes more dense (measured as the leaf area index) and the ϕ beneath the leaves decreases (Fig. 7.17). Variations in the density of a leaf canopy occur in the field as buds break and leaves expand and later senesce and fall. Thus, light-sensitive seeds among vegetation are exposed to changing light environments throughout the growing season, with concomitant effects on their dormancy breakage and germination. However, other environmental factors such as temperature are also influential, so that seed germination is not always predictable from the shade conditions. For example, there is a clear interaction between the different phytochromes and temperature (Sect. 6.6.5). This interaction may be decisive for the form of phytochrome (phyA, phyB, phyE) that will be engaged and, hence, for the ensuing response type. In addition, seasonal conditions during seed maturation may also influence phytochrome-mediated germination.

7.2.4 Nitrate

Nitrate ions have long been known to stimulate germination of seeds of many species, both monocots and dicots, as well as fern spores. Nitrate is part of the global nitrogen cycle and it is present in most soils, often within the range of concentrations that are effective in laboratory germination tests. Nitrate is therefore the foremost inorganic soil component that influences germination.

The ecological significance of nitrate must be considered in conjunction with environmental factors such as temperature, light, and the seed's sensitivity to nitrate

and other chemical soil constituents. Indeed, interactions between such factors and nitrate have been described for a large number of species. To add to the complexity, soil nitrate content, as well as the interacting factors and responsiveness of seeds to them, are all dynamic, displaying fluctuations over shorter or longer periods. In general, germination of most seeds is stimulated within a range of 0–0.05 mol L^{-1} nitrate. The nitrate concentration of the soil fluctuates within this range and therefore might play an ecological role in regulating germination of the soil seed bank.

In many weed species, light and nitrate interact to regulate germination responses. This interaction has been studied in more detail in seeds of *Avena fatua* and *Sisymbrium officinale*. In both species the efficacy of nitrate in stimulating germination depends on the amount of Pfr. In *S. officinale* the dependency on light appears to be absolute. In *Sisymbrium officinale* and *Arabidopsis thaliana*, the effects of Pfr and nitrate on seed germination are reciprocal, i.e., the light requirement of seeds in a soil with low nitrate is higher than that of seeds in nitrate-rich soils. Disturbance of the soil may result in a flush of germination when light is the limiting factor, but soil disturbance may also result in considerable release of nitrate ions. This phenomenon is probably a significant factor in the promotion of weed seed germination, such as *A. fatua*, when summer fallowing is a common practice.

The significance of soil nitrate for seed ecology seems obvious when we assume that a plant that will eventually grow from a seed requires nitrogen for optimal development. However, evidence for a relationship between nitrate concentrations that promote seed germination and those required by the growing plant is largely lacking. A more feasible explanation for the role of nitrate is the ability of seeds to sense changes in the amounts present in their immediate environment. Similar to the shading principle for light, established plants may lower the nitrate content of the soil around their root systems. Nitrate is consumed and nitrification may be inhibited. Thus, the seeds in the immediate environment are depleted of nitrate and germination probability will be reduced. Therefore, the seed's ability to sense both nitrate and FR light contribute to the detection of gaps in the vegetation and, hence, avoid potentially suicidal germination and seedling emergence among competitors, including the mother plant.

7.2.5 Oxygen and Other Gases

The gaseous phase of the soil occupies those pores that are not already filled with water. In addition gases may be dissolved in the soil moisture. Movement of gases through soil is primarily by molecular diffusion but when the soil is waterlogged, gas diffusion is entirely in solution, resulting in a drastic increase in diffusion resistance of several orders of magnitude. In heavy soils and especially in waterlogged soils the oxygen content of the gaseous phase may drop considerably below that of air. The gas phase is also affected by the presence of vegetation. Roots of plants will actively take up oxygen and produce carbon dioxide. In soils with a high organic

content and an active microflora, the oxygen–carbon dioxide balance may shift in a similar way. Although the proportion of oxygen in soil air rarely drops below 19% and carbon dioxide rarely exceeds 1%, extremes may occur at microsites such as those adjacent to plant roots or decaying organic matter, and in soils of flooded areas. In addition to oxygen, carbon dioxide, and nitrogen, soils may contain several other gases and volatile compounds, mostly related to anaerobic conditions and microbial activity. Soils may thus contain methane, hydrogen sulphide, hydrogen, nitrous oxide, and small amounts of carbon monoxide, ethylene, and ammonia.

(1) *Oxygen*. Germination and early seedling growth generally require oxygen at atmospheric levels. Oxygen diffusion can be strongly limited during the lag phase of germination (Sect. 4.4.2) because its diffusion rate is limited by its solubility in water. Moreover, oxygen is often utilized in seed coats and endosperms in non-respiratory reactions. Therefore oxygen concentrations in the embryonic axis may be rather low for some time and therefore seeds must be (temporarily) tolerant of anaerobic conditions. This is particularly true for seeds that germinate under water. Seeds of *Echinochloa crus-galli* germinate well under both anaerobic or aerobic conditions. This trait certainly contributes to its success as an aquatic weed in rice growing areas. The seeds of *Echinochloa* species are all tolerant to ethanol produced during anaerobic germination, which seems unrelated to dormancy breaking. In contrast, incubation under anaerobic conditions delays the induction of secondary dormancy in several species. Seeds of *Viola* species and *Veronica hederifolia* commence germination in 100% nitrogen or 2% oxygen but not in 8% oxygen. Oxygen is required, however, for the release of dormancy during chilling of *Ambrosia artemisiifolia* and during after-ripening of *Avena fatua* and other cereal grains. These examples show that the response to oxygen is highly variable, as is oxygen availability, which can vary due to soil characteristics, such as soil type, water content, and burial depth.
(2) *Carbon dioxide*. As for other gases, the concentration of carbon dioxide in the soil depends on depth, temperature, moisture, porosity, and biotic activity. Carbon dioxide increases with depth, ranging from 1 $dm^3\ m^{-3}$ at the top 10 cm of soil to 80 $dm^3\ m^{-3}$ at 50 cm. These concentrations may increase five- to tenfold during peaks of biological activity in the soil at warmer temperatures. As with oxygen, soil carbon dioxide concentrations are significantly influenced by moisture content, due to the restricted diffusion of gases. Respiratory activity of microorganisms, actively growing plant roots, as well as carbon dioxide evolving from decaying plant material increase with soil moisture content.

Soil carbon dioxide in the range of 20–50 $dm^3\ m^{-3}$ (2–5% by volume) may stimulate germination. This concentration is higher than what is usually found in the soil top layer. However, rainfall may cause an immediate rise in carbon dioxide, its concentration at a depth of 3 cm changing from 8 to 30 $dm^3\ m^{-3}$ (0.8–3%) within hours after rainfall. This rise in CO_2 concentration, rather than moisture content, light, ethylene, or nitrate causes the intermittent flushes of germination of *Echinochloa crus-galli* seeds. However, CO_2 concentrations in the soil are generally below those that stimulate germination. Therefore, it is not likely that the gas plays a significant role in the control of dormancy.

(3) *Ethylene*. Ethylene is a common soil constituent. The gas is produced by both aerobic and anaerobic microorganisms, as well as by plant roots. Ethylene concentrations of several parts per million have been recorded in soils, and vary markedly among soil microenvironments. Ethylene is known as one of the plant hormones (Sect. 2.3.1) that can have a strong influence on plant growth. Both promotive and inhibitory effects of this gas on seed germination have been reported. In addition, it may enhance the positive effect of light and nitrate on germination. In a study of the effect of ethylene on germination of 10 grass and 33 broadleaved weed species, in nine species this was promoted by ethylene in concentrations between 0 and 100 ppm, inhibited in two species; the other species were not affected. Interestingly, the nine species that responded positively to ethylene are now known to be responsive to nitrate as well. Interactions between ethylene and carbon dioxide have been reported also. Curiously, elevated amounts of carbon dioxide may enhance the effect of ethylene on germination, but high amounts generally have an antagonistic effect on its action.

An assessment of the ecological significance of soil ethylene in the germination of seeds in the field is difficult since the gas can both promote and inhibit germination. Perhaps the inhibitory properties of ethylene may be regarded as an adaptation to avoiding competition with neighboring plants. Ethylene concentrations are highest in the rhizosphere because microorganisms therein are capable of synthesizing ethylene. In addition, production of ethylene by microorganisms can be enhanced by compounds in root exudates. These signals from nearby roots via ethylene are apparently used by some parasitic weeds (e.g., *Striga*) to trigger germination. Consequently, injection of ethylene into field soils has been proposed as a method to induce germination of such weed seeds to allow them to be killed and reduce the soil seed bank prior to planting a susceptible crop. However, these seeds also detect specific chemical signals from roots (see next section) and may not respond fully to ethylene.

7.2.6 Other Chemicals

Soils contain a vast array of organic compounds, both volatile and nonvolatile, which are the products of decaying plant and animal remnants and the associated microorganisms. Living plants also produce a wide range of organics, usually in their root exudates. These compounds have the potential to inhibit or stimulate germination. Combustion of plant material by fire also results in the appearance of a number of compounds that may affect germination and seedling emergence.

(1) *Organic inhibitors.* Because the germination of light-independent seeds, which can occur in the dark, is often inhibited in the soil it has often been postulated that chemical inhibitors play a major role therein. These so-called allelopathic substances or allelochemicals form an important group of natural inhibitors. Allelopathy refers to harmful or beneficial effects of higher plants of one species (the donor) on the germination, growth, or development of plants of its own or another species (the recipient).

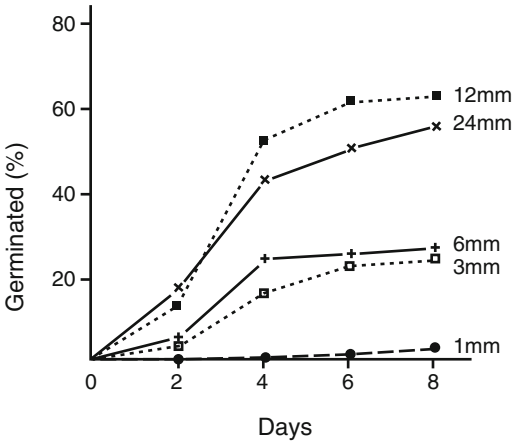

Fig. 7.18 Germination of *Parthenium hysterophorus* achenes placed at various distances apart. From Picman and Picman (1964). Courtesy of Elsevier

Allelopathic inhibition of seed germination may play a role in the regulation of plant succession. For example, pioneer weeds eliminate themselves over time through the production of toxins that inhibit germination of their own seeds (autotoxicity) and of accompanying weeds. Germination of *Aristida oligantha*, a grass that often follows weeds in succession, is not inhibited, however. Alfalfa plants also have an inhibitory effect on the germination of their own seeds. Inhibitors of germination have been detected in extracts from decaying material from, e.g., sorghum and sunflower. Experiments with soil samples have shown that the toxins also leach into the soil from living sunflower organs. However, the accumulated debris displayed greater toxicity than the leachate. Several allelochemicals have been identified. For instance, *cis*-dehydroxy-matricariaester (*cis*-DME) is the active compound in the underground organs of *Solidago altissima*, a weed that succeeds the pioneer *Ambrosia artemisiifolia* in old-field succession, and inhibits germination of its seeds. A soil block 10 cm in depth from the rhizosphere of *Solidago* has been determined to contain 5 ppm *cis*-DME, which is sufficient to inhibit *Ambrosia* seed germination. The inhibitor can persist in soil for several months without decomposition by microorganisms.

Allelochemicals leach from leaves, stems, and roots, and also from seeds. Those of *Parthenium hysterophorus* contain two major water-soluble sesquiterpene lactones: parthenin and coronopilin. Although the seeds (achenes) contain lower amounts than vegetative tissues, their concentrations are high enough to inhibit germination, which decreases with increasing seed sowing density (Fig. 7.18). Also, increasing the washing (leaching) period of seeds to remove the inhibitors increases subsequent germination, demonstrating that they have an autotoxic effect. The toxins are mainly located in the seed coat and may act as a rain gauge, allowing germination only when sufficient inhibitor has been washed out (chemical dormancy, Sect. 6.3.1.3). The germination inhibitors are also effective in the formation of inhibition zones, which deter competitors.

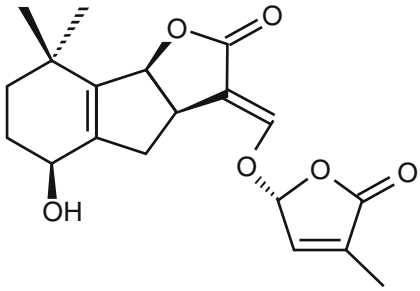

Fig. 7.19 The structure of the strigolactone (+)-Strigol, a germination stimulant of parasitic weed seeds

(2) *Organic promoters: parasitic weeds.* Parasitic weeds cause massive yield losses in agriculture. Broomrapes (*Orobanche* spp., Orobanchaceae) and witchweeds (*Striga* spp., Scrophulariaceae) are serious pests in many countries. *Orobanche* spp. are holoparasites that lack chlorophyll, and therefore obtain water, nutrients, and carbohydrates through the roots of their host. *Striga* spp. are hemiparasites, with reduced photosynthetic activity, and behave as holoparasites.

The first critical step in the life cycle of these parasites—germination of their seeds—is regulated by specific chemical signals exuded by the roots of their host plants, but even preceding this is the early and unambiguous recognition of the correct host. For *Striga* spp. several germination stimulants have been identified from host and non-host plants. Most of them are strigolactones, terpenoid lactones that are derived from carotenoids, including strigol (Fig. 7.19). The chemical communication between parasite and host is central to this recognition.

The physiology of the parasitic weed seed is complex. Newly shed seeds from such parasitic weeds as *Striga* and *Orobanche* spp. possess primary dormancy and require a period of moist conditions of several days to break dormancy and to become responsive to the chemical stimulants from the hosts, such as strigol and orobanchol. Contact with the host stimulant then induces germination. However, with prolonged conditioning, seeds may enter secondary dormancy and become less sensitive to the germination stimulant (Fig. 7.20). These changes in sensitivity suggest that this is a safety mechanism that restricts the period in which the seeds can respond to the germination stimulants produced by host plants. Indeed, there are several reports showing that a later crop-sowing date strongly reduces infection by parasitic weeds. This behavior resembles the "dormancy cycling" as described for nonparasitic weeds (Sect. 7.3.1).

Relatively little is known about the chemical stimulation of germination in root parasites. It is difficult to understand why some have a rather wide host range, while others exhibit an extremely narrow range. It is even more difficult to understand with our presently limited knowledge why false hosts also produce germination stimulants but are not infected. More definite information is needed on the chemical nature of other germination stimulants and their dose–response reactions.

(3) *Organic promoters*: *smoke.* Recurring fires are an integral part of several ecosystems and when such areas are protected from fire, their local ecology becomes severely disturbed. How does the occurrence of a fire stimulate the seeds of certain

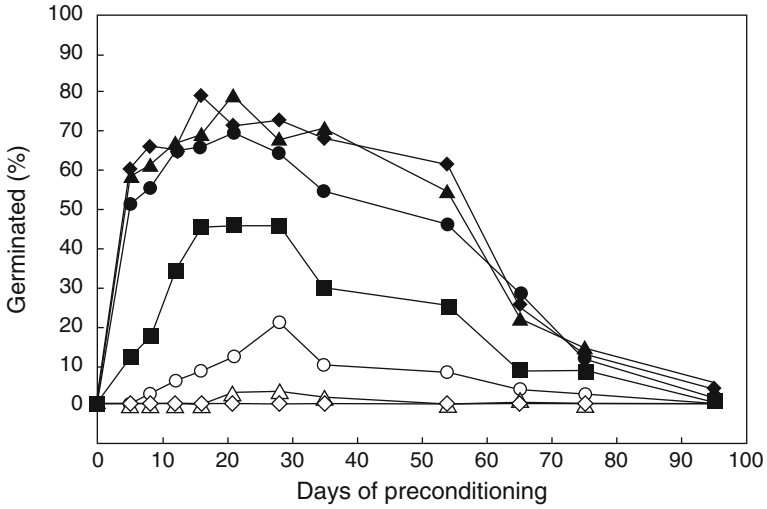

Fig. 7.20 Changes in germination of *Striga hermonthica* seeds in response to strigol with time after preconditioning. Seeds were moist-preconditioned at 30°C for the time indicated and then germinated at 30°C in the dark at a range of GR24 (a synthetic strigolactone) concentrations: 0 (◊), 0.00001 (□) 0.0001 (Δ), 0.001 (○), 0.01 (■), 0.1 (●), 1 (▲) and 10 mg L^{-1} (♦). From Matusova et al. (2004). With permission of Cambridge Univ. Press

species to germinate so quickly and lead to the emergence of new, green seedlings on the charred soil? There are many potential germination stimulants that change in the post-fire environment, including heat scarification, altered light levels (vegetation gaps) and increased nitrate in the soil. However, one of the most important inducers of germination in post-fire environments is smoke itself. Smoke induces germination both directly and indirectly by aqueous or gaseous transfer from soil to seeds. A principal group of active compounds in smoke has been identified as the karrikins (Sect. 6.6.7.3). The positive effect of smoke on seed germination is not limited to species that are native to fire-prone habitats. Smoke (and smoke extracts) appears to be an almost universal stimulator of seed germination and is now widely in use as an ecological and restoration tool throughout the world in a variety of conservation practices, in land management, and for the promotion of wild plants, including indigenous medicinal plants.

Smoke-stimulated germination occurs in 25 chaparral species, representing 11 families. None of these families is known to exhibit heat-shock-stimulated germination, i.e., by short exposures to high or extreme temperatures or temperature differences (Sect. 6.6.7). The quantitatively important gases generated by biomass smoke are generally not effective, except for NO_2. Seeds of smoke-stimulated species appear to have many similar characteristics that separate them from most heat-shock-stimulated seeds, including highly textured outer seed coats, a poorly developed outer cuticle, absence of a dense palisade tissue in the seed coat and a subdermal membrane that is selectively permeable, allowing passage of water but blocking entry of large solutes. It appears that smoke is involved in overcoming different

blocks to germination in different species. There is little doubt that the action of smoke-derived germination stimulants is subject to interactions with other abiotic environmental cues, such as temperature.

7.3 Secondary Dormancy and Seasonal Variation

Temperature acts to regulate germination in the field in several ways (Sect. 7.2.2) but also affects seed survival by determining the rate of deterioration (in moist seeds). Furthermore, temperature during seed development and maturation has a profound influence on performance of the mature seed after shedding (Sect. 6.6.2). Since temperature is relatively constant in its seasonal, monthly, and daily variations, it is arguably the most important environmental cue to synchronize seed germination with conditions suitable for seedling establishment. This is certainly valid for seasonal climate types, but in arid and semi-arid regions water may be the most important cue, whereas in the humid tropics variations in temperature and water availability appear to be virtually absent and hence will not synchronize seed germination with the environment, if this occurs at all.

7.3.1 Dormancy Cycling

In order to synchronize themselves with the seasons, seeds in the soil seed bank must be able to sense and perceive the continuous stream of information about the suitability of the environment for successful seedling emergence and subsequent plant growth. The ecophysiology of dormancy and germination deals with the perception of environmental factors by the seeds and how these are translated into signals within the seed and, ultimately, determine whether the seed will germinate.

Much progress in clarifying the internal processing of external information by seeds has been made with the large group of arable annual weeds of the temperate zones. In these regions seedling emergence is restricted to predetermined periods of the year, and in most cases (summer annuals) within a limited period in the spring, sometimes followed by additional flushes in summer. Examples of this group of summer annuals are *Ambrosia artemisiifolia*, *Polygonum persicaria*, *Chenopodium album*, *Spergula arvensis*, and *Sisymbrium officinale*. Species originating from climates with a hot dry summer and a cool humid winter, such as *Arabidopsis thaliana*, usually germinate in autumn whilst surviving the winter as rosette plants (winter annuals).

Dicotyledonous annual weed species often form large persistent seed banks. Survival of seeds in these seed banks may be as long as decades to perhaps even centuries. Emergence from soil seed banks is strongly stimulated by disturbance or wetting of the soil, e.g., by cultivation (Sect. 7.2.3), but the seasonal timing of emergence appears not to be affected. It therefore seems that the timing of emergence does not depend on prevailing conditions but on a seasonal fluctuation of the environment. In the temperate zones, temperature fluctuations over the year remain

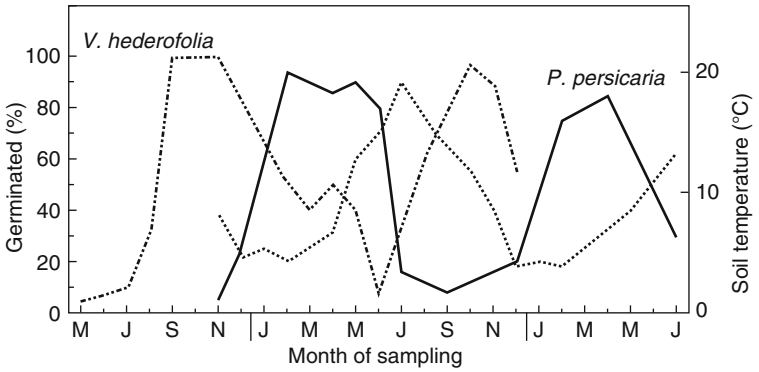

Fig. 7.21 Patterns of seed dormancy during burial. The patterns of germination and dormancy of *Veronica hederofolia* and *Polygonum persicaria* are shown. Seeds of both species were buried in sandy loam at 5 cm *(Veronica)* or 10 cm *(Polygonum)*. Germination at alternating temperatures in the light was tested at intervals. The dotted line shows the average morning soil temperature at the site of burial of *Polygonum*. *V. hederofolia* is a winter annual; *P. persicaria*, a summer annual. Note that the two species enter a deep secondary dormancy at different times of the year, in response to low and high temperatures, respectively. After Roberts and Lockett (1978) and Karssen (1980/81)

within narrow ranges, as opposed to, for example, rainfall, which can be more variable. Cold temperatures experienced by seeds in the seed bank in the winter of the temperate zones results in a fraction of nondormant seeds that may germinate in the spring when conditions for germination are permissive (Sect. 6.6.3). If the environment for germination is not favorable, seeds may gradually become dormant again, entering secondary dormancy. This is induced by the warm summer temperatures in summer annuals, such as *Polygonum persicaria*. In winter annuals, such as *Veronica hederofolia,* the summer temperatures break dormancy whereas the low winter temperatures induce secondary dormancy. Thus, summer annuals germinate in spring and winter annuals in autumn. However, many species may have characteristics of both. For example, *Lamium amplexicaule* and *Arabidopsis thaliana* are considered facultative winter annuals, which means that seeds from these species germinate not only in autumn but a small fraction also in the spring. Accordingly, seasonal fluctuations in temperature are considered the main regulatory factor of annual dormancy cycling (Fig. 7.21).

The range of conditions over which germination and emergence can occur widens during the alleviation of dormancy whereas it narrows during dormancy induction, indicating that dormancy is a relative phenomenon (Fig. 7.7), the expression of which is dependent on the prevailing environmental temperature. As indicated in Chap. 6, cold treatment, as well as after-ripening, also sensitizes the seeds to the environment to become responsive to light, nitrate and other factors. Therefore, germination in the field occurs when the germination temperature window overlaps with the actual field temperature (Fig. 7.22). In summer annuals the window is very narrow or even closed in dormant seeds at the end of the summer season and, hence, germination will not occur. When dormancy is terminated, as a result of the

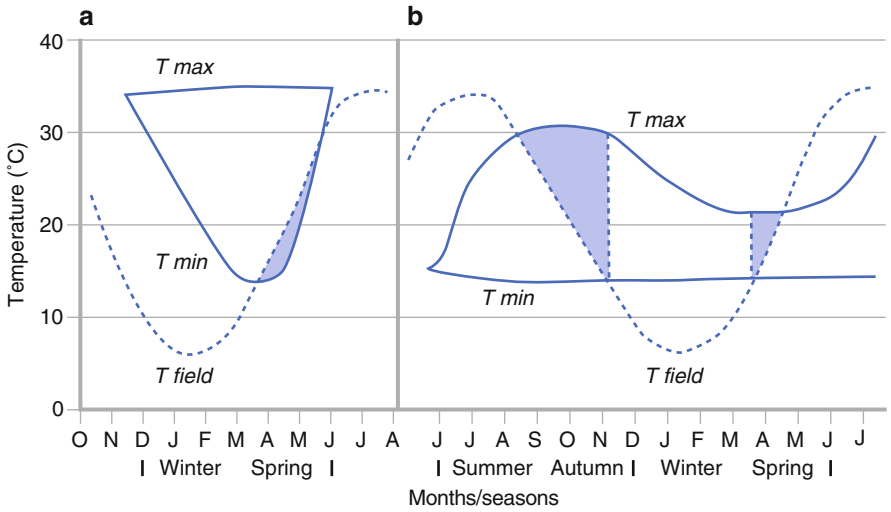

Fig. 7.22 Model to show the relationship between field temperature and the change in the range of temperatures over which germination can proceed. Solid lines represents the maximum (*T max*) and minimum (*T min*) temperatures at which germination is possible. The broken line indicates the mean daily maximum temperature in the field (*T field*). In the blue shaded area the actual and the required temperature overlap. (**a**) Strict summer annual and (**b**) facultative winter annual. From Probert (2000). Courtesy of CAB International

cool winter temperatures, the germination temperature window widens and will eventually overlap with the (increasing) field temperature in spring. However, germination will only occur when the requirements for germination, such as oxygen, water, soil components and possibly light are met. Conversely, induction of dormancy will be associated with a narrowing of the germination temperature window and a decreased responsiveness to environmental factors. Thus, dormancy cycling is a process of alternating perceptiveness of seeds to environmental factors that promote germination. The ecological relevance of dormancy cycling is to prevent seeds from germinating during short spells of favorable conditions in an otherwise unfavorable season. For example, a short spell of relatively high temperatures often occurs in autumn and could lead to germination if seeds are not dormant. Subsequent seedling emergence and establishment may become suicidal when temperatures drop again.

7.3.2 Dormancy Cycling: Mechanisms and Modeling

Based on the long-term effects of temperature on dormancy, i.e., dormancy breaking by chilling temperatures and induction of secondary dormancy by elevated temperatures, descriptive models have been developed. In this way the opening and closing of the "temperature windows" for germination can be modeled from the daily field

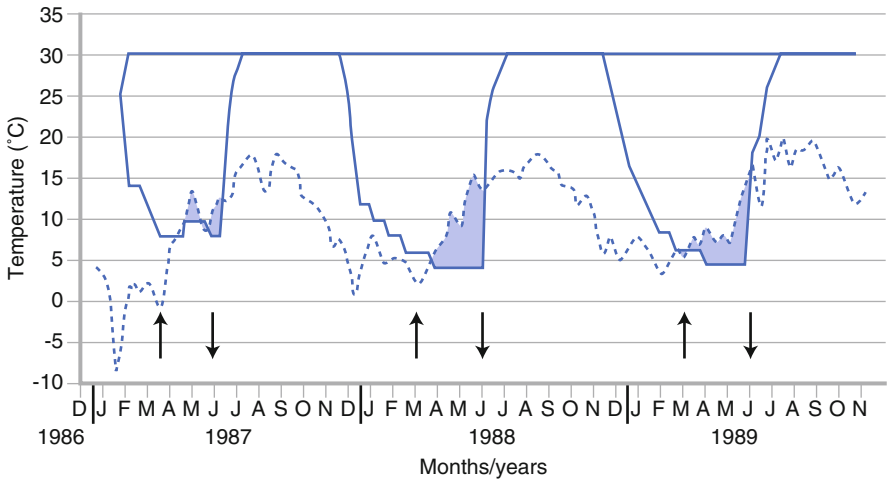

Fig. 7.23 Simulation of seasonal changes in the range of temperatures over which at least 50% of exhumed *Polygonum persicaria* seeds germinate. Solid lines represent maximum and minimum temperature required for 50% germination in water, calculated according to a descriptive model based on thermal time parameters. The dotted line indicates air temperature at 1.50 m. Blue shaded areas indicate overlap of field temperature and germination temperature range. Arrows indicate when germination outdoors in Petri dishes actually increased above (↑) or decreased below 50% (↓). From Probert (2000). Courtesy of CAB International

temperatures during a complete dormancy cycle. The models calculate the temperature sums from the number of days above or below the threshold temperatures for the induction or breaking of dormancy, respectively, during complete dormancy cycles in the field. In many cases this threshold temperature is approximately 15°C. Using a function that relates expected germination to heat and cold sums, temperature, and substrate, equation parameters are selected that provide the best similarities with germination data from laboratory experiments. From this the maximum and minimum temperatures to reach 50% germination are calculated and can then be compared with the real field situation to predict seedling emergence. These models are remarkably predictive of the timing of emergence for some species, but are much less accurate in predicting the number of emerged seedlings (Fig. 7.23).

Although it is now firmly established that temperature is the main driving force of dormancy and that dormancy cycling in the soil can be mimicked by descriptive models, a mechanistic explanation of this phenomenon is lacking. Only very few studies have been devoted to investigating the molecular aspects of dormancy relief and induction in the same seed batch and in the same study. So far reliable data have been obtained only from the *Arabidopsis thaliana* accession Cvi. This normally has a profound primary dormancy that can be broken by after-ripening and/or chilling and secondary dormancy can be induced by prolonged dark incubation at 20°C. An in vitro transcriptomics approach has revealed distinct sets of dormancy- and

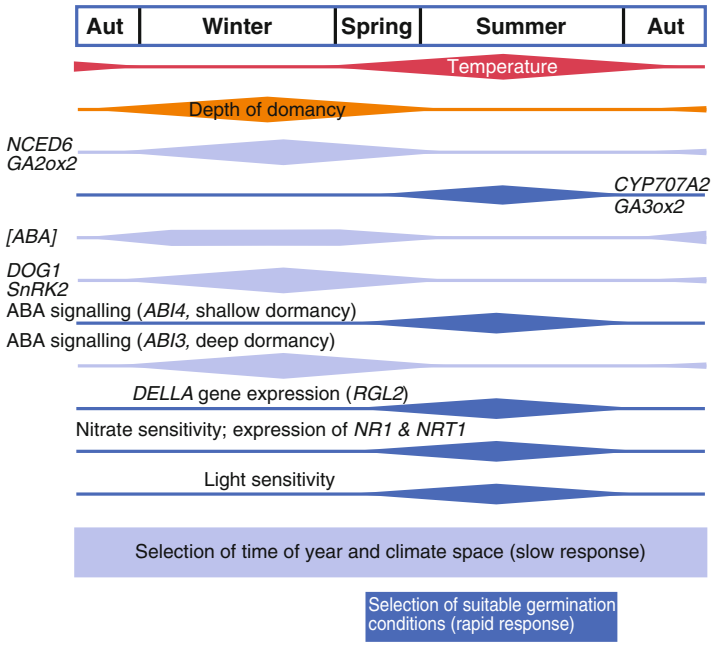

Fig. 7.24 Dormancy cycling in the field as monitored by depth of dormancy, light and nitrate sensitivity and expression of key genes of the winter annual *Arabidopsis thaliana* Cvi dormancy cycling in relation to annual fluctuations in soil temperature. The extent of each of the responses to seasonal variation is indicated by the height of the bars. The light and dark-blue bars at the base of the figure indicate the long- and short-term efficacies of dormancy breaking, respectively. From Footitt et al. (2011). Courtesy of the National Academy of Sciences, USA

germination-associated genes. Each of these consists of several hundreds of genes. It appears that the effects of different environmental factors that break dormancy, including after-ripening, cold, nitrate, and light, are very similar in that their effects on the different gene sets are additive.

The seasonal timing of physiological and molecular events associated with dormancy cycling of *A. thaliana* Cvi seeds in the field is primarily correlated with soil temperature and ABA concentration and sensitivity. The key enzymes of the GA–ABA balance (Sect. 6.6.1.4) identified in the laboratory behave as expected: expression of *NCED6* and *GA2ox2* genes (components of the ABA synthesis and GA inactivating pathways, respectively; Fig. 6.13) increases with increasing ABA concentrations and depth of dormancy during winter. In contrast, abundance of transcripts of the *CYP707A2* and *GA3ox2* genes (important in ABA inactivation and GA synthesis, respectively) decreases when dormancy is lost and ABA contents drop during spring and summer (Fig. 7.24). Similarly, transcripts of ABA-signaling genes from *ABI4* and *ABI3* are correlated with shallow summer dormancy and winter deep dormancy, respectively. *DOG1* and *SnRK* genes (Sects. 6.4.2, 6.6.1) are correlated

with deep winter dormancy only. *DELLA* gene expression, as well as nitrate- and light-sensitivity correlate with shallow summer dormancy. DOG1 is hypothesized to be involved in a thermal-sensing mechanism to influence the (temperature-driven) dormancy level by altering sensitivity to ABA. The abundance of two separate groups of transcripts correlates well with the previously mentioned "long-term" and "short-term" breaking of dormancy (Sect. 6.6).

7.4 Influences of Plant Life Cycle, Distribution and Origin on Germination

7.4.1 Plant Distribution

Different species may have different temperature requirements for germination, which are important in determining the distribution of plants, for they limit germination to regions that have suitable temperatures. It follows, also, that indigenous species of a particular region show characteristic temperature requirements, since they are adapted to the temperature conditions prevailing in their environment.

Members of one family, the Caryophyllacae, differ in their habitat and temperature requirements for germination, and are used here to illustrate this variable relationship. One way of documenting this is to determine, for each species, the time taken at each temperature to reach 50% of maximum germination to produce a germination "signature." The resulting signature curve thus indicates the low and high cutoff temperatures for germinated, or T_b and T_c. (Note that if the germination rates, 1/days to 50% germinated, are plotted rather than the times to germination, the patterns resemble the linear cardinal temperature relationships shown in Fig. 7.8.) Germination signatures of three Caryophyllaceous species are shown in Fig. 7.25, each typifying its geographical origin. The species from the continental grassland (steppe) *(Petrorhagia prolifera)* completes germination quickly at the favorable temperatures (12–40°C), with a high minimum (ca. 8°C) and maximum (ca. 42°C) (Fig. 7.25a, curve b). The Mediterranean species (*Silene echinata*) also completes germination fairly rapidly at median temperatures but, in contrast to the grassland type, has rather low minimum (<5°C) and maximum (ca. 25°C) requirements (curve a). Finally, the European woodland species (*Silene dioica*) is relatively slow to complete germination at median temperatures, with a high minimum (10–15°C) and moderate maximum (ca. 35°C) temperature requirement (curve c). The Mediterranean signature, belonging to the winter annuals, has been interpreted as favoring fall germination of the shed seed, in anticipation of the winter growing season. Seeds of the European woodland species, with a median temperature range, if shed in summer, would complete germination at once, whereas fall-shed seed would have to await the following spring. Here, germination in only spring/summer is encouraged. The grassland species have an opportunist signature and are able to germinate over a wide range of temperatures; they germinate when the seeds are shed in mid- to late summer. Of course, the same species may be found in a wide variety of climatic

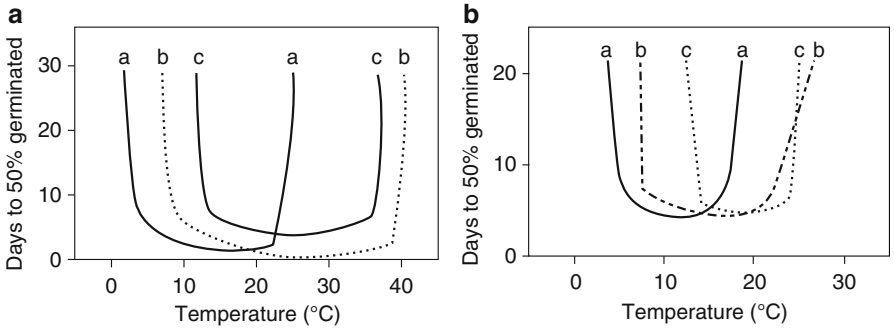

Fig. 7.25 (**a**) Germination "signature" curves. Nondormant seeds of three species were held at different temperatures, and the number of days taken to reach 50% germinated seeds was determined. a, *Silene echinata* (Mediterranean); b, *Petrorhagia prolifera* (continental grassland); c, *Silene dioica* (European woodland). Adapted from Thompson (1973b). (**b**) Germination "signature" curves of *Silene vulgaris* seeds from different regions. Seeds from three geographical localities were tested at a range of temperatures. The number of days for the germinated seeds to reach 50% was determined at each temperature. a, seeds from Portugal; b, seeds from Czechoslovakia; c, seeds from England. After Thompson (1973a)

regions: here, the germination behavior may differ according to provenance. The seed germination signatures of a single species, *Silene vulgaris,* from different regions are shown in Fig. 7.25b. Seeds from three origins show the typical germination signatures of the regional types (Mediterranean, continental grassland, and European woodland—cf. Fig. 7.25a), so clearly adaptation to the local conditions occurs within a species.

7.4.2 Seasonal and Flowering Interactions Affecting Dormancy

There is now developing an understanding that adaptation patterns of plants are highly dependent on perhaps just a few critical stages of the plant life cycle, namely, flowering and germination phenology (the term "phenology" denotes the timing of life cycle events). In populations of many species the timing of (field) germination largely determines their reproductive output (seed production) and how many generations can be completed in a given season or year. In addition, timing of germination is highly dependent on flowering time and, hence, depends on maternal environmental effects on germination and dormancy (Sect. 6.5). Evidently, these effects on dormancy and germination influence the timing of germination and, consequently, plant life cycle and population demography. Figure 7.26 shows several possible life cycles of annual plants. The winter annual life cycle occurs when seeds germinate in autumn (see also Sect. 7.3.1). Seedlings or rosettes overwinter and flowering, seed set and dispersal occur during spring and early summer. The dispersed seeds germinate again in autumn and the winter

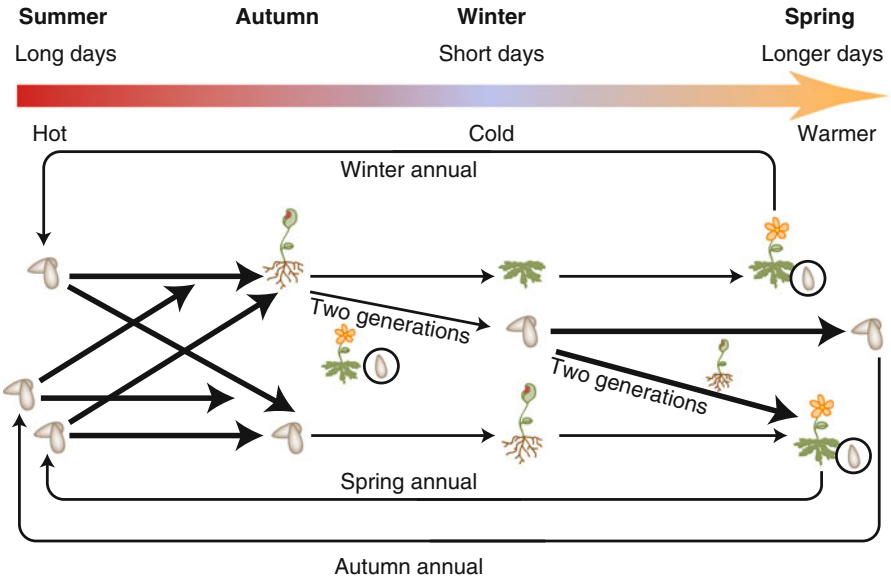

Fig. 7.26 Life cycles of annual plants. Bold lines indicate branch points determined by the germination behavior of seeds ( ) that matured during different seasons. The pathway from flower to seed represents the maternal effects on germination, and this path also completes the life cycle. The life cycle that is expressed depends on which path the seeds follow, which can be a function of when they matured and were dispersed. *Circled Seeds* indicate plants that have produced and shed seed. Adapted from Donohue (2009). Courtesy of the Royal Society of London

annual cycle begins again. Alternatively, the spring annual cycle starts when seeds germinate in spring and grow into mature plants that flower, set seed and disperse their seeds that same spring or summer. These seeds overwinter and do not germinate until the following spring. An autumn annual cycle occurs if seeds that mature in autumn remain dormant and do not germinate until the next autumn. If they germinate in the spring, then a spring annual generation could occur that set seeds in spring/summer and germinate in autumn, resulting in two generations per year instead of one. Many annual (and biennial) plants display such profound phenological variation. Thus, germination timing, along with capacity to flower in different seasons, determines the type of life cycle that is actually expressed.

Apart from the (maternal) environment, genetic factors also play a role in germination phenology, for example dormancy genotypes. Dormancy cycling is a determinant of germination timing, and together with the prevailing germination environment results in narrow seasonal time windows for seedling emergence. It is not known how the maternal environment of the maturing seeds affects dormancy and, consequently, dormancy cycling. However, it has become clear that DOG1 (Sect. 6.4.2) is a critical component in the expression of natural variation of dormancy in *Arabidopsis thaliana* and may be a mediator between the maternal environment and seed phenotype (Fig. 7.24).

Another example of the importance of germination timing can be found in desert populations. A study observing annual populations of 10 species in an undisturbed desert area for 22 years showed that delayed germination (i.e., dormancy) buffers the variation in reproductive success (germination and seedling survival). In other words, seeds remaining dormant in the soil may substitute for lower seed production or germination in a certain year, for instance because of a lack of precipitation. As noted above, in desert climates water and not temperature may be the limiting factor for seedling emergence.

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