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Chapter 11

Germination Ecophysiology

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11.1 Introduction

For parasitic weeds of the Orobanchaceae to emerge successfully above the soil surface and have the potential to produce viable seeds for the next generation, the seeds must first be after-ripened, conditioned, stimulated and germinate. The seedlings must then locate, attach to and penetrate a host (Kebreab and Murdoch 2001). Next to the fertilisation of the ovule, germination is the primary event in the life cycle of flowering plants and successfully consummates the mother plant's investment in its offspring. It is especially significant in annual parasitic plants such as *Orobanche*, *Phelipanche*, *Alectra* and *Striga* species, most of which disperse and regenerate exclusively by seed. Environmental influences during maturation on the mother plant and subsequently in the soil seed bank interact with genotype and are adapted to increase the probabilities that a seed germinates in “the right place and at the right time” and regenerates successfully, completing a full life cycle (Murdoch and Ellis 2000). The key question in this chapter is: what proportion of viable seeds will regenerate successfully? Models to quantify the probability of a successful outcome are described below, focusing on genotype and environment interactions in the individual seed for which

To germinate or not to germinate? That is the question!

Seeds of many species are sensitive to environmental germination triggers to ensure seeds germinate at a time and depth of burial from which they may emerge.

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Such factors may include depth-sensing factors such as light quality and quantity and the amplitude of diurnal temperature fluctuation and seasonal factors such as soil nitrogen status, temperature and soil atmospheric composition (Roberts 1973; Roberts et al. 1987; Murdoch and Ellis 2000). As pointed out, however, by Joel et al. (2006), “the most specialized and intriguing germination mechanisms belong to some parasitic angiosperms that do not germinate until they detect the presence of a host plant”. Adaptations which help to ensure some seeds successfully complete their life cycle include their fecundity, the stimulation of germination by host root exudates (Chap. 10) and the preservation of viability for long periods (Teryokhin 1997).

In terms of fecundity, mature *Orobanche* or *Phelipanche* plants may produce more than a quarter of a million (Parker and Riches 1993) very small seeds (0.2–0.7 mm long $\times$ 0.2–0.5 mm wide; Budantsev 1993, see Chap. 8 and Sect. 9.1). Since seed production is density dependent (López-Granados and García-Torres 1991; Kebreab and Murdoch 2001), it is useful to evaluate seed production per unit area where, for *O. crenata* on a range of legume hosts in Syria, Schnell et al. (1994) reported 0–619,000 seeds m^{-2} in a dry year (1990, 209 mm rainfall) and 1,100–10.6 million seeds m^{-2} on the same hosts in a wetter year (1991, 316 mm). Typically, 10–25 % of seeds produced may be non-viable (Teryokhin 1997).

Fecundity is slightly lower in *Striga*, with average seed numbers per *S. hermonthica* plant on sorghum of 6,700–26,500 (Rodenburg et al. 2006) and 15,600–18,800 on millet (van Mourik et al. 2008). Individual plants may of course produce much higher or smaller outputs. The maximum *S. hermonthica* seed production per sorghum host plant was 757,000 equivalent to 1.57 million seeds m^{-2} (van Mourik 2007), but seed production varies with host and decreases with decrease in crop duration, season length and intercropping with non-hosts (van Mourik et al. 2008). Some genera in the Orobanchaceae have much larger seeds (see Sect. 9.1). For example, across nine species of *Pedicularis* in Tibet, there is a tendency for seed production per plant to decrease with increase in seed size (Guo et al. 2010). The facultative parasite, *Rhinanthus minor*, also has relatively large seeds (4.9 $\times$ 3.8 mm) and produced on average 168 seeds per plant in the UK (Westbury 2004).

11.2 Seed Survival in Dry Storage

Persistence in soil is only possible if seed viability is preserved. Seed storage behaviour is classified as **orthodox** if seed longevity increases in a quantifiable and predictable manner with decrease in temperature and decrease in seed water potential from about –20 MPa to about –350 MPa, whereas **recalcitrant** seeds cannot be dried without losing viability (Ellis and Roberts 1980; Murdoch and Ellis 2000).

O. crenata and *S. hermonthica* seeds may be added to the 81 % of 13,913 species, including 53 from the Orobanchaceae, which exhibit “orthodox” seed

storage behaviour (Kebreab and Murdoch 1999b; Murdoch et al. 2000; Royal Botanic Gardens Kew 2008). None of the 57 species of the Orobanchaceae, for which information on seed storage behaviour is documented, is recorded as recalcitrant although storability is deemed “uncertain” for four relatively large-seeded species: *Melampyrum nemorosum*, *M. pratense* L., *Pedicularis sylvatica* and *Rhinanthus aristatus* (Royal Botanic Gardens Kew 2008). Uncertainty in these four cases merely relates to the fact that their seeds have been recorded as surviving for less than 1 year in the soil (Thompson et al. 1997) rather than to definitive studies of seed storage behaviour.

Kebreab and Murdoch (1999b) stored seeds of *O. minor*, *O. crenata* and *P. aegyptiaca* in 13 environments above saturated salt solutions with equilibrium relative humidities (e.r.h.) between 11 and 85 % and at temperatures from 20 to 60 °C. Survival of dry seeds corresponded to negative cumulative normal distributions. Viability after any time t (days), at temperature T (°C), and e.r.h. r (%) was quantified as follows:

$$v = K_i - t/10^{K_E - C_W r - C_H T - C_Q T^2} \quad (11.1)$$

where v is viability expressed in normal equivalent deviates (NED = probit – 5), K_i is a seed lot constant, the estimated initial viability of the seed lot (NED), and K_E , C_W , C_H and C_Q are species constants. K_E is an extrapolated estimate of the seed longevity at 0 % e.r.h. and 0 °C, C_W is the sensitivity of longevity to changes in e.r.h. and C_H and C_Q are temperature coefficients (Kebreab and Murdoch 1999b).

Although the research was only carried out on single seed lots of each species, the sensitivities to changes in e.r.h. and temperature were similar in the three species and are also similar to those of non-parasitic plant species in different families. As a working hypothesis, therefore, it is suggested that the parameter values for (11.1) should be able to be used with some confidence to predict the relative effects of changes in e.r.h. and temperature on seed longevity for all species and all seed lots of Orobanchaceae exhibiting “orthodox” seed storage behaviour. Caveats are that (1) the seed lots come from a single provenance in the same year (i.e. seeds from different sources and years should not be mixed) and (2) the seed lot has always been stored air-dry and has not been subdivided and then remixed so that the seed lot constant, K_i , remains valid. If these caveats are met, the time taken for viability to drop by one NED or probit (e.g. from 98 to 84 % or from 84 to 50 %) is doubled for each 8.4 % drop in e.r.h. The temperature term in (11.1) is quadratic, and so the sensitivity to temperature varies with temperature such that the relative benefit to longevity of a decrease in storage temperature decreases with decrease in temperature (the Q_{10} decreases).

What actually differs between species is the value of the “species” constant, K_E , which was lower in *O. minor* than in the other two species. This difference means seeds of *O. minor* are predicted to survive only half as long as *O. crenata* and *P. aegyptiaca* (Table 11.1), which may be one of the reasons why the latter two species are more successful as weeds. The higher the initial viability of the seed lot,

Table 11.1 Predicted viability periods

Initial viability	Years for 5 % loss of viability		
% (K_i , in NED)	<i>Phelipanche aegyptiaca</i>	<i>Orobanche crenata</i>	<i>Orobanche minor</i>
98 (2.00)	21	22	10
89 (1.25)	9	10	5
69 (0.50)	5	5	3

The effect of initial viability [K_i , (11.1)] on the predicted period for 5 % viability loss at 5 °C and 55 % equilibrium relative humidity (from Kebreab and Murdoch (1999b) with permission)

the longer the period for a small (5 %) drop in viability (Table 11.1), a consequence of seed survival curves corresponding to negative cumulative normal distributions. In addition, the ability of seeds to survive for several years means that loss of viability is unlikely to limit the longevity of these seeds when in dry soil. The proportion of viable seeds after a period of time in dry storage will, however, vary widely between seed lots of a given species, and the use of the viability equation in the laboratory requires an accurate estimate of initial seed viability, the seed lot constant, K_i .

11.3 Seed Survival in Moist Storage

At water potentials above about -20 MPa and in fully imbibed seeds, (11.1) no longer applies (Roberts and Ellis 1989). As seeds imbibe, metabolism increases, damage may be repaired and microbial attack may be actively resisted. The effect of increasing water potential is thus completely reversed so that seed longevity increases with increase in moisture availability, provided the seeds remain dormant and air is present to allow respiration (Ibrahim et al. 1983; Murdoch and Ellis 2000). Imbibed tissues and hence seed longevity are, however, very vulnerable to high temperatures, and predicted periods for 50 % loss of viability of imbibed seeds of *S. hermonthica*, *O. crenata* and *O. cumana* were, respectively, 98, 60 and 30 h at 45 °C but only 8, 7 and 6 min at 60 °C (calculated from regression coefficients in Dawoud 1995). *S. hermonthica* is, therefore, more tolerant to high temperature and hence should be the most resistant to soil solarisation (see Sect. 22.4.2). At the lower temperatures, likely to characterise most moist soils, fully imbibed seeds of *Orobanche* and *Phelipanche* spp. have been shown to survive for at least 3 months at 30 °C and to show negligible loss of viability over 7 months at temperatures of 10–20 °C provided air is present (Kebreab and Murdoch 1999a, b; Murdoch and Ellis 2000). In comparison to drier seeds whose survival follows the viability equation (11.1), these responses are relatively poorly quantified, but seed survival curves do approximate to negative cumulative normal distributions (Dawoud 1995; Kebreab and Murdoch 1999a, b).

The differences between very dry (< -350 MPa), dry (-350 to -20 MPa) and hydrated (> -20 MPa) seeds may relate to the binding of water (Roberts and Ellis

1989). Water is freely available in hydrated seeds allowing respiration to occur. Conversely, in very dry seeds, water is strongly bound and has little chemical potential, and so its removal has little effect on longevity. In between these extremes, water is weakly bound, and the effects of changes in water potential on longevity can be predicted by (11.1) (Roberts and Ellis 1989).

Whether at high or low water potentials, orthodox seeds of *Orobanche* and *Phelipanche*, if dormant and thus non-germinating, may persist for long periods in the soil seed bank. The main risks to their longevity are probably predation and anaerobiosis. Circumstantial evidence suggesting longevity of 14–20 years in soil for *Orobanche* seed is probably true. For example, López-Granados and García-Torres (1999) reported 98.7 % loss of viability of *O. crenata* seed after 12 years soil burial in Spain. It is also salutary to reflect on the prediction that even such a high percentage seed loss could still leave 3,250 seeds out of 250,000 produced by a single plant. *Orobanche* seed banks exhibit, therefore, “long-term persistence” in the soil seed bank as defined by Thompson et al. (1997) (see Chaps. 19 and 22).

It has generally been assumed that *Striga hermonthica* may similarly survive in the soil for long periods although recent results have been more equivocal. For example, 52 % depletion of a naturally occurring soil seed bank was observed over two wet seasons in Gambia with mono-cropped, unfertilised sorghum (Murdoch and Kunjo 2003), and slow depletion was also reported in Ghana (Sprich 1994). By contrast, a total loss of *S. hermonthica* seed viability occurred after only 3 months burial in Western Kenya (Pieterse et al. 1996). In drier, unimodal rainfall areas¹ of Benin, *S. hermonthica* seed viability declined from 90 to 15 % over 6 months (Gbèhounou et al. 1996a), with almost total loss of viability over two wet seasons (Gbèhounou 1998). Reasons for the discrepancy were resolved by showing that burial of *S. hermonthica* seeds in small mesh packets, as in the Benin and Western Kenyan reports, leads to rapid loss of viability associated with microbial decay (van Mourik et al. 2005).

Several species of hemiparasitic Orobanchaceae only form transient soil seed banks such that their seeds survive for less than 1 year in the soil, for example, *Rhinanthus minor* (Westbury 2004), *Bartsia alpina* L. and the four larger-seeded species mentioned in Sect. 11.2, while others, for example, *Euphrasia stricta* and *E. officinalis*, form short-term persistent seed banks surviving for 1–5 years in the soil (Thompson et al. 1997). In this respect, these hemiparasitic plants do not differ from non-parasitic plants.

¹ One rainy season each year.

11.4 Dormancy and Quiescence

No matter how spectacular the potential longevity, as quantified by the parameter K_E in (11.1), the potential will never be realised if a seed germinates shortly after entering the soil seed bank. Dormancy and/or quiescence are therefore essential for seeds to persist in the soil.

Dormancy is “the failure of a viable seed to germinate given moisture, air and a suitable constant temperature for radicle emergence and seedling growth” (Murdoch 2004). If one of these three requirements for germination of non-dormant seeds is lacking, the seed is arguably quiescent rather than dormant because metabolism will be lower, and growth will resume as soon as the limiting factor is available. As defined, individual seeds either germinate or do not, implying dormancy and quiescence are quantal responses. Unless all or no seeds germinate, germination assays only distinguish two groups of seeds—those which germinate (non-dormant) and those which do not (dormant). Measuring the extent or depth of physiological dormancy in individual seeds is currently impossible, but the variation in percentage germination as a function of the dose of dormancy-breaking treatments reflects variation in dormancy among individuals in the seed population. Like the seed-to-seed variation in periods for which seeds survive, this variation is often well described by the normal distribution function and so can be quantified by the mean and standard deviation of the distribution.

The qualitative distinction between primary and secondary dormancy is useful. **Primary dormancy** (innate dormancy) develops on the mother plant (Murdoch and Ellis 2000). It prevents or reduces both precocious germination and the germination of seeds immediately after shedding. Based on research on various non-parasitic species, the extent of primary dormancy on dispersal from the mother plant is likely to vary widely between seed lots with strong effects of both genotype and the environment. **Secondary dormancy** is induced after shedding (Murdoch and Ellis 2000) and helps to ensure the long-term persistence of the soil seed bank.

Frustration with negative definitions—“failure to germinate”—has led to dormancy being redefined as “a characteristic of the seed that determines the conditions required for germination” (Finch-Savage and Leubner-Metzger 2006) albeit begging the follow-on questions: which characteristic and how do you measure it? This definition also leads to the question: do host root exudates terminate dormancy in obligate parasitic Orobanchaceae or just stimulate their germination? The answer “depends on where one chooses to draw the line between the processes of dormancy and germination”. Exposure to the chemical(s) in host root exudates changes the seed, removing a physiological or metabolic block, so that it can germinate at a suitable temperature in water and, *sensu stricto*, should therefore be regarded as “the last step in the dormancy-breaking process rather than the first step in the germination process” (quotations from Finch-Savage and Leubner-Metzger (2006)). The question is like looking at two sides of a coin. The chemical stimulant relieves the final physiological block to germination, and thus, the dual effect is that it relieves the final block to germination rather like light for

some light-sensitive seeds and in so doing, stimulates germination, i.e. provides the first step of germination.

Primary dormancy of fresh, viable seeds of *Orobanche*, *Phelipanche* and *Striga* spp. can be envisaged as composed of three distinct physiological blocks to germination, which need to be relieved sequentially for germination to occur.

First of all, release from primary dormancy generally requires a period of “dry” storage also known as dry after-ripening. After-ripened seeds are not, however, non-dormant in the sense that they will not germinate spontaneously. The mechanism of after-ripening in seeds probably relates to “degradation of mRNAs and proteins for positive regulators of dormancy and for negative regulators of germination”, and there is a possibility of some gene expression even though the seeds are, by definition, quiescent (Finch-Savage and Leubner-Metzger 2006).

Secondly, the seeds must undergo a short period of imbibed storage (conditioning), during which their ability to overcome the third block increases. Thirdly, the final block to germination is a requirement for stimulation by one or more chemicals exuded by host plant roots (see Chap. 10).

The following discussion mainly concerns publications where an approximately optimal and standard stimulatory treatment has been used.

11.4.1 Relief of Primary Dormancy

After-Ripening Air-Dry, Quiescent Seeds. Quantitative studies of dormancy loss in *Orobanche* seeds in controlled dry storage conditions, other than at “room” temperature, are lacking, and this has not altered since Pieterse and Verkleij (1994) reported that “hardly any reliable data on the occurrence of primary dormancy in *Orobanche* seeds are available” and that “conclusions drawn with respect to primary dormancy are largely based on speculation”. For example, Edwards (1972) reported that several months’ storage was required while Saghir (1986) made the unreferenced remark that seeds may require “a period of up to 2 years for after-ripening to occur”. Research in non-parasitic plants implies that loss of primary dormancy may occur both on and off the mother plant. Moreover, the loss of primary dormancy is a progressive process in the seed population, and the rate of the process varies in a predictable way as a function of the environment (Murdoch and Ellis 2000).

With respect to environmental factors, seed moisture content is critical, but the rate of loss of primary dormancy during after-ripening varies with both temperature and seed moisture content (see Bazin et al. 2011 and references cited therein). Moisture contents (fresh weight basis) of 5–18 % are required, the rate of dormancy alleviation during dry storage generally decreasing with decrease in moisture content (see Probert 2000). In modelling the life cycle of *O. crenata*, Grenz and Sauerborn (2007) specified a soil moisture threshold of 22.5 % below which both primary and secondary dormancy can be relieved although the soil type and water potential are not known. These processes can clearly occur for seeds in secondary

dormancy during warm, dry Mediterranean summers (van Hezewijk et al. 1994b), and equally *O. crenata* could not succeed as a weed where warm, dry conditions never occur (Grenz and Sauerborn 2007).

The influence of temperature on this relief of dormancy was not included by Grenz and Sauerborn (2007) in their model. Circumstantial evidence from the literature suggests, however, that many seeds, including *S. hermonthica* (Murdoch et al. 2000), behave like those members of the Poaceae in which the logarithm of the mean dormancy period is a negative linear function of temperature, the Q_{10} for the relation being typically in the range 2.5–3.8. For example, in *S. hermonthica*, the rate of after-ripening decreases slightly with increase in temperature with a Q_{10} of approx. 3 (Murdoch et al. 2000; Murdoch and Kebreab 2005). If the quantitative effect of temperature on the rate of loss of primary dormancy during dry after-ripening is an approximately conserved trait over species from different families (Murdoch and Ellis 2000), then for species for which experimental evidence is lacking, it would be reasonable to assume a Q_{10} of 3 to predict how periods for loss of primary dormancy would vary with a change in temperature. It follows that there should be an approximate 81-fold increase in the rate of after-ripening at 60 °C as compared to 20 °C. However, it is also important to note that the Q_{10} for loss of viability increases approximately exponentially with increase in temperature (the temperature term in (11.1) being quadratic) compared to a linear temperature term for after-ripening. The net effect is that above certain temperatures, a significant fraction of the seed population may lose viability before it loses dormancy! No information is available on this transition for *Orobanch* or *Phelipanche*, but in the case of *S. hermonthica*, loss of viability becomes significant during after-ripening at about 60 °C and is detectable although not significant at 50 °C (compare Murdoch and Ellis 2000). It is therefore recommended that routine after-ripening for laboratory experiments should *not* be carried out above 40 °C.

The variation in after-ripening periods described in the literature is, however, not only accounted for by differences in storage temperature and moisture. Other factors could include differences within and between species, variation in seed maturation conditions, the different ways in which seeds are processed and differences in germination protocols. The paucity of literature on these topics especially for *Orobanch* and *Phelipanche* spp. may seem surprising given the importance of dormancy in determining the extent of parasitism. These species mainly occur, however, as serious weeds in agro-ecologies which are subject to seasonal drought during which after-ripening will occur naturally. The second phase of dormancy relief, more commonly known as “conditioning” or “pre-conditioning”, is of greater significance in relation to weed control as it occurs in moist soil and immediately precedes germination.

Conditioning Imbibed Seeds. Imbibition is a physical process which activates metabolic pathways in viable seeds. Once imbibed, seeds enter a lag phase when new physiological mechanisms prepare for elongation of the embryonic axis. Completion of seed germination can be temporarily blocked by dormancy, or indeed, dormancy may be relieved during this lag phase. In the Orobanchaceae,

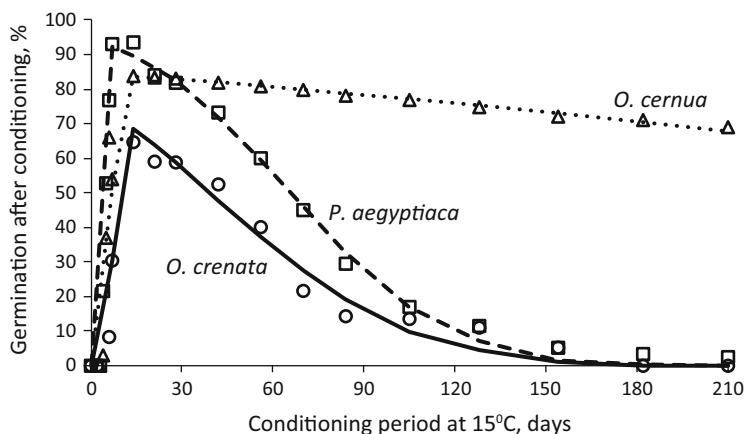


Fig. 11.1 Seed conditioning. Influence of the period of conditioning (at 15 °C) on the seed germination of three parasite species. Germination was stimulated with GR24 and assessed 10 days later (based on data published by Kebeab and Murdoch 1999a)

the process of conditioning has long been recognised as a beneficial seed pretreatment before laboratory experiments (Pieterse 1979). During conditioning, seeds become increasingly sensitive to germination stimulants (Joel et al. 1991; Matusova et al. 2004) over periods of up to about 14 days (Fig. 11.1), the period required decreasing with increase in temperature (Table 11.2). The extrapolated lowest temperatures at which the rate of loss of dormancy is zero, the **base temperature**, varied from -5.4 °C in *O. crenata* to 11.2 °C for *S. hermonthica* (Table 11.2; Vallance 1950). The effect is analogous to stratification in non-parasitic seeds in which seeds show a progressive increase in sensitivity to a subsequent treatment, which overcomes the final block to germination (Murdoch and Ellis 2000).

Respiration of *P. aegyptiaca* increased to a maximum after 3 days of conditioning with a second peak after 11 days and thereafter declined to low levels (Bar-Nun and Mayer 1993; Mayer and Bar-Nun 1994). A similar decline to low levels has also been reported for imbibed, non-germinating seeds of non-parasitic plants (Barton 1945; Ibrahim et al. 1983). Also like some non-parasitic plants (Roberts 1973; Roberts and Smith 1977), respiration prior to germination is at least in part via the cyanide-insensitive respiratory pathway, but this happens in the parasite seeds during early conditioning (Bar-Nun et al. 2003). Interestingly, the final percentage germination of *P. ramosa* did not differ significantly when seeds were conditioned for 14 days at 20 °C with oxygen partial pressures ranging from 1 to 21 % oxygen in the atmosphere (Gibot-Leclerc et al. 2004).

Gene expression occurs actively during conditioning (e.g. Joel et al. 2006) and is perhaps linked to gibberellin biosynthesis (Joel et al. 1991; Song et al. 2005) and other metabolic activities. Exogenous applications of GA₃ increase the subsequent

Table 11.2 Loss of dormancy during conditioning

	<i>Phelipanche aegyptiaca</i>	<i>Orobancha cernua</i>	<i>Orobancha crenata</i>	<i>Striga hermonthica</i>
Base temperature (°C)	0.55	3.42	−5.38	11.2
Approx. median thermal time (°C d) ^a	58.8	69.8	142.9	69.4
Approx. median conditioning periods (days) at:				
10 °C	6.2	10.6	9.3	—
15 °C	4.1	6.0	7.0	18.3
20 °C	3.0	4.2	5.6	7.9
25 °C	2.4	3.2	4.7	5.0
30 °C	2.0	2.6	4.0	3.7
35 °C	—	—	—	2.9

Base temperatures, median thermal times and predicted conditioning periods required at 10–35 °C for loss of dormancy during conditioning

Requirements to sensitise approx. 50 % of parasite seed populations to germination stimulants. Estimates based on parameter values for p_0 and p in (11.2) (Kebreab and Murdoch 1999a) and on comparable figures from Dzomeku and Murdoch (2007b)

^aThermal times for loss of dormancy to increase by three normal deviates or probits from −3 NED (0.1 %) to 0 NED (50 %) Thermal times for approx. complete loss of primary dormancy, i.e. from −3 to +3 NED (99.9 %), are twice those to 50 %

germination, whereas including an inhibitor of GA biosynthesis (e.g. 0.01 mg/L uniconazole) has the converse effect on seeds of *P. ramosa*, *P. aegyptiaca* and *O. minor* (Song et al. 2005). In addition, the concentration of ABA decreased from approx. 250 ng/g seed to 100 ng/g during 6 days of conditioning of *O. minor* in darkness at both 23 and 30 °C (Chae et al. 2004; see Sects. 9.2.1 and 9.4 regarding the timing of expression of an ABA catabolic gene in various seed tissues). Carotenoid biosynthesis inhibitors prevent ABA biosynthesis, and two out of three inhibitors tested by Kusumoto et al. (2006), fluridone and norflurazon, reduced the conditioning period required for germination of *Striga asiatica* seeds. Given the importance of both ABA and gibberellin in control of dormancy and germination of many species (e.g. Finch-Savage and Leubner-Metzger 2006; Shepherd et al. 2007), it is not surprising that changes in plant hormones during conditioning are linked to the increase in seed sensitivity to germination stimulants. ABA is catabolised during conditioning (Fig. 9.3c; see Sect. 9.2.1) and Lechat et al. (2012) showed significant up-regulation of the ABA catabolism gene, *PrCYP707A1*, after stimulating conditioned *P. ramosa* seeds with GR24 (Fig. 9.8b; see Sect. 9.4). Slavov et al. (2004) showed IAA was released by *P. ramosa* seeds after treating with germination stimulant.

Despite some conflicting and inconsistent reports, subsequent germination of *O. crenata* increased significantly with increase in pH levels during conditioning for 14 days at 20 °C from 36 % at pH 4 to about 50 % at pH 6–7 and 62 % at pH 8.5 (van Hezewijk et al. 1994a).

Recent research has suggested that while conditioning is a prerequisite for germination of *Striga* spp. and *O. crenata*, it is not in either *P. aegyptiaca* or *O. cumana* provided germination test periods are extended to about 14 days, because seeds of

the latter two species achieve high germination percentages whether or not they have been conditioned prior to stimulation with GR24 (Plakhine et al. 2009; Plakhine and Joel 2010). Given the need to prolong the germination period, it could still be argued that conditioning occurred prior to germination; it was just that exposure to the germination stimulant occurred earlier. It should also be noted that conditioned seeds responded better to lower concentrations of stimulant. For example, 53 % of conditioned *P. aegyptiaca* seeds germinated with 10^{-8} M GR24 compared to only 25 % of the unconditioned ones (SED 2.56, Fig. 3 in Plakhine et al. 2009). So, while the earlier literature implied that conditioning was a prerequisite before exposure to stimulant, it is now more appropriate to say it is beneficial, but the sequence of dormancy-relieving treatments is less critical in some species than previously thought.

11.4.2 Secondary Dormancy

Prolonging conditioning beyond the optimum leads to an induction of secondary dormancy (Fig. 11.1). The term “wet dormancy” was introduced by Vallance (1950) for this process in *S. hermonthica*. Induction of secondary dormancy during prolonged moist aerobic treatments also occurs in non-parasitic species of other plant families, e.g. *Rumex* spp. and *Picea sitchensis* (Totterdell and Roberts 1979; Jones et al. 1997). Interestingly, the rate of induction of secondary dormancy in imbibed *R. crispus* seeds decreased with decrease in temperature (from 20 to 1.5 °C, Murdoch and Ellis 2000), whereas the converse occurs in *Orobanch*e and *Striga* seeds in which rates of induction of secondary dormancy were respectively fastest during prolonged conditioning at 10 and 17.5 °C and decreased to a minimum above about 20 and 25 °C (Kebreab and Murdoch 1999a; Song et al. 2005; Dzomeku and Murdoch 2007a), which indicates dissimilarity in secondary dormancy mechanisms.

Relief of secondary dormancy is usually achieved in laboratory experiments by drying, reconditioning and restimulating the seeds (Kebreab and Murdoch 1999a). This observation implies some similarity in the mechanism of secondary dormancy to the requirement for after-ripening, which is acquired during maturation on the mother plant (see Sect. 11.4.1).

11.4.3 Modelling Conditioning

Although variation within homogeneous seed populations is normally distributed, non-normal responses are observed during conditioning because up to three processes are occurring during this pre-germination phase, as demonstrated for seeds of *O. cernua*, *O. crenata* and *P. aegyptiaca* (Kebreab and Murdoch 1999a) and *S. hermonthica* (Dzomeku and Murdoch 2007b). Provided that the germination tests

were carried out identically, germination (G) after conditioning in water for t days ($0 \leq t \leq 210$ days) at temperature T (from $10 \leq T \leq 30$ °C) is then the product of the proportions of the seed population that have (a) lost primary dormancy (Φ_d^{-1}), (b) not entered secondary dormancy (Φ_s^{-1}) and (c) at 30 °C only retained viability (Φ_v^{-1}), according to the following equation:

$$G = [\Phi_d^{-1}(K_d + (p_0 + pT)t)] [\Phi_s^{-1}(K_i + (s_m + sr^T)t)] \times [\Phi_v^{-1}(K_i + \beta_{30}t)] / \Phi^{-1}(K_i) \quad (11.2)$$

where Φ^{-1} indicates back-transformation from NED to proportions; K_d and K_i are respectively the initial levels of non-dormancy and viability in NED when $t = 0$ days; p_0 and p quantify a linear increase in the rate of loss of primary dormancy with increase in temperature; s_m , s and r are an asymptotic decrease in the rate of induction of secondary dormancy with increase in temperature; and β_{30} is the rate of loss of viability at 30 °C (Kebreab and Murdoch 1999a). Examples for seeds conditioned at 15 °C are illustrated in Fig. 11.1.

The counter-intuitive inference from (11.2) is that the sensitisation to germination stimulants associated with loss of dormancy during conditioning is both independent and concurrent with the desensitisation to germination stimulants associated with induction of secondary dormancy. The hypothesis of independence and concurrence is based on a similar idea proposed by Totterdell and Roberts (1979) and was used by Grenz and Sauerborn (2007) to model seed bank dynamics of *O. crenata*, and it is consistent with the mechanism of secondary dormancy suggested in Sect. 11.4.2. Vleeshouwers and Bouwmeester (2001) contended, however, that only one process could take place at a time.

Using a much larger set of data in which *S. hermonthica* seeds were conditioned not only at different temperatures but also at different water potentials and in different concentrations of urea, Dzomeku and Murdoch (2007b) preferred a sequential model in which seeds first lose primary dormancy and can only then have secondary dormancy induced in them. As a step to resolving this question, multiplicative and sequential models could be compared statistically on the same datasets.

Water stress and urea during conditioning both reduce subsequent germination of *S. hermonthica* (Dzomeku and Murdoch 2007a, b), while water stress reduced the subsequent germination rate of *P. ramosa* (Gibot-Leclerc et al. 2004) and also final germination percentages of *P. aegyptiaca*, *P. ramosa* and *O. minor* seeds especially if a -2 MPa treatment was applied at relatively low (13 °C) or high (28 °C) conditioning temperatures (Song et al. 2005). Interestingly, the rate of induction of secondary dormancy appeared not to be affected by decrease in water potential (to -2 MPa) during conditioning (Song et al. 2005). For the same three species, Song et al. (2006) demonstrated that germination after prolonged conditioning can be enhanced by the use of the growth promoters, gibberellin (GA_3 ,

10 mg L⁻¹), fluridone (10 mg L⁻¹) and brassinolide (1 mg L⁻¹), combinations of pairs of these chemicals being particularly effective.

The variation between species (and often also between populations of the same species) in the effects of conditioning is particularly interesting. For example, *P. aegyptiaca* lost dormancy most rapidly and *O. crenata* most slowly (Table 11.2, Fig. 11.1), perhaps reflecting the absolute conditioning requirement of the latter (Plakhine et al. 2009). Lowest temperatures for loss of dormancy during conditioning vary between species, *O. cernua* showing relatively little induction of secondary dormancy compared to *P. aegyptiaca* and *O. crenata* (Fig. 11.1). Similarly, Song et al. (2005) found that *O. minor* was much less susceptible to secondary dormancy compared to *P. aegyptiaca* and *P. ramosa*. Interestingly, Gibot-Leclerc et al. (2004) found induction of secondary dormancy in *P. ramosa* to a greater extent at 30 °C than at lower temperatures, whereas the asymptotic decrease in the rate of induction of secondary dormancy with increase in temperature in (11.2) was based on a minimal induction of secondary dormancy at 30 °C (Kebreab and Murdoch 1999a). A further contrast is found in Song et al.'s (2005) results for *P. ramosa*, which showed little difference in the rate of induction of secondary dormancy over the temperature range 13–28 °C and at water stress levels of 0 to –2 MPa.

It is therefore clear that responses to conditioning are not at all conserved in different species, base temperatures, thermal times and rates of induction of secondary dormancy all varying markedly between species and often also between seed lots of the same species (Table 11.2, Fig. 11.1). Conditioning is therefore likely to be a highly adaptive trait in parasitic seeds. Further research to explore this adaptation in different seed lots of the same species and in different species could assist in predicting the potential spread of these species with climate change.

11.5 From Relief of Dormancy to the Initiation of Germination

If the seed ultimately fails to germinate, adaptations to maintain viability, avoid predation and prevent germination in unfavourable conditions will have been with no advantage as far as the individual seed is concerned. Using the banking analogy, some seeds need to be transferred from a deeply dormant “savings” account to a less or non-dormant “current” account. These latter seeds need to be at a low enough level of dormancy so as to be capable of responding to the chemicals exuded from host plant roots.

11.5.1 Annual Cycles in Dormancy

Annual cycles in which physiologically based dormancy is relieved and induced during the course of a year occurred in buried seeds of *O. crenata* in Syria, Egypt and Spain (Van Hezewijk et al. 1994b; López-Granados and García-Torres 1999) as they do in many non-parasitic annuals with persistent soil seed banks in both temperate and tropical soil environments (Baskin and Baskin 1985, 1998; Benech-Arnold and Sanchez 1995; Murdoch and Ellis 2000). *O. crenata* seeds, which after-ripened in the soil in summer, would then be exposed to some moisture, lose their primary dormancy and become able to germinate in response to germination stimulant in the autumn or winter (Van Hezewijk et al. 1994b). Secondary dormancy was then induced at low winter temperatures (compare Sect. 12.2) followed by its being progressively relieved during warm dry summer conditions, a similar pattern recurring over at least 6 years (López-Granados and García-Torres 1999). Evidence for a comparable annual dormancy cycle in other species of *Orobanchaceae* is not known, but it is speculated that differences in dormancy cycles are likely due, for example, to the obligate requirement for conditioning in *O. crenata*, but not in *P. aegyptiaca* or *O. cumana* (Plakhine et al. 2009; Plakhine and Joel 2010) and differences in rates of induction of secondary dormancy (Fig. 11.1).

This annual dormancy cycle is not found in quiescent *Orobanchaceae* seeds stored dry in controlled constant environments, but in *S. hermonthica*, Gbèhounou (1998) suggested that there was an endogenous dormancy cycle in dry-stored seeds. While such cycles have sometimes been suggested in other species, the absence of control or monitoring of temperature and humidity during laboratory storage means the cycle needs confirmation. For seeds buried in the soil, changes in dormancy were, however, evident ensuring the seeds were ready to germinate at the end of the dry season (Gbèhounou et al. 1996b).

11.6 Germination

For species which respond to germination stimulants, the percentage germination achievable varies with the amounts and type of germination stimulants exuded by the host (see Chap. 10). In the field, the concentration sensed by the seed is a function of soil moisture and proximity of the seed to active host roots, and these are also the most important factors determining whether or not germination occurs. Many factors influence the proportion of seeds which germinate at any given stimulant concentration. Promotion of suicidal germination (see Sect. 22.4.5) by application of stimulants to soil has achieved some success in glasshouse experiments (Kgosi et al. 2012), but not so far in commercial agricultural systems. Research supplementing synthetic stimulants with growth promoters may improve the reliability of the treatment (Song et al. 2006; see Sect. 10.4.1).

Whether the goal is the stimulation of suicidal germination or prediction of infestations (Sect. 23.4), research has quantified germination responses in relation to both **germination rate** (germination per unit time) and final **percentage germination**.

Soil fertility and in particular the presence of ammonium ions or urea tend to be inhibitory (Pieterse 1996). In studies of five weedy parasitic *Orobanch* species, Westwood and Foy (1999) showed that while ammonium ions inhibit germination slightly, their main effect was to reduce radicle elongation after germination, approximately 80 % reduction in radicle length occurring after 10 days in 25 mM ammonium sulphate compared to the water control. Temperature and moisture are the main environmental factors that determine germination of non-dormant seeds in the field. Water stress often limits germination (Benech-Arnold and Sanchez 1995), while temperature not only influences germination through its effects on seed viability and dormancy but also affects the germination process itself.

11.6.1 *Effects of Fluctuating and Constant Temperatures*

Relief of dormancy and promotion of germination by fluctuating temperatures in non-parasitic plants have been interpreted ecologically as depth and seasonal sensing mechanisms of small seeds, which increase the likelihood of successful regeneration (Roberts et al. 1987). Seeds of the small-seeded, parasitic members of the Orobanchaceae need to detect their proximity to the roots of host plants rather than the soil surface, and so a positive response to fluctuating temperatures might actually be selected against, as it would indicate proximity to the soil surface where density of host roots might be lower.

Racovitza (1959) suggested that germination of seeds of *P. ramosa* may be enhanced by a 6–8 °C fluctuation of temperature. Strictly, however, to demonstrate unequivocally that alternating temperatures affect germination, the constant temperature controls should include the mean, minimum and maximum temperatures of the alternating temperature regime. Comparing germination at a 15/25 °C (12 h/12 h) alternation with the mean temperature of the regime (20 °C) as a constant temperature control, Van Hezewijk (1994) found a deleterious effect of the alternating temperature regime on germination of *O. crenata*.

The use of a temperature gradient plate by Kebreab and Murdoch (1999c) allowed testing a total of 78 different combinations of daily minimum and maximum temperature regimes, each with either 8 or 16 h/day at the maximum/minimum temperature. Germination after up to 30 days was compared with 13 constant temperature controls for non-dormant seeds of *P. aegyptiaca*, *O. cernua*, *O. crenata* and *O. minor* and for *P. aegyptiaca* and *O. crenata* seeds with secondary dormancy. The expected absence of a positive response to temperature fluctuation was confirmed, and indeed, as observed by Van Hezewijk (1994), alternating temperatures tended to be deleterious. Alternating temperatures never increased germination compared to the corresponding mean temperatures, and at wider amplitudes,

alternating temperatures decreased germination percentage. Four characteristics of the temperature regime (whether constant or alternating) appeared to affect germination percentage: (a) the mean temperature, (b) the maximum temperature, (c) the temperature range or amplitude and (d) the period spent at the maximum temperature each day, the latter two modifying the effect of maximum temperature (Kebreab and Murdoch 1999c).

Variation in germination responses could be accounted for by a multiplicative probability model which implied that there were two cardinal temperatures determining whether or not an individual seed would germinate in a given regime: (a) a mean temperature, which had to be exceeded, and (b) a maximum temperature, which must not be exceeded. These two limits were modelled on the bases that they were independent in individual seeds and were normally distributed in the seed population. In general, a very sharp decline in germination was noted in temperature regimes in which one or both temperatures exceeded 25 °C, indicating that the adverse effect of alternating temperatures was mainly due to the maximum temperature (Kebreab and Murdoch 1999c). Eizenberg et al. (2003) reported a similarly dramatic effect in seeds of *O. cumana* whose germination decreased from 88 to 38 % with only a 3 °C increase in mean temperature at alternating temperatures of 26/18 °C and 29/21 °C, respectively (14 h/10 h).

The acceptance of a model with two cardinal temperatures implies that individual seeds vary in the temperature range over which they will germinate. Integration of these ranges gives an overall range of temperature, final germination percentage varying within that range (Table 11.3). The overall range itself varies between species and may also vary between populations of a given species.

It is also important to recognise that the optimal temperature for maximum final germination percentage is much lower than the optimal temperature for rate of germination. Water stress narrows the temperature range for germination (Kebreab and Murdoch 2000). For example, germination of *P. aegyptiaca* exceeded 90 % from 11 to 29 °C in water but only 70–75 % over the range of 17–21 °C at –1.25 MPa (Kebreab and Murdoch 2000).

11.6.2 *Thermal Time and the Rate of Germination in the Laboratory and Field*

The success of germination in the field is often linked to the time it takes for seeds to germinate or the reciprocal of time, the rate of germination. Progress of germination in a seed population has commonly been described by **thermal time** or **hydrothermal time** models, the latter taking account of both temperature and water potential (see Kebreab and Murdoch 1999d; Bradford 2002; Allen et al. 2007). Thermal time models have been developed to simulate seed bank dynamics (Grenz et al. 2008) and subsequent development (Manschadi 1999; Ephrath and Eizenberg 2010).

Table 11.3 Optimum temperatures and thermal times for germination of *Phelipanche* and *Orobanch*e species

	Temperature range for germination (°C)	Temperature for maximum final germination (°C)			Temperature for maximum rate of germination (°C)	Median thermal time for germination (°C d)	Standard deviation of thermal time for germination (°C d)
		No dormancy	Secondary dormancy				
<i>P. aegyptiaca</i>	5–32	18–21	17.5–19.5	29	52.4	15.2	
<i>O. crenata</i>	8–29	18	17.5	29	52.0	20.4	
<i>O. cernua</i>	5–32	15	–	29	47.0	15.6	
<i>O. minor</i>	8–29	17–20	–	26–29	37.6	10.4	
<i>O. cumana</i>	5–32	–	–	26	46.4	10.5	

Based on temperature gradient experiments (Kebreab and Murdoch 1999c), germination tests continued for 30–50 days according to species and temperature (Kebreab and Murdoch 1998, 1999d). Median thermal times in °C days (°C d) are estimates based on a common base temperature of 4.9 °C

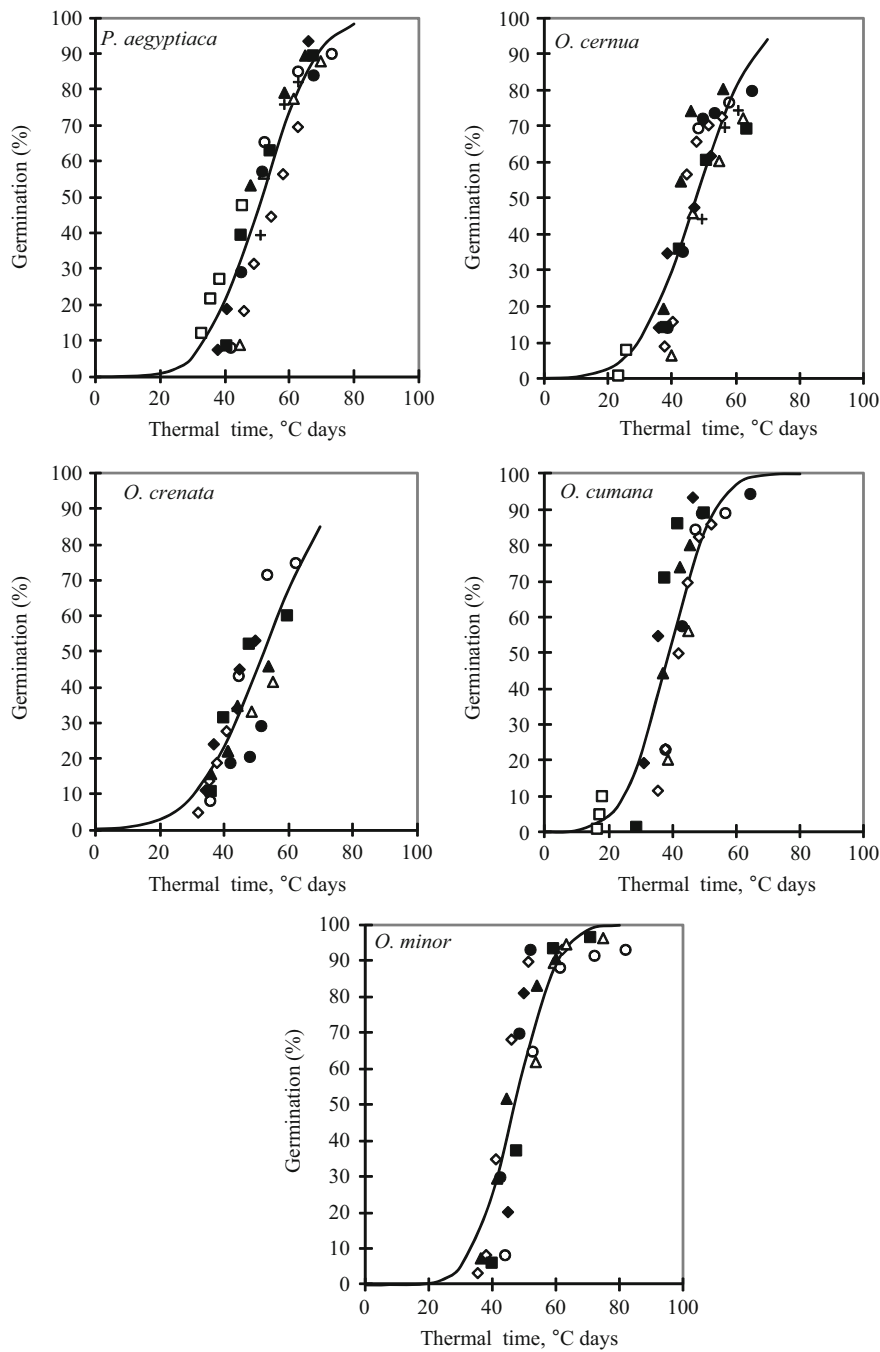


Fig. 11.2 Thermal times for progress of germination of different parasites. Progress of germination at various temperatures: 5 °C (*open squares*), 8 °C (*open diamonds*), 11 °C (*open triangles*),

Thermal time for progress of germination is approximately normally distributed within a seed lot (Covell et al. 1986; Ellis et al. 1986; Kebreab and Murdoch 1999d, Fig. 11.2) and is always calculated above the estimated base temperature at which, by extrapolation, the rate of germination is predicted to be zero. In *S. hermonthica*, the base and optimum temperatures for rate of germination were 22.7 and 40 °C in seeds conditioned at 20 °C compared with 18.9 and 32–35 °C for seeds conditioned at 30 °C (Aflakpui et al. 1998).

The variation in base and optimal temperatures with conditioning temperature is particularly interesting because Ellis and Butcher (1988) found that base temperature varied little between autumn and spring sown onion seeds and suggested it was probably a species characteristic, i.e. every individual seed of every seed lot of a given species has the same base temperature. In studies of germination rates of *P. aegyptiaca*, *O. crenata*, *O. cernua*, *O. minor* and *O. cumana*, separate base temperatures for each species were tabulated by Kebreab and Murdoch (1998), and further analysis showed that a base temperature of 4.9 °C was not only constant within each seed population, but it did not differ significantly between all five species (Kebreab and Murdoch 1998). Supporting evidence comes from Van Hezewijk et al. (1991), who reported a base temperature of approx. 5 °C for *O. crenata*, and Grenz et al. (2008) who used 5 °C for *O. cumana*. Eizenberg et al. (2012) achieved excellent predictions of attachments of *O. cumana* to sunflower roots using the base temperature of the sunflower host (4 °C) while noting that models of attachment are only applicable above base temperatures for growth of both parasite (5 °C) and host (see Sect. 23.4). The germination (G in NED or probits) after t_g (days) of non-dormant seeds of these five species when germinated at a mean temperature, T , with 10^{-5} M GR24 at a water potential of 0 MPa (water) can thus be predicted as follows:

$$\text{Probit } (G) = [t_g(T - T_b) - \theta_{T(50)}] / \sigma_{\theta_T} \quad (11.3)$$

where T_b is the base temperature, $\theta_{T(50)}$ is the median thermal time to germination in water (Table 11.3) and σ_{θ_T} is the standard deviation of thermal times (°C d, Table 11.3, Fig. 11.2).

Base temperature and thermal time both increase, however, as a linear function of the decrease in water potential (Kebreab and Murdoch 1999d). The effect of conditioning temperature on base temperature of *S. hermonthica* (Aflakpui et al. 1998) emphasises the caution needed. It is not known how these effects of water potential differ between seed lots or species. The highest water potential at which seeds of *P. aegyptiaca* were predicted to be unable to germinate (the base water potential at which the rate of germination is predicted to be zero) varied, however,

Fig. 11.2 (continued) 14 °C (open circles), 17 °C (filled squares), 20 °C (filled diamonds), 23 °C (filled triangles), 26 °C (filled circles) and 29 °C (plus symbols), using a common base temperature of 4.9 °C for all species. Normal distributions were fitted according to (11.3) (reanalysis of data in Kebreab and Murdoch 1998)

between individual seeds (mean -1.96 MPa and standard deviation 0.33 MPa at 20°C). The median base water potential was approx. -2 MPa at $14\text{--}23^{\circ}\text{C}$ and increased at both higher and lower temperatures, meaning *P. aegyptiaca* seeds were more susceptible to water stress when also subjected to either low or high temperature stress.

11.7 Conclusion

Adaptations to holo- and hemiparasitism are seen in many chapters of this book, not least in seed characteristics. All aspects of the seed cycle can be seen as maximising the likelihood of successful attachment to a host plant, but variations between species have also been evident. These variations in combination with those regarding the response to germination stimulation facilitate adaptations to different agro-ecologies and different hosts, since germination is the primary event driving infestations of annual weeds. The concepts, results and models considered in this chapter have important ramifications for integrated weed management (see Chaps. 22 and 23). As an example, changes in the dormancy of buried seeds underpin delayed sowing practices which exploit induction of secondary dormancy, and so there is clearly little point in using such approaches for species such as *O. cernua* and *O. minor* in which secondary dormancy is induced slowly.

Despite the small size of the seeds, they also seem well adapted to form a persistent soil seed bank, survival of at least some seeds until conditions are right for germination being assured by their fecundity, small size (avoiding predation) and their ability to maintain viability while preventing germination by dormancy.

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