Ongoing projects serve to highlight the commitment of *New Phytologist* to mathematical modelling and theoretical approaches across the four sections of the journal – such as in the application of modelling to understanding the evolution of phenotypic plasticity (discussed in the 'eco-devo' feature forthcoming in April) and the use of three-dimensional modelling to probe structure–function relationships in plants, using computer simulations (structure–function modelling feature forthcoming in June). Both these issues will be available as free content for three-month periods in 2005.

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Commentary

Threshold models applied to seed germination ecology

Seed dormancy is a complex phenomenon by which seeds schedule their germination to coincide with favorable periods for seedling establishment. Dormant seeds do not complete germination even though environmental conditions (e.g. water, temperature) would normally be conducive to it. Once dormant seeds have received required signals from the environment, which are specific to each species, dormancy is alleviated and germination can proceed. The alleviation of dormancy is often regulated by environmental factors such as temperature and light that can inform the seed about its location in the soil, whether it is shaded by other plants, the season of the year and other information relevant to its 'decision' as to whether to germinate at a given time (Benech-Arnold *et al.*, 2000). The work of Batlla & Benech-Arnold on dormancy of *Polygonum aviculare* seeds (see pp. 445–452 in this issue) illustrates how multiple environmental cues can interact to affect the germination potential of a seed population.

'The concept of a distribution of threshold sensitivities among seeds in a population has resulted in a remarkably robust yet simple mathematical model'

Polygonum aviculare and threshold modelling

Batlla & Benech-Arnold show that dormant seeds of *Polygonum aviculare* are unable to germinate in either light or dark, but when imbibed and held at chilling temperatures, the seeds become responsive to red light through the action of phytochrome. The sensitivity of the seeds to light is increased by exposure to a chilling temperature ('stratification'), as is known to occur in various species (e.g. lettuce; VanDerWoude, 1985). Further, Batlla & Benech-Arnold showed that this change in light sensitivity occurs in proportion to the accumulation of 'stratification thermal time', or the difference between the maximum effective temperature (17°C in this case) and the storage temperature (< 17°C) multiplied by the duration of chilling; the lower the temperature below the threshold, the more rapid the increase in light sensitivity (i.e. loss of dormancy). In related work, Batlla & Benech-Arnold (2004) showed that chilling also resulted in a decrease in the threshold water potential at which seeds of the same species could complete germination, and that this decrease also occurred in proportion to the accumulation of stratification thermal time.

These studies contribute to a growing body of evidence that threshold models are useful for describing and quantifying the responses of seeds to diverse conditions, including temperature, water, light, afterripening, chilling and other dormancy-breaking factors (reviewed in Bradford, 1995, 2002; Allen, 2003; Finch-Savage, 2004). Threshold models are based on the concept that the magnitude or speed of a biological response is proportional to the difference between the level of a signal input and the threshold sensitivity for that input. Thus, the response of a given seed in terms of when and whether it completes germination is determined by its sensitivity threshold in relation to the current signal input from the environment – the greater the signal level above the threshold, the more rapid the response. In addition, populations of seeds, particularly those of weedy or native plants, tend to vary widely in the depth of dormancy or the extent of dormancy-breaking conditions that are required to allow germination. Such population variation extends the viable duration of seed banks in soil and spreads the risk that germination will occur in an unfavorable environment with subsequent death of the seedlings. The concept of a distribution of threshold sensitivities among seeds in a population has resulted in a remarkably robust yet simple mathematical model that can account for many aspects of seed dormancy and germination behavior (Bradford, 1996, 2002; Rowse & Finch-Savage, 2003; Finch-Savage, 2004).

Quantifying changing sensitivity

An underappreciated aspect of this threshold model concept is that rather than identifying static parameters of a seed population, the model can quantify the changes in sensitivity that occur as seeds enter or leave dormancy. As noted above, Batlla & Benech-Arnold have identified changes in light sensitivity and water potential thresholds due to chilling in *P. aviculare*, and Allen and coworkers showed that changes in water potential thresholds were associated with the loss of dormancy in *Bromus tectorum* seeds during dry afterripening (Christensen *et al.*, 1996). Similar results were found for true potato (*Solanum tuberosum*) seeds in response to afterripening and dormancy-breaking chemicals (Alvarado & Bradford, 2005). Loss of dormancy in *Aesculus hippocastanum* seeds was associated with a lowering of the minimum temperature for germination during stratification (Steadman & Pritchard, 2004). Alvarado & Bradford (2002) and Rowse & Finch-Savage (2003) demonstrated that the reduction in germination that occurs between the optimum and the maximum germination temperatures is a consequence of an increase in the water potential threshold for germination as temperature increases. Thus, shifts in the median sensitivity of a seed population to environmental factors, along with the variation among seeds in their individual sensitivities, can account for a wide array of seed germination and dormancy phenotypes.

Population responses to light

This integrative aspect of population-based threshold models can be illustrated by further examining data presented by Batlla & Benech-Arnold (2005). The responses of germination to light intensity as a function of accumulated stratification thermal time from their fig. 3 are reproduced here (Fig. 1, symbols). The light intensity is quantified as the ratio of the far-red-absorbing form of phytochrome to total phytochrome (Pfr/P). They fit a trilineal model to these data that describes an initial unresponsive period, a linear increase in sensitivity to light and then a maximum response for a given Pfr/P ratio (see fig. 3 of Batlla & Benech-Arnold, 2005). The extension of the population-based threshold concept to these data provides an alternative modeling approach. Assume that there is a range of sensitivities to light (i.e. of threshold Pfr/P ratios required for germination) within the seed population, illustrated here by a normal frequency distribution (Fig. 2). Without chilling, all of the seeds require very high (unattainable) Pfr/P ratios, so that the seeds are
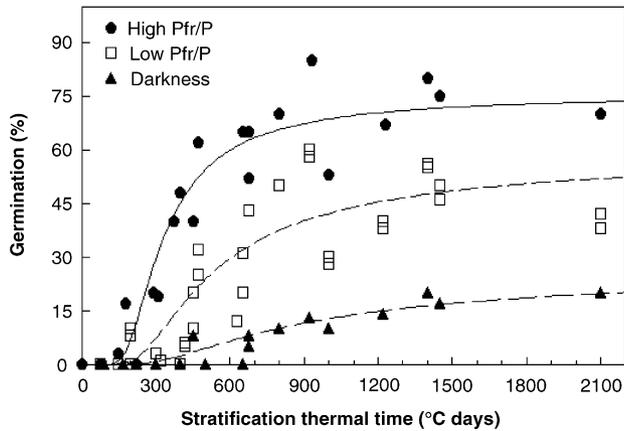
Fig. 1 Germination of *Polygonum aviculare* seeds after different periods of chilling (expressed on a stratification thermal time scale) and at light levels that result in different ratios of the far-red-absorbing (Pfr) form of phytochrome relative to total phytochrome (P) (from Batlla & Benech-Arnold, pp. 445–452). The symbols are the experimental data, and the curves are predicted based upon the population distributions and shifting light requirement thresholds in response to chilling.
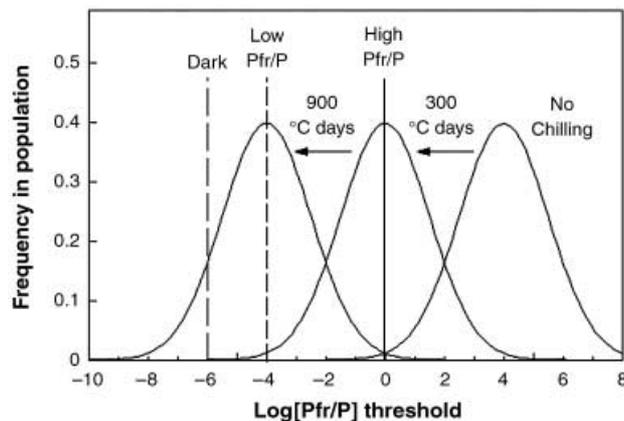

Fig. 2 Theoretical threshold distributions of the sensitivity of the seed population to the Pfr/P ratio. The sensitivity to light is shown as a normal frequency distribution. Initially, the sensitivity to light is low (i.e. a very high (unattainable) Pfr/P ratio would be required to stimulate germination). With the accumulation of chilling, the sensitivity distribution shifts toward lower Pfr/P ratios (i.e. the seeds become more responsive to light). The vertical lines indicate the approximate Pfr/P ratios that correspond to the different light treatments. The fractions of the sensitivity distributions that are to the left of these lines correspond to the fractions of the seed populations that are able to germinate at those Pfr/P ratios.

insensitive to light. With accumulated thermal chilling time, this sensitivity distribution shifts to lower Pfr/P ratios, such that some seeds can now germinate in the light, and the higher the Pfr/P ratio, the larger the fraction of the population for which the threshold is exceeded and which can therefore germinate. With further chilling, the sensitivity distribution shifts even lower, to the extent that some seeds
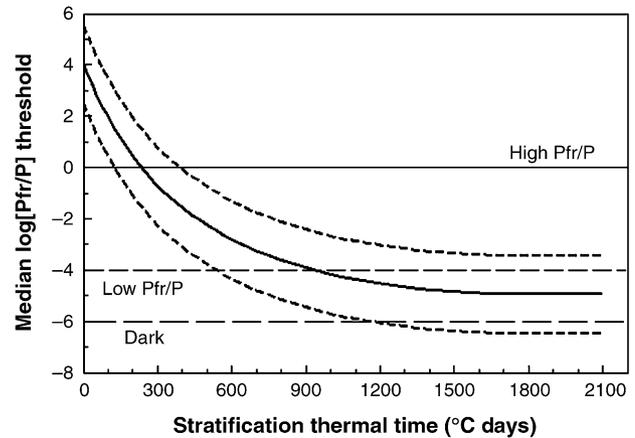

Fig. 3 Theoretical change in sensitivity to Pfr/P ratio as a function of stratification thermal time. As the sensitivity of the seed population to light increases with chilling time, the median threshold shifts to lower Pfr/P ratios (solid curve). The dashed lines indicate one standard deviation around the median to represent the variation among seeds in their thresholds. The horizontal lines correspond to different Pfr/P ratios. The fraction of the seed population that is below these horizontal lines (i.e. has a sensitivity threshold lower than the Pfr/P ratio established by the light conditions) corresponds to the percentage that can germinate at each light level.

can germinate in the dark and the majority of seeds germinate in the light. The distribution of sensitivities among seeds in the population automatically accounts for the sigmoidal shape of the response curves. For any given light level (Pfr/P ratio), as the sensitivity threshold distribution shifts to lower values with thermal chilling time, the sigmoidal increase in germination response is automatically generated (curves in Fig. 1). Thus, to characterize the effects of chilling on the response to light, one needs only a single relationship between the accumulated stratification chilling time and the decrease in median threshold Pfr/P ratio (Fig. 3), along with the variation in light sensitivity within the seed population (the standard deviation of the frequency distribution). The smooth curve shown in Fig. 3 and the log Pfr/P axis of Fig. 2 may not be strictly correct, as germination responses to light are generally biphasic, corresponding to the VLFR and LFR response ranges (e.g. VanDerWoude, 1985). Thus, there may be more of a quantum change in light sensitivity rather than the quantitative change illustrated here. Nonetheless, the general concept of increasing fractions of the seed population becoming more sensitive to light with thermal chilling time can be adapted to different sensitivity scales.

Perspectives

The case illustrated here by the work of Batlla and Benech-Arnold and those reviewed above show that threshold models for different environmental stimuli can be combined for greater explanatory power. In the example here, the

concept of stratification thermal time allowed the dormancy loss kinetics at different chilling temperatures to be conveniently described on a single thermal time scale. By further characterizing the change in light sensitivity with a second threshold distribution that can shift in response to accumulated stratification thermal time (Fig. 2), the response of the entire seed population to any light level after any stratification temperature and duration might be readily modeled using only a few parameters (Figs 1 and 3). Further, as has been argued previously (Bradford, 1995, 2002; Allen & Meyer, 1998), the ability of these models to closely match actual seed behavior suggests that they have biological significance, rather than merely empirical utility. Understanding seed dormancy and its alleviation by environmental signals is equivalent to understanding the physiological, biochemical and molecular bases of sensitivity distributions and how these are shifted in response to both external and internal signals. By combining quantitative mathematical models that can characterize seed dormancy states with modern genetic and molecular techniques such as quantitative trait locus identification (Alonso-Blanco *et al.*, 2003) and microarray analyses of gene expression responses to environmental signals (Yamauchi *et al.*, 2004), we can envision a path to deciphering how seed populations make life and death decisions about when or whether to germinate.

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Understanding a flammable planet – climate, fire and global vegetation patterns

The extraordinary intellectual achievement of the 19th century German botanist Andreas Schimper was his book *Plant-Geography upon a Physiological Basis* (Schimper, 1903). Through sheer force of imagination and by drawing on numerous written observations from around the world, he described the correspondence between global climate and vegetation zones. Such 19th century global ecological syntheses were superseded in the 20th century because attention was directed to specific questions using the hypothetico-deductive approach. However, growing concern over global environmental change and the advent of powerful space-age and computer technologies has seen the pendulum swing away from narrowly focused analyses back towards global synthesis.