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# A simulation model for seasonal changes in dormancy and germination of weed seeds

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## Abstract

A model has been developed to simulate the annual dormancy cycle of seeds of light-requiring species in the seed bank and the germination of exhumed seeds after irradiation. Simulation of dormancy and germination is based on a physiological model concerning the action of phytochrome in the seed. Dormancy is related to the amount of a hypothetical phytochrome receptor, which fluctuates in an annual pattern. Relief of dormancy is equivalent to an increase in the amount of receptor, and induction of dormancy is equivalent to a decrease in the amount of receptor. Annual changes in temperature are the driving force for annual changes in the amount of phytochrome receptor in seeds that are buried in the seed bank. From the average amount of phytochrome receptor in the seeds of a population, the model calculates the germination percentage that is reached when a seed sample from the population is exhumed, irradiated and incubated at a given temperature in darkness. In the model, relief of dormancy results in a widening of the range of temperatures over which germination can occur, and induction of dormancy results in a narrowing of this range. Model parameters were estimated by fitting the model to data from a burial experiment with seeds of *Polygonum persicaria* L., *Chenopodium album* L. and *Spergula arvensis* L. At regular time intervals during 3 years, subsamples of these seeds were exhumed and tested for germination in the laboratory. The simulation model gave a good description of the observed cyclic changes in germinability of exhumed seeds.

**Keywords: *Chenopodium album*, dormancy pattern, germination, *Polygonum persicaria*, simulation model, *Spergula arvensis*, weed seeds**

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## Introduction

Viable seeds can be dormant when their germination is inhibited by a physiological internal block, so that they cannot germinate in an otherwise favourable environment (Bewley and Black, 1982). Dormancy may be partial, in that it curtails the range of environmental conditions in which germination is possible, but does not block germination completely. Seeds in persistent seed banks are often subject to annual cycles in the intensity of dormancy (Karssen, 1982; Baskin and Baskin, 1985). Seed dormancy is regulated by temperature (Totterdell and Roberts, 1979; Bouwmeester and Karssen, 1992). In summer annuals, for example, low winter temperatures release seed dormancy and high summer temperatures induce seed dormancy.

Quantification of seasonal changes in dormancy of buried weed seeds may be an important step towards understanding and eventual prediction of seasonal emergence patterns of weeds. Existing simulation models (e.g. Spitters, 1989; Bouwmeester and Karssen, 1992, 1993a, b, c) use descriptive approaches to quantify seasonal changes in dormancy. These simulation models are based on an ecophysiological conceptual model of seed dormancy, in which the degree of dormancy is expressed as the width of the temperature range over which seeds are able to germinate. Seeds that are non-dormant germinate over a wide range of temperatures. When dormancy is induced, the temperature range over which the seeds can germinate becomes narrower, until full dormancy is reached and germination cannot take place at any temperature (Vegis, 1964; Karssen, 1982). Seasonal patterns in dormancy of buried seeds are reflected in seasonal changes in the width of the temperature range suited for germination. Germination in the field is restricted to the period when the field temperature overlaps this range. Spitters (1989) used a fixed relationship between the calendar date and the temperature range over which seeds are able to germinate. With help of this

relationship, he simulated the seasonal patterns of field germination in *Ambrosia artemisiifolia* and *Lamium amplexicaule*. Bouwmeester and Karssen (1992, 1993a, b, c) developed a descriptive model of the seasonal changes in dormancy of four weedy species (*Polygonum persicaria*, *Chenopodium album*, *Spergula arvensis* and *Sisymbrium officinale*). In their model, dormancy patterns result from the simultaneous action of a dormancy-breaking and a dormancy-inducing factor, both of which are regulated by soil temperature. The dormancy-breaking factor is the cold sum, calculated as the period spent below a critical border temperature; the dormancy-inducing factor is the heat sum, calculated by accumulating the temperature during burial. A quadratic regression function related germination of exhumed seed samples to cold and heat sum, germination temperature, the presence or absence of nitrate and the temperature during a period prior to exhumation.

Spitters (1989) stated that forecasting seedling flushes could be improved by introducing more causality in his simulation model. He claimed that this may be achieved by storing the degree of dormancy as an integral, the value of which changes in time according to rates of induction and relief of dormancy. These rates depend on the factors controlling dormancy. Bouwmeester and Karssen (1992) stated that knowledge of the physiological processes responsible for the changes in dormancy should lead to a more mechanistic approach of the simulation of dormancy patterns.

Recently, a descriptive model of dormancy cycling in seeds was hypothesized (Hilhorst, 1993, 1998; see also Derkx and Karssen, 1993; Hilhorst *et al*., 1996), which may be used in developing a quantitative model for dormancy patterns. In the model it is assumed that alterations in properties of cellular membranes are involved in the regulation of dormancy (Hilhorst, 1998). The main reasons for this assumption are that (1) membranes have been suggested to be the primary target for temperature perception at the cellular level, and temperature plays a decisive role in the regulation of dormancy; and (2) a number of factors affecting membranes (such as high temperatures and several chemical compounds) are also known to affect dormancy and germination. The hypothetical model was also built on the evidence that changes in dormancy of seeds of *Sisymbrium officinale* and *Arabidopsis thaliana* coincided with changes in sensitivity or responsiveness to naturally occurring factors that stimulate germination, such as light and nitrate (Derkx and Karssen, 1993; Hilhorst, 1998). The model is considered to apply to a group of temperate weed species, and here we describe it for a summer annual weed species (Fig. 1). The initial state of the membrane is that of a dormant, imbibed seed at low temperature (1). Breaking of dormancy at low temperatures implies synthesis of a phytochrome receptor protein $X_a$ (2). Increase of the temperature increases membrane fluidity, which makes lateral movement of the receptor possible (3). Nitrate activates the exposed receptor (4). By irradiation with red light Pr is transformed to Pfr, which binds to the activated receptor (5). The presence of the $X_a$–Pfr complex triggers biosynthesis of gibberellins (GA) (6) and enhances the sensitivity of receptors to GA (7). Binding of GA to its receptors (8) induces germination. High summer temperatures cause degradation of the phytochrome receptor protein ($X_a$) and thus induce dormancy (1).

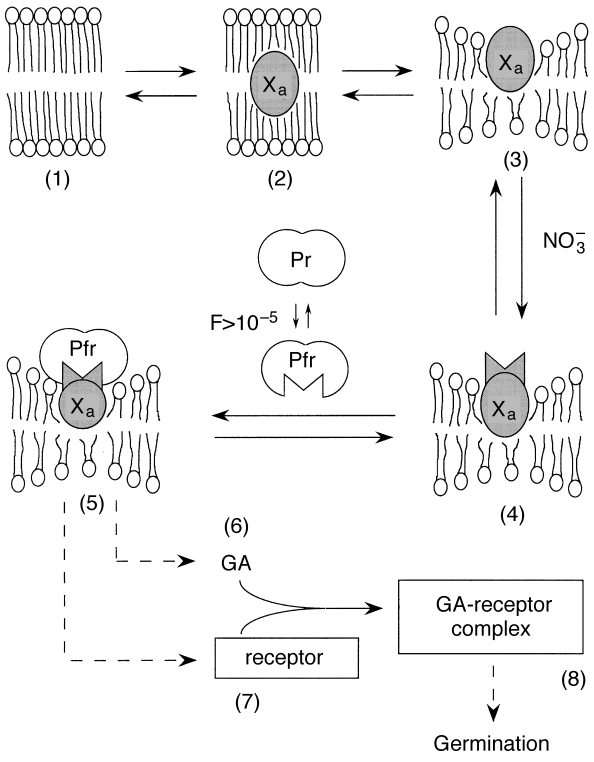


**Figure 1.** Model for breakage and induction of dormancy, and stimulation of germination in a light-requiring summer annual. The initial state of the membrane is that of a dormant, imbibed seed at low temperature (1). Breaking of dormancy at low temperatures implies synthesis of a phytochrome receptor protein, $X_a$ (2). Increased temperature increases membrane fluidity, which makes lateral movement of the receptor possible (3). Nitrate activates the exposed receptor (4). Irradiation by red light with a fluence, F, higher than $10^{-5}$ mol $m^{-2}$ transforms Pr into Pfr. Pfr binds to the activated receptor (5). The presence of the $X_a$–Pfr complex triggers biosynthesis of gibberellins (GA) (6) and enhances the sensitivity of receptors to GA (7). Binding of GA to its receptors (8) induces germination. (After Hilhorst, 1993).

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Both of these conceptual dormancy models have their specific merits. The ecophysiological concept, in which dormancy is associated with the width of the temperature range for germination, can be related easily to weed seed germination in the field. The biochemical concept, in which dormancy is associated with the amount of a phytochrome receptor, provides a possible mechanism for changes in dormancy at a molecular level. The quantitative model described in this paper is based on an integration of both concepts. It allows for prediction of dormancy and germination on the basis of environmental factors.

The aim of this study was to quantify the relationships in the hypothesized biochemical model by Hilhorst (1993, 1998), using data from a burial experiment with seeds of three arable weed species to test whether seasonal changes in the germination-permissive temperature range can be explained by the model.

## Materials and methods

### *Description of the simulation model*

The simulation model uses the amount of the membrane-located phytochrome receptor protein that was hypothesized by Hilhorst (1993, 1998) as a measure for the degree of dormancy. The dormancy model simulates seasonal changes in the amount of the receptor in buried seeds, driven by seasonal changes in temperature. As yet, the hypothetical receptor cannot be measured. In experiments it can only be made visible indirectly, by conducting germination tests over a range of conditions. The dormancy model in this study is therefore coupled to a germination model. From the amount of phytochrome receptor, the germination model calculates germination percentages of seed samples that are irradiated with red light and tested for germination in the presence of nitrate over a range of temperatures.

The structure of the simulation model follows the conceptual model in Fig. 1. The dormancy part of the model is depicted in Fig. 1, (1) and (2), and the germination part of the model in Fig. 1, (3) through (8). The variables and parameters used in the model are listed in Tables 1 and 2. In the regulation of seasonal changes in dormancy and germination, temperature plays a dual role (Bouwmeester and Karssen, 1992). Field temperature determines the seasonal changes in dormancy of buried seeds, while the temperature at which germination is tested influences the expression of the dormancy pattern. In the model, the dual role of temperature is reflected in the use of Tb (burial temperature) in the simulation of dormancy, and Tt (test temperature) in the simulation of germination. Tb represents the daily average temperature in the field, and Tt the constant temperature in the germination test. In the next subsections, the different parts of the simulation model will be described in detail using Fig. 1 as a guide.

**Table 1.** Abbreviations used in the model

| | |
|---|---|
| $I$ | Rate of dormancy induction |
| $R$ | Rate of dormancy release |
| Tb | Temperature during burial |
| Tt | Temperature in the germination test |
| $X_a$ | Available receptor |
| $X_a$–Pfr | Phytochrome–receptor complex |

#### *Dormancy cycle [Fig. 1, (1) and (2)]*

In accordance with the biochemical model described by Hilhorst (1998), the properties of the membrane in which the receptor is located determine the availability of the membrane-bound phytochrome receptor protein. The degree of dormancy is inversely related to the total amount of available receptor $X_a$. The absolute amount of available receptor cannot be quantified. In the model only relative changes in the amount of $X_a$ are important, and it is therefore a dimensionless quantity.

The temperature relationships for the release and induction of dormancy are based on those suggested for *P. persicaria*, *C. album* and *S. arvensis* by Bouwmeester (1990). Dormancy release has a species-specific temperature optimum, ranging from 0°C to 15°C. The induction of dormancy increases linearly with increasing temperature. We assumed that, as far as the processes included in the model are concerned, release of primary and secondary dormancy are identical and we did not distinguish between them.

#### *Release of dormancy [Fig. 1, from (1) to (2)]*

During periods of dormancy release, the rate at which the amount of available receptor increases, $dX_a/dt$, is called the rate of release of dormancy, $R$ ($day^{-1}$). Values of $R$ are always greater than or equal to zero. In the model, $R$ reaches its maximum value at the optimum temperature for dormancy release and decreases linearly to zero at both sides of the temperature optimum:

$$R = 0 \text{ if } Tb < TR_{min} \quad (1a)$$

$$R = (Tb - TR_{min})(R_{max}/(TR_{opt} - TR_{min})) \text{ if } TR_{min} < Tb < TR_{opt} \quad (1b)$$

$$R = (TR_{max} - Tb)(R_{max}/(TR_{max} - TR_{opt})) \text{ if } TR_{opt} < Tb < TR_{max} \quad (1c)$$

$$R = 0 \text{ if } Tb > TR_{max} \quad (1d)$$

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**Table 2.** Definitions of the model parameters and their estimated values

| Parameter | Description (dimension in parentheses) | *Polygonum persicaria* | *Chenopodium album* | *Spergula arvensis* |
|---|---|---|---|---|
| Dormancy | | | | |
| $X_i$ | Initial amount of $X_a$ (dimensionless) | 0.109 | 0.175 | 0.170 |
| $X_{min}$ | Lower limit of $X_a$ (dimensionless) | 0.000 | 0.159 | 0.151 |
| $X_{max}$ | Upper limit of $X_a$ (dimensionless) | 1 | 1 | 1 |
| $TR_{min}$ | Minimum temperature for the release of dormancy (°C) | 0.5 | 0.3 | 4.1 |
| $TR_{opt}$ | Optimum temperature for the release of dormancy (°C) | 1.8 | 9.0 | 14.4 |
| $TR_{max}$ | Maximum temperature for the release of dormancy (°C) | 15.5 | 16.6 | 21.2 |
| $R_{max}$ | Maximal rate of release of dormancy ($day^{-1}$) | 0.0239 | 0.0117 | 0.0184 |
| $TI_{min}$ | Minimum temperature for the induction of dormancy (°C) | 8.1 | 8.9 | 2.4 |
| $a$ | Proportionality factor between the temperature and the rate of induction of dormancy ($day^{-1}$ °$C^{-1}$) | –0.00109 | –0.00084 | – |
| $TI_{opt}$ | Optimum temperature for the induction of dormancy (°C) | – | – | 10.6 |
| $TI_{max}$ | Maximum temperature for the induction of dormancy (°C) | – | – | 20.9 |
| $I_{max}$ | Maximal rate of induction of dormancy ($day^{-1}$) | – | – | –0.00869 |
| Germination | | | | |
| $TE_{min}$ | Lower temperature limit for $X_a$ exposure (°C) | 1.7 | 3.1 | 0.2 |
| $TE_{max}$ | Temperature above which the total amount of $X_a$ is exposed (°C) | 37.1 | 15.3 | 6.2 |
| $k_d(20)$ | Rate constant of dark reversion at 20°C ($h^{-1}$) | 0.0394 | 0.0638 | 0.0527 |
| $Q_{10,dr}$ | $Q_{10}$ of dark reversion (dimensionless) | 5.0 | 9.2 | 3.6 |
| $[X_a–Pfr]_{thr}$ | Threshold for the activity of $X_a$–Pfr (dimensionless) | 0.111 | 0.209 | 0.157 |
| *et*(20) | Average escape time at 20°C (h) | 10 | 10 | 10 |
| $Q_{10,et}$ | $Q_{10}$ of escape (dimensionless) | 4 | 4 | 4 |

A dash indicates that the parameter is not used for the species in question. Values for *et*(20) and $Q_{10,et}$ were fixed before the calibration.

where Tb is the field temperature (°C), $TR_{min}$, $TR_{opt}$ and $TR_{max}$ are the minimum, optimum and maximum temperature for the release of dormancy (°C), and $R_{max}$ is the maximum rate of dormancy release ($day^{-1}$).

### *Induction of dormancy [Fig. 1, from (2) to (1)]*

During periods of dormancy induction, the rate at which the amount of available receptor decreases, $dX_a/dt$, is called the rate of induction of dormancy, $I$ ($day^{-1}$). Values of $I$ are always less than or equal to zero. In the model the temperature dependence of $I$ is described as follows:

$$I = 0 \text{ if } Tb < TI_{min} \quad (2a)$$

$$I = a\,(Tb - TI_{min}) \text{ if } Tb > TI_{min} \quad (2b)$$

where Tb is the field temperature (°C), $TI_{min}$ is the minimum temperature for the induction of dormancy (°C) and $a$ is the slope of the curve ($day^{-1}$ °$C^{-1}$).

Experiments with *Rumex* spp. and *P. persicaria* showed that even at constant temperatures a cyclic change in germination capacity may occur (Totterdell and Roberts, 1979; Bouwmeester and Karssen, 1992). We interpreted this by assuming that the dormancy cycle can reverse from release to induction and vice versa without a change in the temperature conditions. Totterdell and Roberts (1979), however, explained their results by assuming simultaneous and independent processes of relief and induction of dormancy. Their concept was elaborated by Jones *et al*. (1997) and by Kebreab and Murdoch (1999) to describe loss and induction of dormancy in seeds of *Picea sitchensis* and *Orobanche* spp. We reasoned, however, that in order to describe multiple dormancy cycles, the most straightforward concept would be an alternation of dormancy release and induction. In our model it is assumed that an internal switch causes the reversal from release to induction and from induction to release. The dormancy cycle of a seed shifts from induction to release when $X_a$ equals its lower limit, $X_{min}$, and from release to induction when $X_a$ equals its upper limit, $X_{max}$. The internal switch determines whether the prevailing temperature has a dormancy-relieving or a dormancy-inducing effect, and periods of dormancy release and dormancy induction are strictly separated.

Output from this part of the model is the amount of $X_a$ in the average seed in the population. The structure of the model complies with the suggestion by Spitters (1989) of storing the degree of dormancy in an integral (i.e. $X_a$) that changes according to rates of induction and relief of dormancy. Among the seeds in the population, there is a variation in the degree of dormancy. In the model this variation is simulated by a random generator drawing from a normal distribution of $X_a$ around the simulated average.

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*Germination [Fig. 1, (3) to (8)]*

The processes that determine the action of phytochrome in the seed constitute the germination part of the model (cf. Vleeshouwers *et al*., 1995). The phytochromes are a family of photoreceptors that are involved in the reaction of seeds to different light stimuli (Shinomura, 1997; Casal and Sánchez, 1998; Casal *et al*., 1998). Phytochrome A (phyA) mediates the very-low-fluence response (VLFR), and phytochrome B (phyB) the low-fluence response (LFR). The germination data that will be simulated by the model are induced by a saturating pulse of red light. It seems obvious, therefore, that the model should concentrate on phyB. However, the other phytochromes may also play a role (Casal and Sánchez, 1998): (1) in some cases a red pulse triggers both a VLFR and a LFR, implying that reversion by a subsequent far-red pulse is only partial; the response mediated by phyB is additional to that mediated by phyA; (2) there may be an interaction between phyA and phyB; and (3) the LFR is possibly also mediated by phyD. The phytochrome reactions assumed in the model may therefore apply to the phytochrome dominating the process, possibly phyB, or may constitute the resultant of different types. The model does not intend to cover the diversity in phytochrome processes, but rather investigates whether an inherently approximate quantification of phytochrome reactions may be a first step in modelling the physiological processes involved.

The germination process of light-requiring seeds is triggered by red irradiation, converting the physiologically inactive form of phytochrome (Pr) to its active form (Pfr) (Bewley and Black, 1982). The germination process has to be supported by the presence of Pfr for a certain period, the escape time, but ceases if the lifetime of Pfr is shorter than the escape time. Both the rate at which the processes that have to be supported by Pfr proceed (determining the escape time) and the rate at which Pfr reverts to Pr in darkness are temperature dependent (Bewley and Black, 1982). Photoconversion itself is independent of temperature (Nyman, 1963). A flash of light that produces some Pfr thus starts off a race between action and disappearance of Pfr within seeds. The outcome of this race (i.e. the final germination percentage) can be manipulated by choice of temperature (Borthwick, 1972). In our model the idea put forward by Borthwick (1972) is elaborated by introducing seed dormancy (i.e. the amount of $X_a$) as an additional factor determining the outcome of the race.

The processes denoted (3) to (8) in Fig. 1 represent the germination process in a seed with a certain amount of $X_a$ when it is irradiated by red light.

*Exposure of receptor [Fig. 1, (3)]*

In order to be able to bind Pfr, the receptor should be exposed at the outside of the membrane. Hilhorst (1993, 1998) hypothesized that membrane fluidity increases with increasing temperature, which makes lateral movement of the receptor possible. The model assumes that the fraction of $X_a$ that is exposed, $f_{exp}$, increases linearly with temperature:

$$f_{exp} = 0 \text{ if } Tt < TE_{min} \tag{3a}$$

$$f_{exp} = (Tt - TE_{min})/(TE_{max} - TE_{min}) \text{ if } TE_{min} < Tt < TE_{max} \tag{3b}$$

$$f_{exp} = 1 \text{ if } Tt > TE_{max} \tag{3c}$$

where Tt is the temperature in the germination test (°C), $TE_{min}$ is the lower temperature limit for $X_a$ exposure (°C) and $TE_{max}$ is the temperature above which the total amount of available receptor is exposed (°C).

*Binding of Pfr to the receptor [Fig. 1, (4) and (5)]*

The exposed receptor is activated by nitrate, enabling it to bind Pfr [Fig. 1, (4)] (Hilhorst, 1993, 1998). From data of Hilhorst (1990), it can be inferred that after red irradiation at the intensity used in our experiments all receptors are occupied. Thus, through irradiation of the seeds, all exposed (and activated) receptors are occupied, and an amount of phytochrome–receptor complex, $X_a$–Pfr [Fig. 1, (5)], is formed, equalling $f_{exp} \times X_a$.

*Dark reversion [Fig. 1, from (5) to (4)]*

The simulation model attributes all Pfr decrease after the red irradiation to dark reversion. There is no clear evidence that Pfr destruction plays a role in seeds (Bewley and Black, 1982), which is supported by an *in vivo* study of phytochrome in seeds of *Pinus nigra* (Orlandini and Malcoste, 1972). The *in vivo* kinetics of dark reversion can be described by an exponential decrease of the amount of Pfr (Orlandini and Malcoste, 1972; Schäfer and Schmidt, 1974). In the model, it was assumed that the decrease in $X_a$–Pfr after irradiation has a similar time course:

$$[X_a\text{–Pfr}]_t = [X_a\text{–Pfr}]_0 \times \exp(-k_d\, t), \tag{4}$$

where $[X_a\text{–Pfr}]_t$ is the amount of occupied receptor at time t, $[X_a\text{–Pfr}]_0$ is the amount of occupied receptor immediately after irradiation ($= f_{exp} \times X_a$), and $k_d$ is the rate constant of dark reversion ($h^{-1}$).

The rate of dark reversion strongly increases with increasing temperature (Taylorson and Hendricks, 1969). In the model this temperature dependence is quantified by $Q_{10,dr}$, and all rates of dark reversion are related to the rate of dark reversion at 20°C. The

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$k_d$ at the test temperature Tt (°C), $k_d$(Tt), is calculated as:

$$k_d(Tt) = k_d(20) / (Q_{10,dr}^{((20-Tt)/10)}), \quad (5)$$

where $k_d$(20) is the $k_d$ at 20°C in $h^{-1}$.

### *Period of $X_a$–Pfr action*

Data from Karssen (1970) for *Chenopodium album* show that seeds need a threshold concentration of Pfr to stimulate germination. In the model this is interpreted as a threshold amount of $X_a$–Pfr, denoted $[X_a\text{–Pfr}]_{thr}$, because only receptor-bound Pfr promotes germination. With help of equation (4), it can be calculated that the period in which $X_a$–Pfr promotes germination after a red light pulse at the test temperature, *pt*(Tt) in h, is equal to

$$pt(Tt) = (\ln([X_a\text{–Pfr}]_0 / [X_a\text{–Pfr}]_{thr})) / k_d(Tt). \quad (6)$$

### *Escape time*

In the model it is assumed that the germination process requires the presence of $X_a$–Pfr until it reaches a stage from where it can proceed independently of the presence of $X_a$–Pfr. At that stage the escape time has passed. Hilhorst (1993, 1998) suggested that the steps following the binding of Pfr to its receptor are synthesis of GA and activation of GA receptors. For the calculation in the model, however, it is not essential what part of the germination process is dependent on $X_a$–Pfr.

Escape times decrease with increasing temperature (Bewley and Black, 1982). In the model this temperature dependence of the escape time is quantified by $Q_{10,et}$, and all escape times are related to the escape time at 20°C. The average escape time, *et*(Tt) in h, at the test temperature Tt (°C) is calculated as:

$$et(Tt) = et(20) \times (Q_{10,et}^{((20-Tt)/10)}), \quad (7)$$

where *et*(20) is the average escape time at 20°C in h.

Borthwick *et al*. (1954) showed the distribution of escape times in a seed population of *Lactuca sativa* at 20°C. In accordance with these data, the model assumes a normal distribution of escape times within a population. A random generator drawing from this distribution simulates the variation in escape times in a seed population around the average that is calculated by the model.

### *Visible germination*

The model simulates the germination percentage by counting the number of seeds for which the period of Pfr action, *pt*(Tt) [equation (6)] exceeds the escape time *et*(Tt) [equation (7)]. The time of visible germination (protrusion of the rootlet) is not calculated. For this purpose the model could easily be extended with a calculation based on a temperature sum (Benech-Arnold and Sánchez, 1995).

Overall, the model input consists of the field temperature in the period when the seeds are buried (the driving variable for the dormancy model) and the temperatures used in the germination tests carried out after exhumation of the seeds (the driving variable for the germination model). All seeds were irradiated with red light and incubated in $KNO_3$, so that light and nitrate were not limiting and germination depended only on the test temperature. Outputs of the model are the germination percentages in the tests.

## *Parameterization of the model*

Specific data to parameterize the above-mentioned equations for *Polygonum persicaria*, *Chenopodium album* and *Spergula arvensis* are lacking. Therefore, parameters for the model relationships were estimated by calibrating the model with experimental germination data for *P. persicaria* (Bouwmeester and Karssen, 1992), *C. album* (Bouwmeester and Karssen, 1993a) and *S. arvensis* (Bouwmeester and Karssen, 1993b). In the experiments, which started in December 1986, seed lots of *P. persicaria*, *C. album* and *S. arvensis* were buried in the field at 10 cm in loamy sand. At regular intervals during three consecutive years, subsamples of these seeds were exhumed. They were divided into smaller portions and incubated in Petri dishes in 50 mM $KNO_3$. Seeds were irradiated for 15 minutes with red light, and germination was assessed in darkness at 10, 20 and 30°C for *P. persicaria* and *C. album*, and at 2, 15 and 30°C for *S. arvensis*. Subsamples were exhumed and tested for germination at 19 times during the experiments. In the calibration, parameter values were determined for which the simulated results fitted best to the observed data. The Price algorithm contained in the FSEOPT program developed by Stol *et al*. (1992) was used in the calibration procedure. For the burial temperature (Tb) the daily average temperature at a depth of 10 cm in bare soil, measured at the meteorological station 'Haarweg' in Wageningen, was used. A detailed description of the calibration method can be found in Vleeshouwers (1997).

Three species parameters were not estimated in the calibration, but were parameterized with a pre-set value that was the same for all three species, viz. $X_{max}$, *et*(20) and $Q_{10,et}$. This was done for the following reasons.

(1) The amount of receptor is measured on a relative scale. The absolute quantities of receptor that are present in seeds are not known, and in the model only relative differences are important. Since the absolute amounts of $X_a$ and $X_{max}$ do not affect the calculations, we fixed the amount of $X_a$ at which reversal from dormancy release to induction occurs ($X_{max}$) at an arbitrary value of 1. In the

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model this implies that the amount of $X_a$ is expressed as a fraction of the amount present at reversal.

(2) The model calculates whether or not the seed will germinate by comparing the period of $X_a$–Pfr action and the escape time. In this calculation it is only important which of these periods is longer. The period of $X_a$–Pfr action is determined by the parameters $k_d(20)$ and $Q_{10,dr}$. The escape time is determined by the parameters *et*(20) and $Q_{10,et}$. Since only the ratio between these periods is important, the parameters estimated in the calibration are actually the ratios $(k_d(20))^{-1}/et(20)$ and $Q_{10,dr}/Q_{10,et}$. To be able to compare the estimated parameter values for $k_d(20)$ and $Q_{10,dr}$ to data from literature, the value of *et*(20) was fixed at 10 h, as reported by Borthwick *et al.* (1954) for *Lactuca sativa*, and the value of $Q_{10,et}$ was fixed at 4, as was reported by Taylorson and Hendricks (1969) for *Amaranthus retroflexus*.

In all three species, the standard deviation of the distribution of $X_a$ in the model was set to 0.1. Using a pre-set value for the standard deviation was necessary for technical reasons. The use of a non-fixed value in the calibration would interfere with finding the best parameter set. The standard deviation of the distribution of escape times was estimated at 0.2 times the average escape time, which was derived from data of Borthwick *et al*. (1954). Since calibration was done with three summer annuals and the simulation started in December, the model was initialized in a state of dormancy release.

To enable comparison with other models, a coefficient *C* is introduced that calculates the percentage variance accounted for by the model,

$$C = 1 - \frac{\sum (y_{obs} - y_{sim})^2}{\sum (y_{obs} - \bar{y}_{obs})^2} \quad (8)$$

where $y_{obs}$ is the observed and $y_{sim}$ is the simulated value.

### *Evaluation of the model*

The model was evaluated with help of field emergence patterns of *P. persicaria* and *C. album* observed in Lelystad, The Netherlands (Van den Brand, 1986). The emergence patterns were observed in separate plots with a diameter of 50 cm in which seeds of the weed species were sown in 1978. In subsequent years, seed input was from plants that matured within the plots. Once a year, in autumn, the seeds were mixed through the soil by tillage to a depth of 20 cm. Each year, the plots were lightly fertilized. Observation of seedling emergence in the plots extended from 1979 until 1983. The simulations by the model were based on the daily minimum and maximum air temperatures at 1.50 m, measured by the meteorological station at Swifterbant, 7 km from the experimental site.

## Results and discussion

Preliminary results of the simulation model showed that both *C. album* and *S. arvensis* deviated in one species-specific aspect from the basic model structure for the dormancy cycle. *C. album* differs from the two other species in the study in that the dormancy cycle does not only reverse from induction to release of dormancy when the amount of available receptor reaches its minimum, but also when the field temperature reaches $TI_{min}$. The criteria for reversal used in the model are that either in autumn the average temperature over the previous 10 days drops beneath $TI_{min}$, or that the amount of $X_a$ reaches $X_{min}$. *S. arvensis* differs from the two other species in the study in that above a certain optimum temperature, *I* decreases with increasing temperature [cf. equation (2)].

$$I = 0 \text{ if } Tb < TI_{min} \quad (9a)$$

$$I = (Tb - TI_{min})(I_{max}/(TI_{opt} - TI_{min})) \text{ if } TI_{min} < Tb < TI_{opt} \quad (9b)$$

$$I = (TI_{max} - Tb)(I_{max}/(TI_{max} - TI_{opt})) \text{ if } TI_{opt} < Tb < TI_{max} \quad (9c)$$

$$I = 0 \text{ if } Tb > TI_{max} \quad (9d)$$

where Tb is the field temperature (°C), $TI_{min}$, $TI_{opt}$ and $TI_{max}$ are the minimum, optimum and maximum temperature for the induction of dormancy (°C), and $I_{max}$ is the maximum rate of dormancy induction ($day^{-1}$).

### *Model performance*

Optimum parameter values for each species are shown in Table 2. The results of the exhumation experiments with *P. persicaria*, *C. album* and *S. arvensis* are shown in Fig. 2, together with the simulated curves resulting from the optimum parameter set in the calibration. The experimental and simulated curves show that germination of exhumed seeds rose and fell in an annual pattern. In general, the dormancy changes were fitted well. Fluctuations in the simulated germination percentages on a smaller time scale reflect the random variation in the population and not short-term oscillations in dormancy.

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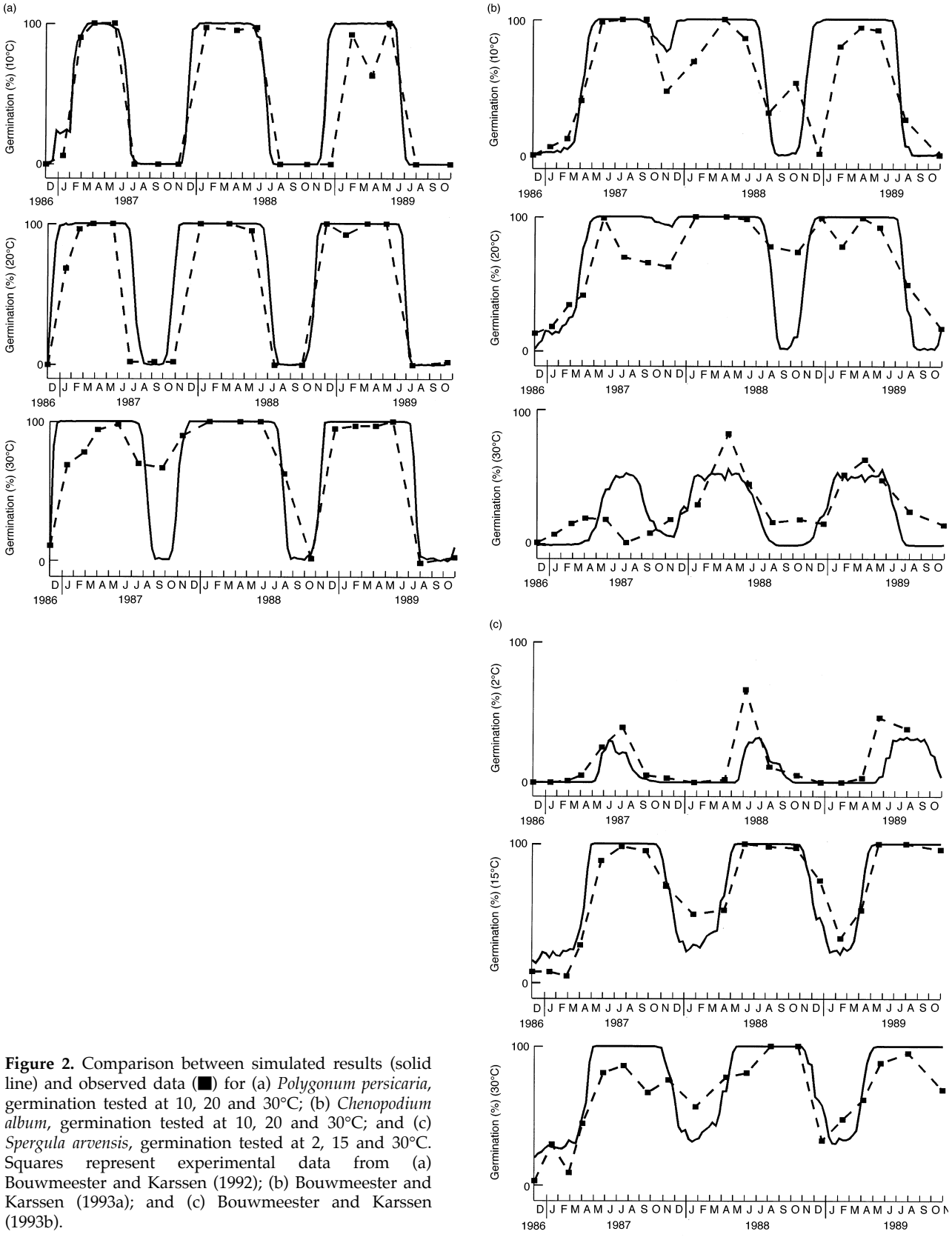


**Figure 2.** Comparison between simulated results (solid line) and observed data (■) for (a) *Polygonum persicaria*, germination tested at 10, 20 and 30°C; (b) *Chenopodium album*, germination tested at 10, 20 and 30°C; and (c) *Spergula arvensis*, germination tested at 2, 15 and 30°C. Squares represent experimental data from (a) Bouwmeester and Karssen (1992); (b) Bouwmeester and Karssen (1993a); and (c) Bouwmeester and Karssen (1993b).

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The model was compared to the one by Bouwmeester and Karssen (1992, 1993a, b), which was fitted to the same data set, by examining values of coefficient *C* [equation (8)]. For *P. persicaria*, *C. album* and *S. arvensis*, the model gave *C* values of 0.74, 0.55 and 0.85, respectively. The model by Bouwmeester and Karssen (1992, 1993a, b) gave *C* values of 0.69, 0.56 and 0.78, respectively. It should be noted that neither of the models has been calibrated with a maximal value of *C* as a criterion. The numbers of parameters included in both models are approximately the same. It appears that the most important improvement of the present model compared to the one by Bouwmeester and Karssen (1992, 1993a, b) is not the higher percentage variance accounted for, but the concrete formulation of the parameters in the model in terms of physiological seed characteristics, which may provoke new research questions. Furthermore, we consider it an advantage of the model that it can generate cyclic changes in dormancy under constant temperatures, as shown by Totterdell and Roberts (1979), which cannot be achieved with the model by Bouwmeester and Karssen (1992, 1993a, b).

A sensitivity analysis of the parameters in the model revealed that there were no important differences in the sensitivity of the model to the different parameters (Vleeshouwers, 1997). No key parameters can be identified that have a disproportionally strong influence on the model output.

### *Evaluation of parameter estimates*

In this study all parameters in the model were estimated by calibration. It would be a challenge for seed scientists to design experiments to determine the parameters experimentally. An evaluation of the validity of the parameter values estimated in the calibration can be made by comparison with values reported in literature. Apart from the field experiments that were used in the calibration, Bouwmeester (1990) and Bouwmeester and Karssen (1992, 1993a, b) reported a number of data on dormancy release and induction of the three species in this study from experiments under controlled conditions. In an experiment with *P. persicaria*, dormancy was relieved faster in a pretreatment at 2°C than at 6°C and 10°C, and was not relieved at all at 15°C (Bouwmeester, 1990). This agrees very well with the model, in which $TR_{min}$ was estimated at 0.5°C, $TR_{opt}$ at 1.8°C, and $TR_{max}$ at 15.5°C (Table 2). In the calibration $TI_{min}$ was estimated at 8.1°C. This estimate seems high in comparison with data by Bouwmeester and Karssen (1992), who found that induction of dormancy in *P. persicaria* also occurs at 2°C. However, their experiments also showed that induction of dormancy at 2°C and 10°C is much slower than at 15°C. Experiments with *C. album* showed that release of dormancy proceeds faster at 10°C than at 2, 6 and 15°C (Bouwmeester and Karssen, 1993a, and unpublished results). Again, this agrees well with the model, in which the maximum rate of dormancy release is reached at 9.0°C (Table 2). Induction of dormancy in *C. album* occurs at 15°C, but not at 10°C (Bouwmeester and Karssen, 1993a), which agrees well with the minimum temperature for the induction of dormancy of 8.9°C in the model. Experimental results on *S. arvensis* showed that no release of dormancy occurs at 2°C. When the temperature increases, the rate of release increases to a maximum at 15°C, and then decreases to zero at 20°C (Bouwmeester and Karssen, 1993b). These data correspond well with the model, in which the minimum, optimum and maximum temperatures for dormancy release were estimated at 4.1, 14.4, and 21.2°C, respectively (Table 2). In the experiments with *S. arvensis*, dormancy induction was maximal at 10°C, lower at 6°C and 15°C, and about zero at 2°C and 20°C. These values also agree well with the model, in which $TI_{min}$ was estimated at 2.4°C, $TI_{opt}$ at 10.6°C, and $TI_{max}$ at 20.9°C (Table 2).

The parameter $TE_{min}$ represents the theoretical minimum temperature at which germination can take place. The estimated values range from 0.2 to 3.1°C. These values are in accordance with the minimum germination temperature of so-called psychrophilic or cold-resistant weed species, ranging from 2 to 4°C (Fisyunov, 1976). Lauer (1953) reported germination of *C. album* and *S. arvensis* at 2–5°C, but the minimum germination temperature for *P. persicaria* was 20–25°C. However, *P. persicaria* still germinated in a test at 3–4°C (Vleeshouwers, unpublished data). It should be noted that the parameter $TE_{max}$ cannot be regarded as the theoretical maximum temperature for germination. The maximum temperature for germination is determined by the temperature relationships of Pfr action and Pfr disappearance. No published data are available that can be used as an estimate for $TE_{max}$.

Taylorson and Hendricks (1969) studied dark reversion and escape times in *Amaranthus retroflexus*. They roughly estimated the half-time for dark reversion at 20°C to be 1.3 days, which implies a $k_d(20)$ of 0.0222 $h^{-1}$. The model parameters range from 0.0394 $h^{-1}$ to 0.0638 $h^{-1}$, which seem to be physiologically relevant values judging from their order of magnitude. The $Q_{10,dr}$ they estimated was 16. They considered this seemingly high value not unreasonable as the interaction of a protein and a chromophore is involved. The values estimated in our model were lower (from 3.6 to 9.2). The value estimated for $[X_a–Pfr]_{thr}$ in *C. album* (0.209) lies within the range of Pfr to total phytochrome ratios found to

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promote germination of this species (Karssen, 1970), from about 0.05 to 0.4.

According to the model, the phytochrome receptor level required to induce maximal germination, defined as 99%, in *P. persicaria*, *C. album* and *S. arvensis*, amounts to 20%, 53% and 34%, respectively, of the level maximally present in the seeds. The percentages are of the same order of magnitude as for *Sisymbrium officinale* given by Hilhorst (1990), who calculated that the receptor level required to achieve full germination amounts to 40% of the maximal level.

In general, the parameters that produce a good fit between the model output and the experimental data have physiologically meaningful values when compared with independent experimental measurements reported in the literature.

### *Dormancy cycles: a comparison of the species*

The temperature dependence of the rate of dormancy release and induction for the three species is shown Fig. 3. *P. persicaria* and *C. album* only differ in the temperature optimum for dormancy release ($TR_{opt}$), which is higher for *C. album,* and in the maximal rate of dormancy release ($R_{max}$). *S. arvensis* has higher temperature requirements for dormancy release and lower temperature requirements for dormancy induction than both other species. For *S. arvensis*, the optimum temperature for the induction of dormancy is 10.6°C. *P. persicaria* and *C. album* are likely to have a temperature optimum for the induction of dormancy as well, but it is apparently so high that during the experiment it was not or seldom reached in the field at a depth of 10 cm, and therefore cannot be estimated from the available data. Dedicated laboratory experiments may be used to estimate the optimum and maximum temperatures for dormancy induction in these two species. The slope of the curve showing the increase in dormancy induction rate with increasing temperature between $TI_{min}$ and $TI_{opt}$ for *S. arvensis* equals 0.00106 $day^{-1}$ $°C^{-1}$, and this is of the same order of magnitude as parameter *a* for *P. persicaria* and *C. album*.

The model offers a basis for characterization of annuals on a continuous scale from pure winter annuals to pure summer annuals. A winter annual character coincides with a high $TR_{opt}$ and a low $TI_{opt}$. A summer annual character coincides with a low $TR_{opt}$ and a high $TI_{opt}$. For the three species in this study, the summer annual character becomes more pronounced in the order *S. arvensis*, *C. album* and *P. persicaria*.

Figure 4 shows the simulated changes in the minimum and maximum temperature required for 50% germination in 50 mM $KNO_3$ after irradiation with red light, during the period when the burial

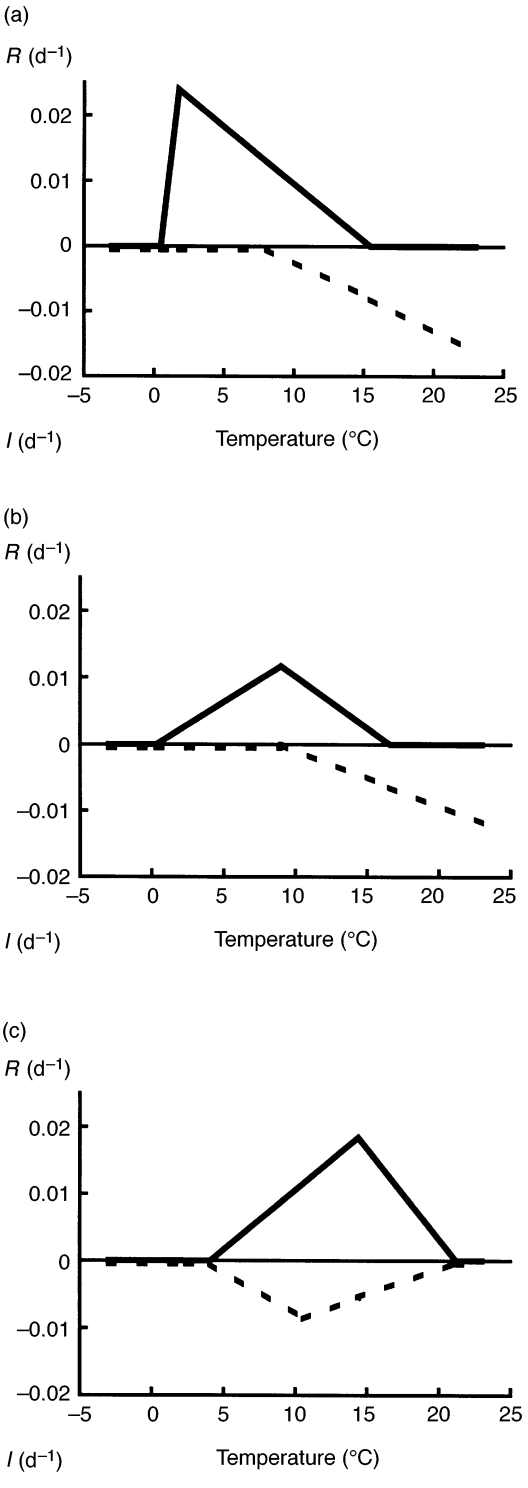


**Figure 3.** Temperature dependence of the rate of dormancy release (solid line) and induction (dashed line) in (a) *Polygonum persicaria*; (b) *Chenopodium album*; and (c) *Spergula arvensis*. Note that release and induction of dormancy occur in separate periods, thus resulting in a cyclic increase and decrease in the availability of the phytochrome receptor.

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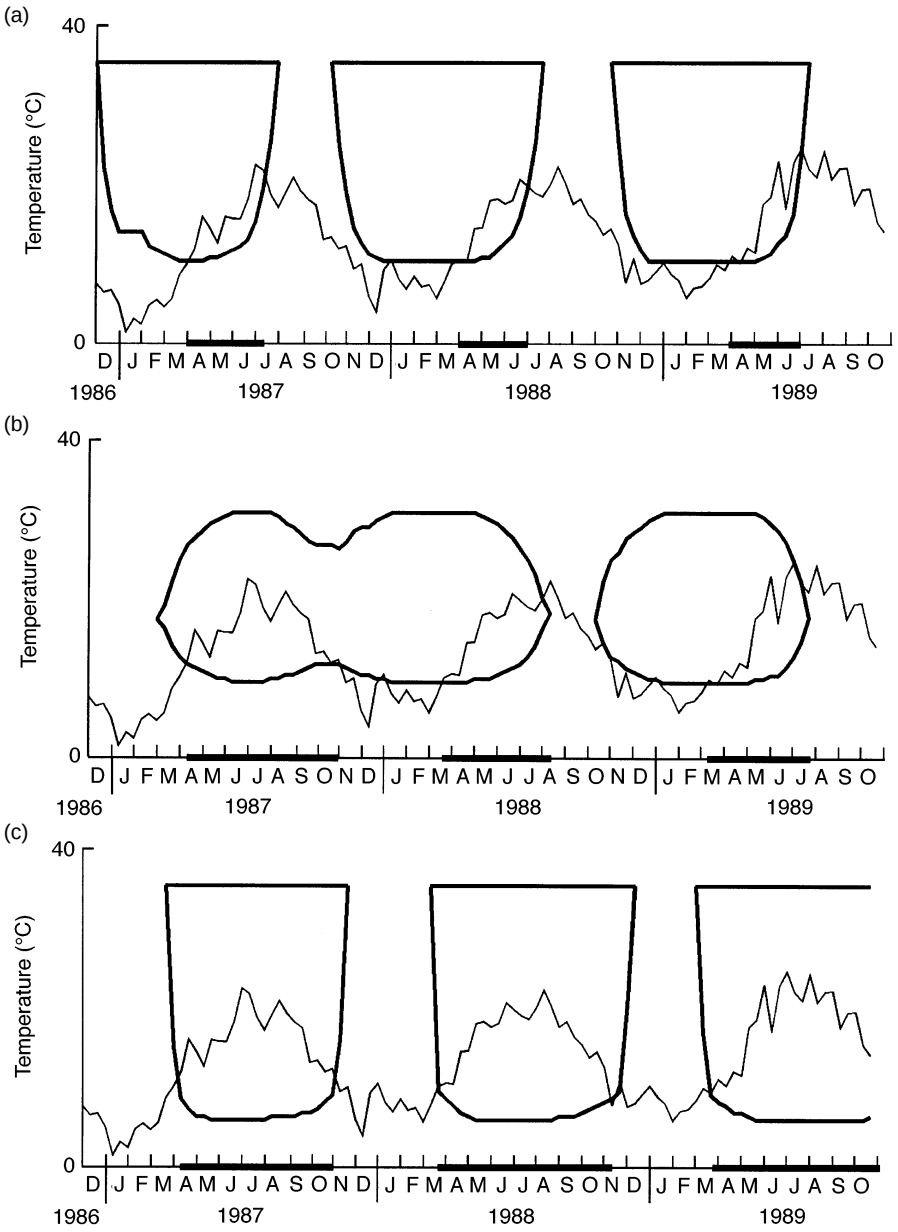


**Figure 4.** Simulated seasonal changes in the range of temperatures over which exhumed seeds germinate in (a) *Polygonum persicaria*; (b) *Chenopodium album*; and (c) *Spergula arvensis*. Thick lines represent the minimum and maximum temperature for 50% germination in 50 mM $KNO_3$ after red irradiation. The thin line indicates soil temperature at –10 cm. The bold line segments on the *x*-axis indicate periods when field and germination temperatures overlapped.

experiment was conducted. Considering the test temperatures used, extrapolation of the temperature range was restricted to the range 0–35°C. Figure 4 demonstrates that the simulation model, based on the hypothesis of Hilhorst (1993, 1998) that dormancy is related to the amount of a membrane-located phytochrome receptor, exhibits an annual widening and narrowing of the temperature range for germination and is thus compatible to the theory of Karssen (1982). The model can build a bridge between the dormancy concepts of Hilhorst (1993, 1998) and Karssen (1982).

The output of the model, as presented in Fig. 4, may be used in predicting weed germination in the field. Essentially, the experimental treatment of the seeds – consisting of exhumation, irradiation and

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germination in darkness – corresponds with the effect of soil disturbance in the field. A major difference, however, is that exposure of the weed seeds to daylight during soil cultivation may be too short to induce an effect similar to that of the saturating red light irradiation in the laboratory. Ideally, the model should not only generate germinability at a range of temperatures, but also at a range of fluences. This may be done in an empirical way, by adding a number of light dose–response curves to the model (e.g. Derkx and Karssen, 1993). To include the effect of short irradiations during soil cultivation in the simulation model, explicit incorporation of the VLFR may be required, which is not feasible at present. Another difference between the experimental treatment that is described by the model and the field situation is that seeds in the field will experience diurnal temperature fluctuations, which may enhance their germination. Additional research on the temperature dependence of the processes in the model would be required to include the stimulating effect of alternating temperatures on germination.

For all three weed species the germination period in the field (given sufficient exposure to light), depends on changes in both the minimum temperature required for germination and the prevailing soil temperature (Fig. 4). In December of the second and third year, the temperature range for germination of *P. persicaria* is maximal. However, only in March–April has the soil temperature risen such that germination in the field can occur. In *C. album* the timing of field germination depends more on the annual fluctuation in the soil temperature than on the annual fluctuation in the minimum temperature for germination. Since broadening of the temperature range for germination in *S. arvensis* coincides with the increase of soil temperature in spring, and narrowing of the temperature range for germination coincides with the decrease of temperature in autumn, changes in dormancy and changes in the soil temperature reinforce each other in the timing of germination in the field.

### *Evaluation of the model*

Assessing the goodness of fit when the model is fitted to dormancy patterns observed in the field is not a discriminative test of the model. Independent datasets are necessary to validate the model. The best way to test the model performance would be to compare simulated germination data with experimental results of germination tests over a range of test temperatures, using seeds that were pretreated at different temperature regimes ('burial temperatures') in the laboratory. These data are not available at present. There are, however, data from field experiments in the literature that may be used to test the model.

The general trend in the periodicity of field emergence in the three species that was calculated by the model for The Netherlands compares well to seasonal emergence patterns in temperate regions reported in the literature (Fig. 5). In both the field observations and the simulations, emergence of *P. persicaria* is restricted to the spring season. Emergence of *C. album* starts in spring, extends into the summer and occasionally into late autumn, and emergence of *S. arvensis* occurs throughout the growing season.

Field emergence patterns of *P. persicaria* and *C. album* observed in Lelystad, The Netherlands (Van den Brand, 1986) were also used to evaluate the model. In Fig. 6 the field observations are compared to the simulations made with the model. Simulation results are depicted in the same way as in Fig. 4. When comparing observed and simulated data, it should be noted that Van den Brand (1986) cumulated seedling numbers per month and presented the data as relative distributions of monthly totals over the year. Model simulations were done on a daily time basis. The plots in which seedling emergence was observed were disturbed once a year, in autumn. This implies that the emergence flush in the field coincides with the moment when the field temperature first overlaps the germination-permissive temperature range. The duration and cessation of the overlap are not reflected in the field emergence data. This would only occur when the soil is disturbed repeatedly during the season, bringing seeds from deeper layers to the surface. Both in *P. persicaria* and in *C. album*, the model is able to explain the major differences in seedling emergence between the years. For *P. persicaria*, 1981 was the only year when emergence started in March, and also the only year when the temperature exceeded the lower temperature limit for germination as early as in March. Assuming that field emergence starts when the temperature is close to the lower limit of the temperature range for germination, and that field emergence peaks when it exceeds the lower temperature limit, emergence patterns in 1981 and 1983 can be explained. The model explains the start of field emergence in April 1979 and 1982, but not the relative seedling numbers emerged in April and May. For *C. album*, 1981 was the year when field emergence in March was highest, and also the only year when the temperature was close to the minimum temperature for germination in March. In 1983 the temperature exceeded the lower temperature limit for germination in April, while in the other years this happened in May. This agrees fully with the timing of the emergence peaks, which was in April in 1983, and in May in the other years.

In order to predict field emergence patterns of weeds in specific circumstances, changes in dormancy should be well described on the time scale of days or weeks. Figure 2 suggests that this may not be the case.

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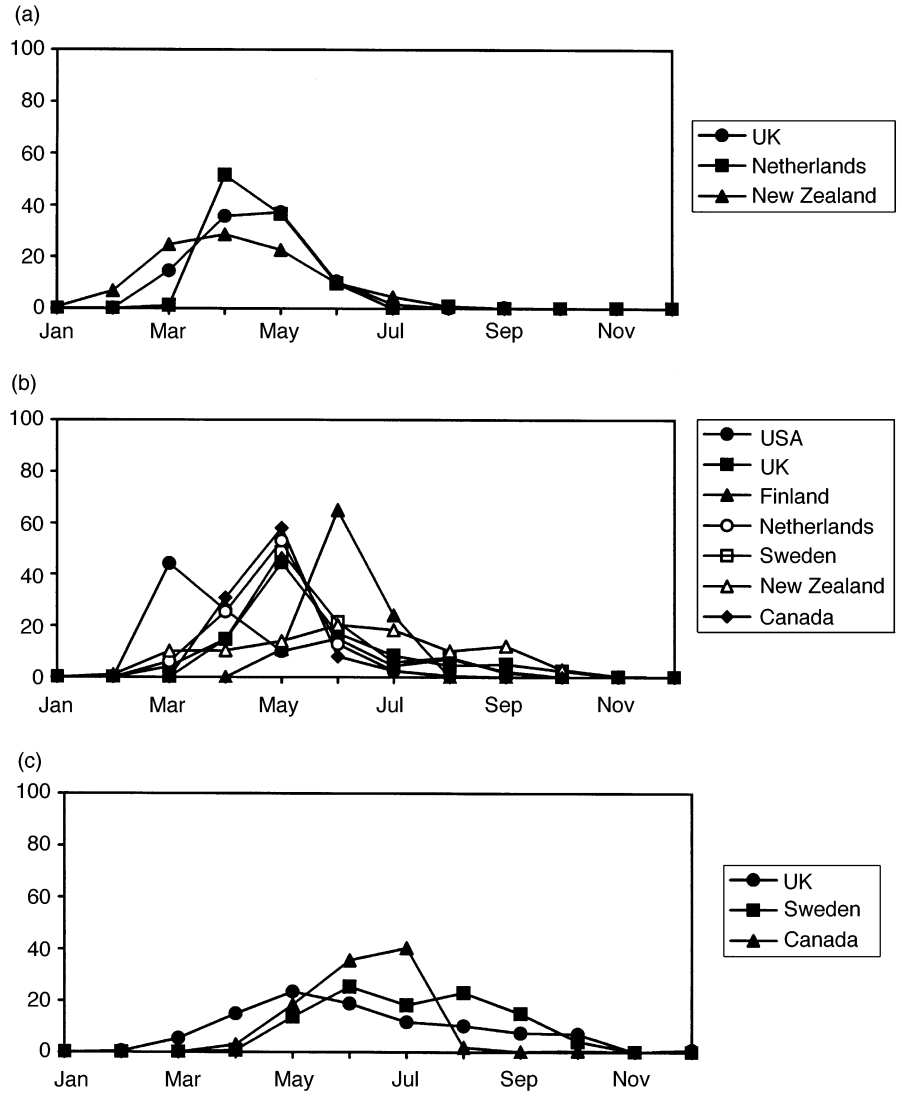


**Figure 5.** Seedling emergence patterns in the field, as observed by several authors. Data are averaged per country. (a) *Polygonum persicaria*: UK, Chancellor (1964), Roberts and Neilson (1980); Netherlands, Van den Brand (1986); New Zealand, Popay *et al.* (1995). (b) *Chenopodium album*: USA, Ogg and Dawson (1984); UK, Roberts (1964), Roberts and Feast (1970), Lawson *et al.* (1974); Finland, Erviö (1981); Netherlands, Van den Brand (1986); Sweden, Håkansson (1992); New-Zealand, Popay *et al.* (1995); Canada, Chepil (1946). (c) *Spergula arvensis*: UK, Roberts and Feast (1970), Lawson *et al.* (1974); Sweden, Håkansson (1992); Canada, Chepil (1946). Note that the time axis for the observations of Popay *et al.* (1995) from New Zealand was shifted by 6 months, to enable comparison with the patterns from the northern hemisphere.

Comparison with experimental data has affirmed that, as yet, the model is not accurate enough to be used in the prediction of field emergence patterns (Vleeshouwers and Kropff, 2000). Apart from being useful for generating and exploring hypotheses on the physiology of dormancy and germination, the present significance of the model lies in the characterization of species and their dormancy patterns in different climatic conditions.

## Conclusion

A simulation model for seed dormancy was developed that uses the hypothetical amount of available membrane-located phytochrome receptor protein as a measure for the degree of dormancy. On the basis of this amount, it calculates germination percentages of seed samples that are irradiated with red light and tested for germination at different

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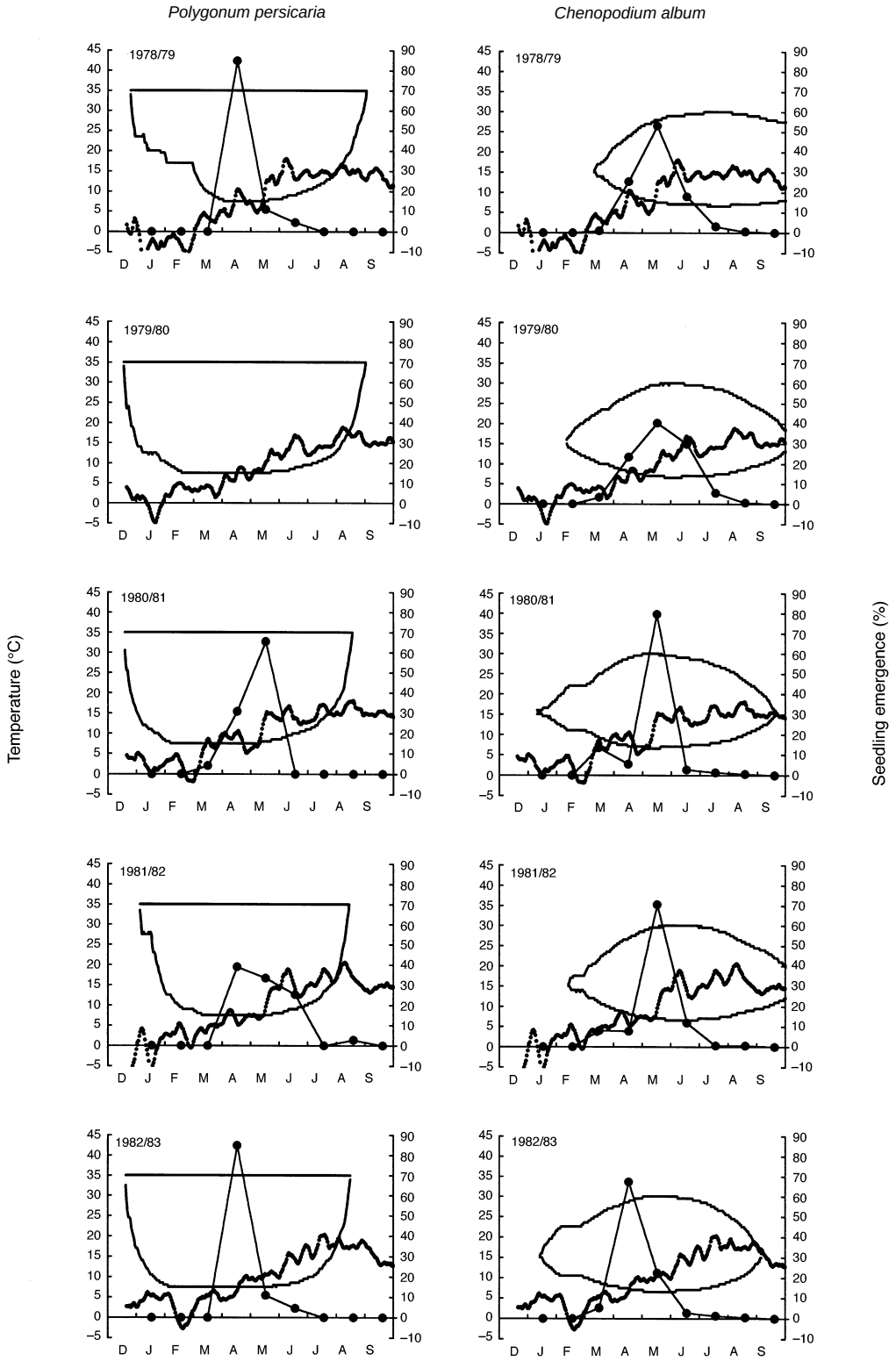


**Figure 6.** Field emergence patterns of *Polygonum persicaria* and *Chenopodium album* in Lelystad, The Netherlands, in the years 1979–1983 (•—•) (Van den Brand, 1986), compared to simulated changes in the temperature range for germination, and its overlap with the field temperature. The emergence pattern of *P. persicaria* in 1980 was not given by Van den Brand (1986), since seedling numbers were very low. The emergence pattern of *P. persicaria* in 1983 was not given either, but it was reported to be almost equal to that in 1979.

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temperatures. The estimates of physiological parameters in the model seem to be of biological dimensions. It would be a challenge for seed scientists to try to actually measure these parameters. The model output can also be presented as the width of the temperature range in which germination occurs, and as such bridges the gap between the biochemical concept of dormancy hypothesized by Hilhorst (1993, 1998), in which dormancy is related to the amount of phytochrome receptor, and the ecological concept put forward by Karssen (1982), in which dormancy is related to the temperature range over which seeds germinate.

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