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# The dual role of temperature in the regulation of the seasonal changes in dormancy and germination of seeds of *Polygonum persicaria* L.

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**Summary.** The role of temperature in the regulation of seasonal changes in dormancy and germination was studied in seeds of *Polygonum persicaria*. Seeds were buried in the field and under controlled conditions. Portions of seeds were exhumed at regular intervals and germination was tested over a range of conditions. Seeds of *P. persicaria* exhibited a seasonal dormancy pattern that clearly showed the typical features of summer annuals, i.e. dormancy was relieved at low winter temperatures, the germination peak occurred in spring and dormancy was re-induced in summer. The expression of the dormancy pattern was influenced by the temperature at which germination was tested. At 30° C exhumed seeds germinated over a much longer period of the year than at 20° or 10° C. Nitrate added during the germination test occasionally stimulated germination. The seasonal changes in dormancy of buried seeds were regulated by the field temperature. Soil moisture and nitrate content did not influence the changes in dormancy. The fact that, on the one hand, field temperature determined the changes in dormancy and, on the other hand, germination itself was influenced by temperature, was used to describe the seasonal germination pattern of *P. persicaria* with a model. Germination of exhumed seeds in Petri dishes at field temperature was accurately described with this model. Germination in the field was restricted to the period where the range of temperatures over which germination could proceed (computed with the model) and field temperature overlapped.

**Key words:** *Polygonum persicaria* – Dormancy pattern – Germination – Model – Weed seeds

Studies with both artificially buried and natural seed populations have shown that the emergence of many species occurs in a seasonal pattern. Emergence is often restricted either to spring-early summer (summer annuals) or to autumn and/or winter sometimes with additional flushes in spring (winter annuals). Frequent cultivation of the soil increases the number of emerging seedlings for most species, but it does not essentially influence the periodicity of emergence (Roberts and Feast 1973; Roberts and Lockett 1978).

Restriction of emergence to a fixed interval of the year may be caused by seasonal limitations in the number of seeds in the soil. This is particularly true for grasses that form transient seed banks that exist only for a limited period of the year. However, most dicotyledonous annuals form persistent seed banks that are present during all seasons but vary seasonally in volume (Thompson and Grime 1979). For those species the seasonal emergence pattern was shown to be caused by a seasonal variation in dormancy of the seeds in the seed bank (Karssen 1982; Baskin and Baskin 1985). Both relief and induction of dormancy occur at fixed seasons only. As a consequence, low levels of dormancy and emergence are restricted to a species-specific interval of the year. Dormancy prevents germination in the seasons of least favourable conditions for plant survival. Thus, summer annuals are dormant in summer and autumn, dormancy is relieved during winter and, if suitable conditions prevail, they germinate in spring. If germination is prevented, because suitable conditions are lacking, secondary dormancy is induced in summer. For winter annuals it is just the opposite. Their seeds are dormant in winter and spring. Dormancy is relieved during summer and, provided that suitable germination conditions are present, they can germinate in autumn. If germination is prevented secondary dormancy develops during winter. Often dormancy induction during winter is slow, such that germination may also occur in (early) spring.

The seasonal character of the changes in dormancy suggests that dormancy is mainly regulated by field temperature. Totterdell and Roberts (1979) hypothesized that the loss of dormancy at low temperatures of seeds of *Rumex obtusifolius* and *R. crispus* was the result of two

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subprocesses: (i) *Relief* of primary dormancy and (ii) *induction* of secondary dormancy. They suggested that relief of primary dormancy only occurred at temperatures below a certain value. This critical temperature was estimated to be 15° C for the *Rumex* species. It was hypothesized that this relief of primary dormancy was independent of the actual temperature so long as it was below 15° C. In the opinion of Totterdell and Roberts (1979), induction of secondary dormancy occurred at all temperatures with the rate of induction increasing with increase in temperature. They hypothesized that the effect of a temperature pretreatment on dormancy of the *Rumex* species depended on these two subprocesses. This implies that, although relief of primary dormancy occurred equally at all temperatures below 15° C, temperatures just above zero caused the most effective net relief of dormancy (= stratification), because the rate of induction of secondary dormancy was lowest at these low temperatures. Espeby (1989) reported that also for *P. lapathifolium* subsp. *lapathifolium* stratification was better at 1° C than at 5° C.

Although Totterdell and Roberts (1979) used the term stratification for the net result of the two subprocesses, we prefer the use of "dormancy relief" or "dormancy induction" as the net result of a temperature pretreatment. Therefore, where these terms are further used the net result of the two subprocesses is meant. When e.g. germination increases over time, due to a pretreatment at a certain temperature, dormancy is said to be relieved, although both subprocesses as defined by Totterdell and Roberts may occur simultaneously.

Germination tests by Baskin and Baskin (1980, 1981a, b, 1983a, b, 1984) with exhumed seeds of several species over a range of temperatures showed that relief of dormancy is characterized by a widening of the range of temperatures over which germination can proceed, whereas during induction of dormancy this range becomes narrower. Germination in the field may occur when the actual field temperature is within this germination-temperature range. This implies that temperature in the field has a dual effect. On the one hand, it is the driving force for the changes in dormancy and therefore determines the *width* of the germination-temperature range. On the other hand, germination itself depends on whether the actual temperature is within this range.

The present study analyses the dual role of temperature in the regulation of the seasonal fluctuations in dormancy and germination of *Polygonum persicaria* seeds. Emergence of this species is restricted to April–May both in The Netherlands (Van den Brand 1986, 1987) and Great Britain (Roberts and Neilson 1980). In a preliminary study, seasonal fluctuations in the germination capacity at one test temperature were reported (Karssen 1980/81). In the present experiments, fluctuations in dormancy are studied both in burial experiments in the field and under controlled conditions in incubators. We also studied whether in addition to temperature, fluctuations in soil moisture content and nitrate level have an effect on the dormancy pattern. Stimulation of germination of *P. persicaria* seeds by nitrate has been reported (Vincent and Roberts 1977, 1979; Karssen 1980/81). Although incidental tests in darkness showed that *P. persicaria* seeds also germinate to a certain extent without light, it was decided to limit the present experiments to light-induced germination. Studies of Baskin and Baskin with several species (1980, 1981a, b, 1983a, b, 1984) showed that the germination temperature range in darkness was much smaller than in light. Overlap between the range and the estimated field temperature hardly ever occurred in darkness.

## Materials and methods

### *Seeds*

Seed lots were collected in October 1986 from small populations of *P. persicaria* in the vicinity of Wageningen. After collection seeds were air dried, rubbed mechanically to remove perianth segments, sieved and winnowed to remove small and light seeds and then stored dry at 2° C until December 1986.

### *Burial in the field*

In December 1986 one seed lot of *P. persicaria* was divided into 48 portions, that were packed separately in envelopes made of fine mesh nylon gauze. Each envelope of seeds was buried in sandy loam in a plastic net pot (∅ 10 cm), that permitted good contact with the surrounding soil. To prevent loss of soil during handling, the pots were lined with gauze. The soil that surrounded the seeds prevented light reaching the seeds during exhumation.

The pots with the seeds of *P. persicaria* were either buried in the field in sandy loam or, at the same location under a transparent plastic roof in a 100-l polyethylene container, sunk in the ground and holding the same soil as in the field. All seeds were buried at a depth of approx. 10 cm below the surface.

Using a tube attached to the bottom of the container and connected to a reservoir, the container could be supplied with water from underneath. The moisture content of the soil was regulated at 10–20% (dwt). Seeds buried in the field were exposed to the natural fluctuations in soil moisture content. At regular intervals the moisture content of the soil from the different treatments was determined in subsamples of approx. 70 g (dwt) taken from a depth of 10 cm, by weighing before and after drying in an oven for 8 h at 130° C. The nitrate content of the soil from the different treatments was determined at regular intervals according to the method of Houba et al. (1986).

Soil temperatures measured at 10 cm in the container showed minor discrepancies from temperatures measured in the field. The latter temperatures were identical to those recorded at a meteorological station at Wageningen. Therefore the recordings of the meteorological station were used. Temperature data were averaged over 10-day periods.

### *Germination tests*

At regular intervals, one portion of seeds was exhumed from both treatments to test germination. During transport to the laboratory the pots were covered with black polyethylene. The seeds from each envelope were divided into smaller portions. These portions were incubated in 50-mm Petri dishes on one layer of filter paper (no. 595, Schleicher and Schüll, Dassel, Germany) and imbibed in Milli-Q water or 50 mM $KNO_3$. Seeds were irradiated for 15 min with red light, which was obtained by filtering light from six red fluorescent tubes (TL 20W/15 Philips, Eindhoven, The Netherlands) through one layer of 3-mm plexiglas (red 501, Röhm & Haas, Darmstadt, Germany), the irradiance at seed level being 250 $\mu W \cdot cm^{-2}$.

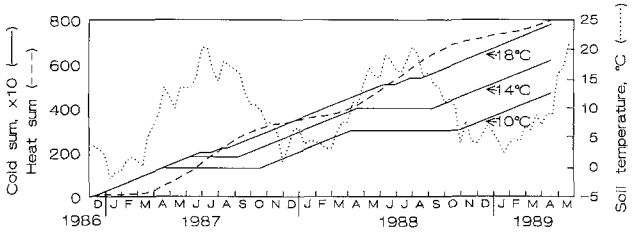


**Fig. 1.** Changes in soil temperature at 10 cm *(dotted line)* and in cold sum (*C*) *(solid line)* and heat sum (*H*) *(dashed line)* during two and a half years of burial. For each period of 10 days that the mean soil temperature was below a critical temperature the value of *C* was raised by an arbitrary value 1. To illustrate the effect of the value of the critical temperature on *C*, it was calculated using critical temperatures of 10°, 14° and 18° C. *H* was calculated by summing the value of the mean soil temperature of every 10-day period

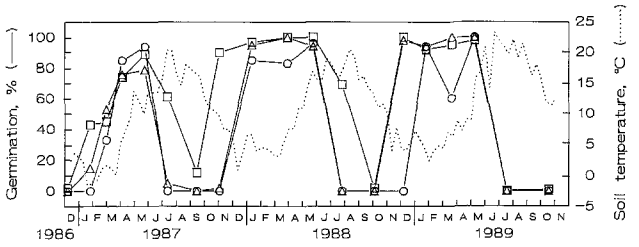


**Fig. 2.** Seasonal variation in germination of exhumed seeds of *Polygonum persicaria* at different test temperatures. Seeds were buried in portions of 1.8 g in December 1986 in sandy loam under field conditions and exhumed a regular intervals. Germination was tested in Petri dishes with single replicates of approx. 35 seeds, at 10° (○), 20° (△) or 30° C (□) in water after a 15-min red light irradiation. The *dotted line* indicates the soil temperature at 10 cm in bare soil

Petri dishes were placed in closed plastic boxes to prevent loss of moisture. Germination tests occurred in cooled incubators (Gallenkamp, Crawley, UK, T ± 1° C) or outdoors at a height of 1.5 m in the shade in the plastic boxes, covered with black polyethylene.

Handling of exhumed seeds occurred in dim green safelight, obtained by filtering light from one green fluorescent tube (TL 40W/17, Philips, Eindhoven, The Netherlands) through two layers yellow no. 46 and two layers blue no. 62 Cinemoid filters (Strand Electric, London, UK).

Between 6 and 14 days after incubation, depending on the test temperature, when no additional germination occurred, both germinated and non-germinated seeds were counted to determine germination percentage. Protrusion of the radicle was the criterion for germination. The temperature during the outdoor germination tests was obtained from the meteorological station at Wageningen.

### *Burial under controlled conditions*

Seeds of *P. persicaria* were buried in sandy loam in black 9-cm plastic Petri dishes between two layers of fine mesh gauze and pretreated at various temperature regimes. At regular intervals, and at each change of temperature one Petri dish was removed from the incubators to test the germination capacity of the seeds.

At the start of the experiment soil moisture content was 18%. Because Petri dishes were kept in plastic boxes lined with moist filter paper, soil moisture content only changed slightly.

### *Statistical procedures*

Statistical procedures were performed with the statistical package SAS (Anonymous 1985). The germinated fraction (*G*) was transformed with an arcsin transformation, $2 \times \arcsin \sqrt{G}$, to get approximately normally distributed data with an equal variance. Results from calculations were transformed back to germination percentages to facilitate comparison with other data.

From the soil temperature data obtained from the meteorological station at Wageningen, both a cumulative dormancy breaking and a dormancy inducing factor were calculated (Fig. 1). They are indicated as cold and heat sum *(C* and *H)*, respectively. We applied the hypothesis of Totterdell and Roberts (1979) and assumed that (i) relief of dormancy is independent of the actual temperature as long as it is below a critical temperature and (ii) the rate of induction of dormancy inreases with increase in temperature. Therefore, (i) the value of *C* was raised by an arbitrary value 1 for each period of 10 days that the mean soil temperature (at 10 cm) was below the critical temperature and (ii) *H* was calculated by summing the mean soil temperatures of each succesive 10-day period. Different critical temperatures were used for the calculation of *C* to determine which temperature was suitable for *P. persicaria*. When the mean soil temperature in a 10-day period was below 0° C, which occurred only three times during the experiment, neither *C* nor *H* were changed. *C* and *H* were never reset to zero, because the determination of the moment this should occur would have been unreliable. Therefore, both factors increased throughout the experiment, *C* only in some parts of the year (when the field temperature was below the critical temperature), *H* continuously (Fig. 1). This implies that time was necessarily involved in both parameters.

Based on *C* and *H*, a model for the changes in dormancy of *P. persicaria* was developed. Selection of parameters for the model occurred with forward and backward stepwise regression (procedure Stepwise, SAS; Anonymous 1985). The significance level for entry into the model was 0.15.

The best value of some parameters (e.g. the threshold temperature to calculate *C*) was tested by fitting equations with all selected parameters using different values for the parameters to be tested (procedure Generalized Linear Models, SAS; Anonymous 1985). Parameter values that gave highest correlation and lowest estimated variance were chosen.

## Results

### *Germination of exhumed seeds*

Germination of exhumed seeds showed a seasonal pattern of dormancy that started directly after burial of the seeds in December 1986 with an alleviation of dormancy (Fig. 2). Re-induction of dormancy occurred in spring-early summer 1987. The pattern was repeated in the following 2 years. A Friedman test showed that the rank sums for the three test temperatures were significantly different ($P = 0.017$). The rank sums for 10°, 20° and 30° C were 30.5, 37.0 and 46.5 respectively, whereas in the absence of differences between the temperatures a rank sum of 38.0 would have been expected. Thus, in general more *P. persicaria* seeds germinated at 30° C than at 20° and 10° C. Consequently, at 30° C seeds germinated during a longer period of the year than at 20° and particularly at 10° C.

Nitrate slightly stimulated germination of exhumed seeds at the three test temperatures but only during the first 6 months of the experiment (data not shown).

### *Control of dormancy pattern*

The above results show that the conditions during the germination test, particularly temperature, influenced the

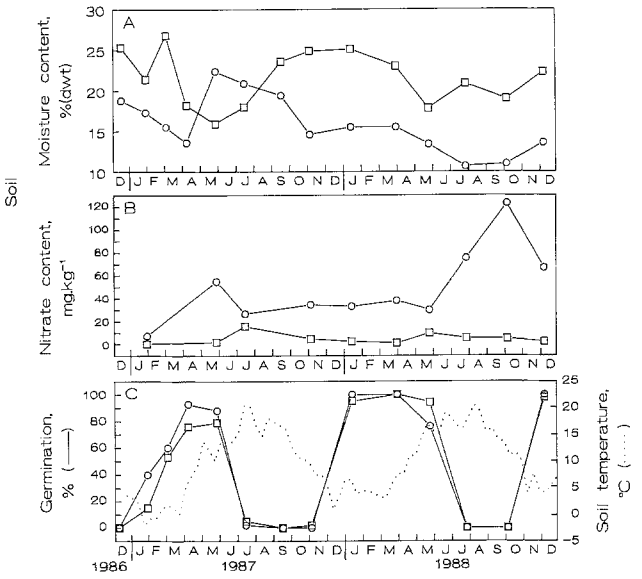


**Fig. 3A–C.** Changes in **A** soil moisture, **B** soil nitrate content and **C** soil temperature (*dotted line*) during burial of seeds of *Polygonum persicaria* and **C** changes in germination of exhumed seeds (*solid lines*). Seeds were buried under field conditions as in Fig. 2 (□) or in sandy loam in a 100-1 plastic container, sunk in the ground and covered with a transparent plastic roof (○). In the container, soil moisture content was regulated at 10 to 20% (dwt). At regular intervals, soil nitrate and moisture content were determined and germination tested as in Fig. 2 at 20° C in water

*expression* of dormancy. A question that has to be answered is which factor(s) control(s) the *changes* in dormancy.

*Soil moisture and nitrate content.* To study the effect of soil moisture on changes in dormancy, seeds were buried either outdoors in sandy loam exposed to the natural fluctuating moisture content or, under a transparent roof, in a container with sandy loam with a more or less constant soil water content. In the uncovered situation, the soil moisture content showed a seasonal fluctuation: moisture content was lowest in May in both years and highest during winter (Fig. 3A). In the covered treatment the soil moisture content also varied, but did not show the same seasonal fluctuations as occurred in the uncovered location.

The two treatments showed large differences in soil nitrate content (Fig. 3B). The nitrate content of the covered treatment was always higher than that of the uncovered location. It increased during summer, particularly in the second year. A Spearman rank correlation test showed the absence of a relationship between germination and both moisture ($r = 0.076$; $P > 0.5$) and nitrate content ($r = -0.135$; $P > 0.5$).

*Temperature.* Comparison of the germination data in Figs. 2 and 3C with the mean soil temperature in the field suggests that dormancy induction occurred when temperature rose above approx. 10–15° C, whereas dormancy relief started when temperature dropped below these values. The hypothesis that field temperature controlled the dormancy pattern was tested (i) in an experiment under controlled conditions and (ii) by applying an elaborated version of the above described theory of Totterdell and Roberts (1979) to the data acquired in our field experiments.

(i) Fig. 4 compares the fluctuations in germination of exhumed seeds that had been buried in the field for 8 months (Fig. 4A) or had been pre-incubated in Petri dishes with soil at 2° C (Fig. 4B) or at a sequence of temperatures starting at 2° C and rising stepwise to 10° (Fig. 4C) or 15° C (Fig. 4D). In contrast to Fig. 2, germination occurred in 50 mM $KNO_3$ instead of water. During the first 3 months (Fig. 4A) or 75 days (Fig. 4B–D), relief of dormancy was very similar for the four treatments. Induction of dormancy had started at the end of the experiment for all treatments except the 2° C→6° C→10° C treatment (Fig. 4C). When seeds were pretreated at 2° C, dormancy induction was only seen in germination tests at 20° and 30° C (Fig. 4B), whereas after pretreatment in the field (Fig. 4A) and at a temperature program rising to 15° C (Fig. 4D), dormancy induction was most evident in germination tests at 10° and 20° C. Apparently, dormancy is either re-induced at constant 2° C or at a rising temperature when it is in-

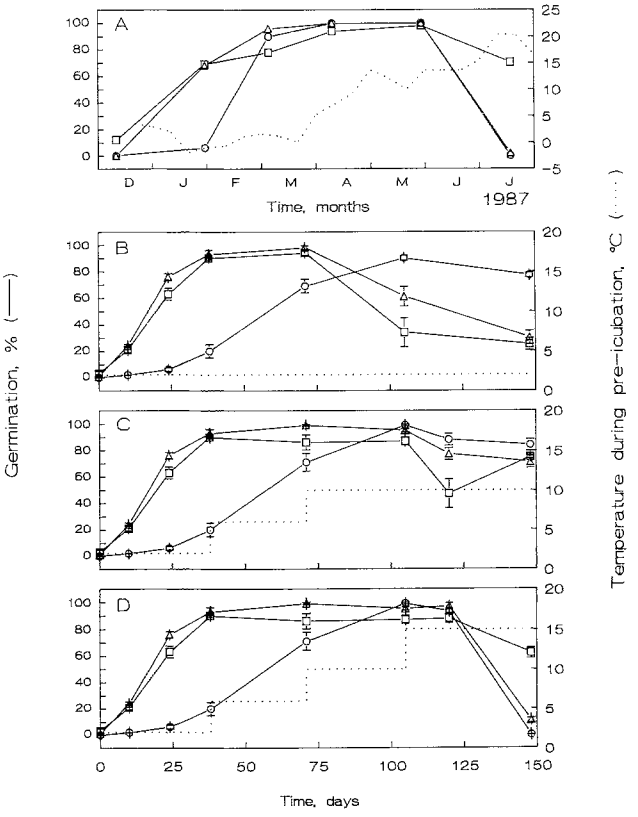


**Fig. 4A–D.** Effect of pretreatment temperature on dormancy of *Polygonum persicaria*. **A** Seeds were buried in the field, exposed to field temperature or **B** seeds were pretreated in sandy loam in black 9-cm plastic Petri dishes between two layers of fine mesh gauze at 2° C or **C** at temperatures rising stepwise from 2° to 6° and 10° or **D** to 15° C. Seeds were "exhumed" at regular intervals. Germination was tested with single test samples of approx. 35 seeds (**A**) or triplicates of approx. 55 seeds (**B, C, D**) in 50 mM $KNO_3$ in Petri dishes at 10° (○), 20° (△) or 30° C (□) after red light irradiation for 15 min. *Vertical bars* indicate standard error. The *dotted line* indicates the temperature during "burial"

creased to 15° C although it is expressed differently. There is a striking similarity between the results of the latter experiment and the pattern observed in the field experiment (compare Fig. 4A to 4D). In the field, a rise above approx. 10°–15° C seems critical for dormancy induction. In a parallel experiment, results similar to those of Totterdell and Roberts with the *Rumex* species were obtained with *P. persicaria:* In the range of 2, 6, 10 and 15° C, stratification of *P. persicaria* occurred faster, the lower the pretreatment temperature. Dormancy was not relieved at 15° C (data not shown).

(ii) For the application of the theory of Totterdell and Roberts to our data, it was assumed that the subprocesses of dormancy relief and induction were regulated by $C$ and $H$, respectively. However, in contrast to Totterdell and Roberts, who only discussed stratification (=loss of primary dormancy), we aimed to explain repeated cycles of dormancy relief and induction. Although dormancy of *P. persicaria* seeds was also induced after 100 days at constant 2° C (Fig. 4B) and this result can not be explained by the involvement of just $C$ and $H$, the observation was ignored during the development of the model, since such long periods of low temperatures do not occur in the temperate zone.

Thus, dormancy ($D$) is a function of $C$ and $H$:

$$D=f(C, H) \tag{1}$$

In Fig. 5 some transformed germination data from Fig. 2 are expressed as a function of the germination temperature. It is clear that the expected transformed germination ($G_t$) at a certain moment can be described by a quadratic function of the germination temperature ($T_g$).

$$G_t = a \cdot T_g^2 + b \cdot T_g + c \tag{2}$$

where $a$, $b$ and $c$ are the coefficients of the quadratic function.

Germination of exhumed seeds fluctuates throughout the year as a function of dormancy (Fig. 2). In addition, germination of exhumed seeds is affected by the conditions of the germination test. It was assumed that one or more of the coefficients $a$, $b$ and $c$ is are a function of dormancy and/or of the factors that influence the result in the germination test, such as the composition of the germination medium ($M_g$), that is in the current study the presence or absence of $KNO_3$.

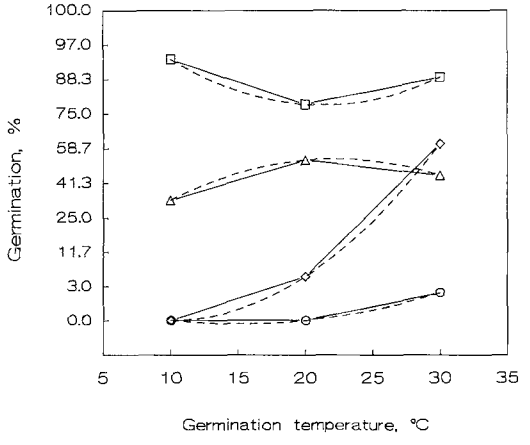


**Fig. 5.** Germination data of *Polygonum persicaria* from Fig. 2 (on an arcsin scale) as a function of germination temperature *(solid line)*. Quadratic curves *(dashed line)* are shown to indicate the quadratic character of the relationship between germination temperature and germination. (○) December 1986, (△) March 1987, (□) May 1987, (◇) July 1987

The observation that dormancy induction at 2° C was primarily seen in germination tests at 20° and 30° C (Fig. 4B) and induction of dormancy at rising temperatures in tests at 10° and 20° C, suggests that temperature shortly before exhumation influenced germination directly and not through $C$ and $H$ alone. Therefore also then mean pretreatment temperature ($T_p$) during a period ($\delta t$) prior to exhumation ($T_{p,\delta t}$) was introduced as possibly influencing $a$, $b$ and $c$. In summary:

$$a, b, c=f(C, H, M_g, T_{p,\delta t}) \tag{3}$$

Substituting Eq. 3 in Eq. 2 gives:

$$\begin{aligned} G_t=f(&C\cdot T_g^2, H\cdot T_g^2, M_g\cdot T_g^2, T_{p,\delta t}\cdot T_g^2, T_g^2,\\ &C\cdot T_g, H\cdot T_g, M_g\cdot T_g, T_{p,\delta t}\cdot T_g, T_g,\\ &C, H, M_g, T_{p,\delta t}) \end{aligned} \tag{4}$$

The parameters that maximized the fit of the data of our germination tests at 10°, 20° and 30° C in water and $KNO_3$ were selected from Eq. 4. The model was developed in June 1989 and therefore data from the germination tests in July and October 1989 were not used. Consequently, these data were suited to test model performance.

For $\delta t$ in $T_{p,\delta t}$ a period of 30 days gave the best fit. With $T_{p,30}$, a critical temperature of 15° C for the calculation of $C$ gave the highest correlation ($r^2=0.76$) and the lowest estimated variance ($\hat{\sigma}^2=1348$). Therefore $C$, computed with a critical temperature of 15° C and $T_{p,30}$ (the mean soil temperature in the 30 days before exhumation) were used in the model. The expected transformed germination ($G_t$) could be estimated by:

$$\begin{aligned} G_t = &(-0.005\ C+0.003\ H+0.040\ T_{p,30}+0.065)\ T_g^2+\\ &(1.785\ C-0.113\ H-1.479\ T_{p,30}+0.658\ M_g)\ T_g+\\ &7.366\ T_{p,30}-10.081 \end{aligned} \tag{5}$$

When a model was developed with the parameter time (weeks of burial) instead of $C$ and $H$, $r^2$ decreased from 0.76 to 0.33 and $\hat{\sigma}^2$ increased from 1348 to 3421.

### *Germination under field conditions*

The model (Eq. 5) was developed with results of germination tests with exhumed seeds in incubators. The intriguing question now is whether the tests of exhumed seeds at the different constant temperatures in incubators do indeed explain the seasonal emergence pattern in the field.

To test the model, calculated data were compared to data collected in outdoors experiments. Germination of exhumed seeds was tested in Petri dishes placed outdoors at a height of 1.5 m. Also in these tests (Fig. 6, dotted lines), germination fluctuated in a seasonal pattern. Comparison with Fig. 2 learns that germination occurred during a much shorter period of the year than at constant temperatures in incubators. Addition of nitrate during the germination test stimulated germination in spring.

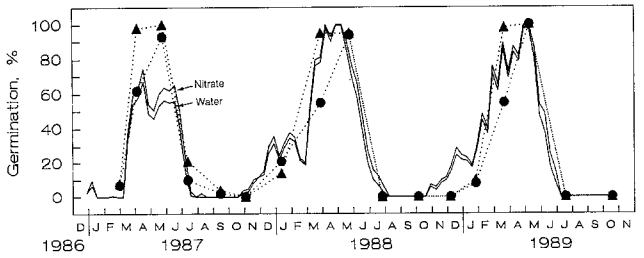


**Fig. 6.** Expected *(solid line)* and observed *(dotted line)* germination of *Polygonum persicaria* in Petri dishes outdoors as a function of exhumation date. Germination was tested in Petri dishes with single replicates of approx. 35 seeds after 15 min red light irradiation, in water (●) or 50 mM $KNO_3$ (▲). The Petri dishes with seeds were incubated in airtight plastic boxes covered with black polyethylene, placed outdoors at a height of 1.5 m in the shade. Expected values were calculated using Eq. 5. See text for explanation

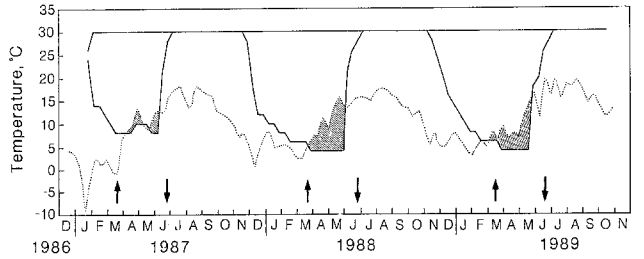


**Fig. 7.** Seasonal changes in the range of temperatures over which at least 50% of exhumed *Polygonum persicaria* seeds germinate. *Solid lines* represent maximum and minimum temperature required for 50% germination in water, calculated with Eq. 5. The *dotted line* indicates air temperature at 1.5 m (see text for explanation). *Hatched areas* indicate overlap of air temperature and germination-temperature range. *Arrows* indicate the moment germination in Petri dishes outdoors actually increased above (↑) or decreased below 50% (↓) (data from Fig. 6)

When air temperature at 1.5 m was used as $T_g$ in Equation 5, the germination pattern outdoors in water and nitrate was simulated fairly accurately (Fig. 6, solid lines). Interestingly, although data obtained after May 1989 were not used to develop the model, outdoor germination in July and October 1989 was closely predicted.

Figure 7 shows the changes in the minimum and maximum temperature required for 50% germination ($T_{g,\min}$ and $T_{g,\max}$) in water, calculated with Eq. 5. These calculations were restricted to the range of 0°–30° C to maintain ecological significance. $T_{g,\min}$ and $T_{g,\max}$ were only calculated for germination in water, since germination in water and nitrate were fairly similar (Fig. 6).

The periods of predicted field germination/emergence are the periods where the field temperature overlapped with the germination-temperature range (hatched areas; Fig. 7). The arrows indicate the moments that germination in Petri dishes placed outdoors actually inreased (↑) or decreased (↓) to 50% (data from dotted lines in Fig. 6). There was a good agreement between the calculated periods of germination and the actual results of outdoor germination tests.

## Discussion

The present data have shown that germination of seeds and emergence of seedlings in the field during the course of the year depend on the one hand on the actual conditions that control germination and on the other hand on the conditions that preceded and that control dormancy. Both aspects will be discussed.

### *Germination of exhumed seeds*

Results of germination tests with exhumed seeds of *P. persicaria* during the first year of burial agreed to most emergence data reported in literature (Roberts and Neilson 1980; Van den Brand 1986, 1987). Germination and emergence occurred in April–May (Fig. 6). In the second and third year, germination in water and nitrate occurred as early as March in some tests. However, in the studies of Roberts and Neilson (1980) and Van den Brand (1986) in some years emergence also occurred as early as March. Moreover, it has to be considered that particularly at low temperatures emergence occurs several weeks after germination.

### *Control of germination*

*Test temperature.* The effect of the test temperature on the expression of dormancy is seen clearly in Fig. 2. At a test temperature of 30° C germination of exhumed seeds occurred during a much longer period of the year than at 20° or 10° C. It is obvious that information about the range of temperatures over which germination can proceed is essential for the prediction of germination (Figs. 6, 7). The germination-temperature range as calculated with Eq. 5 predicted fairly well the period during which at least 50% germination occurred under field conditions (Fig. 7).

The germination-temperature range of *P. persicaria* showed the typical features of a summer annual. Germination was usually best at the higher temperatures and changes in dormancy were obtained by changes in the minimum temperature suitable for germination (Figs. 2, 7). Germination could occur in the field when the rising field temperature overlapped with the minimum temperature required for germination. These features closely resemble those of other typical summer annuals e.g. *Ambrosia artemisiifolia* (Baskin and Baskin 1977, 1980), *Verbascum blattaria* and *V. thapsus* (Baskin and Baskin 1981b) and *Rumex crispus* (Baskin and Baskin 1978) and *R. obtusifolius* (Van Assche and Vanlerberghe 1989).

*Nitrate.* A stimulatory effect of nitrate on germination of *P. persicaria* has been reported before. Stimulation occurred particularly after chilling in light (Vincent and Roberts 1977, 1979) but also in darkness (Karssen 1980/81). Germination of seeds of *Polygonum lapathifolium* subsp. *lapathifolium* pretreated in water in Petri dishes, was also stimulated by nitrate (Bouwmeester 1990). Germination of exhumed seeds of *P. persicaria* was however only slightly stimulated by applied nitrate, particularly during early spring (Fig. 6).

The different reaction of fresh and buried seeds to applied nitrate might be a function of differences in their endogenous nitrate content. Fresh seeds of *Polygonum* species contain very low levels of nitrate [approx. 0.2 μmol · $g^{-1}$ seed (dwt), data not shown] and therefore an effect of applied nitrate as found by Vincent and

Roberts (1977, 1979), Karssen (1980/81) and Bouwmeester (1990) is to be expected. During burial in soil, nitrate uptake from the soil solution may saturate the requirement for nitrate. Hence, additionally applied nitrate will not stimulate germination.

*Control of dormancy*

*Soil moisture and nitrate content.* Seasonal fluctuations in soil moisture or nitrate content are no prerequisite for changes in dormancy of *P. persicaria* (Fig. 3). Also during pretreatment in Petri dishes changes in dormancy occurred, despite the absence of changes in moisture content (Fig. 4B–D).

*Temperature.* Dormancy of summer annuals is usually relieved by low temperatures (Baskin and Baskin 1977; Karssen 1982). Vincent and Roberts (1977, 1979) and Staniforth and Cavers (1979) showed that dormancy of *P. persicaria* was indeed relieved by a chilling pretreatment for 4 weeks at 1° C and 15 weeks at 4° C, respectively. The latter authors showed that there was no difference between a 15-week dormancy breaking treatment during winter in the field or on moist filter paper at 4° C. However, extending the pretreatment at 4° C up to 19 and 25 weeks caused induction of secondary dormancy. This is in agreement with the present results (Fig. 4B). Apparently, dormancy induction is eventually inevitable even at chilling temperatures.

Under field conditions, dormancy induction in summer annuals occurs in summer at high temperatures (Baskin and Baskin 1977, 1985; Karssen 1982). Both the present burial experiment with *P. persicaria* and the experiments of Totterdell and Roberts (1979) with *Rumex obtusifolius* and *R. crispus* seem to suggest that 15° C is the crucial temperature for dormancy relief and induction for some summer annuals.

*Model performance*

The model fairly accurately described and even predicted germination under field conditions. The large decrease of $r^2$ and increase of $\hat{\sigma}^2$ when $C$ and $H$ were replaced by the parameter time, indicates the validity of the use of cold and heat sum as a basis for the simulation of the dormancy pattern of *P. persicaria.*

Knowledge of the physiological processes responsible for the changes in dormancy should lead to a more mechanistic approach of the simulation of dormancy patterns. In addition, detailed knowledge about processes influencing temperature and nitrate in the soil and about the exposure to light during soil disturbance are a prerequisite for an accurate prediction of emergence in the field.

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