The effect of water stress on the temperature range for germination of *Orobanche aegyptiaca* seeds

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Abstract

Non-dormant seeds of *Orobanche aegyptiaca* were incubated at water potentials of 0 to –1.33 MPa and at constant temperatures from 5 to 29°C. Effects of water potential and temperature on final germination were modelled. In general, germination increased with increased temperature from 5 to 20°C and decreased above 26°C. Maximum germination occurred at 20–26°C and 0 MPa. Germination was reduced as the water potential decreased. Water potential also affected the temperature range over which high germination was observed; at 0 MPa high germination occurred over 9° (17–26°C) compared with 3° at −1.25 MPa (17–20°C). The optimum germination temperature also tended to decrease with a decrease in water potential. Final germination could be accounted for by seed-to-seed variation in the population assuming that each seed had a minimum temperature for germination and a maximum temperature above which it would not germinate. Seed-to-seed variation in these characteristics was assumed to be normally distributed, and it was further assumed that the two characteristics were independent. Effects of water potential on these temperature requirements were quantified, and the resulting empirical model accounted for final germination with reasonable accuracy (R^2 = 0.96).

Keywords: broomrape, modelling, *Orobanche aegyptiaca*, germination, temperature, water potential

Introduction

The effect of temperature on the rate of germination at sub-optimal temperatures can be described by a thermal time model (Bierhuizen and Wagenvoort, 1974; Garcia-Huidobro *et al*., 1982).

$$\theta_{T(g)} = (T - T_b)t_{(g)}, \quad (1)$$

where $\theta_{T(g)}$ is the thermal time required for germination of fraction g (°C d), T is the temperature (°C), T_b is the base temperature at which the germination rate is zero and $t_{(g)}$ is the time taken (d) for cumulative germination to reach fraction g.

Similarly, the effect of reduced water potential can also be described in a predictable manner by a hydrotime model (Gummerson, 1986; Bradford, 1990, 1997).

$$\theta_H = \left(\psi - \psi_{b(g)}\right)t_{(g)}, \quad (2)$$

where θ_H is the hydrotime constant (MPa d), ψ is the seed water potential (MPa) and $\psi_{b(g)}$ is the base water potential that facilitates radicle emergence of fraction g of the population.

Gummerson (1986) proposed that the thermal and hydrotime models could be combined into a single 'hydrothermal time' model. Bradford and co-workers (Dahal *et al*., 1993; Dahal and Bradford, 1994; Bradford, 1995; Dahal *et al*., 1996) further developed and applied this model which assumes the hydrothermal time for germination is constant in a seed lot and that there is no interaction between base temperature and water potential or between base water potential and temperature.

Interactions of temperature and water potential were, however, noted by Dahal and Bradford (1994) in tomato, and Christensen *et al*. (1996) suggested varying the mean base water potential with temperature in fully ripened *Bromus tectorum* L. seeds, although this adjustment was not necessary in modelling germination during after-ripening of the same species. Kebreab and Murdoch (1999b) have likewise demonstrated that such interactions do exist in some species and that hydrothermal time did not explain the variation observed in germination progress of *O. aegyptiaca* Pers. This observation led to the development of a new modified thermal time model that described the progress of germination at any water potential and temperature.

$$\text{Probit}(g) = \left[t_{(g)}\left(T - T_{b(0)} - m_b\psi\right) + m_T\psi - \theta_{T(50)}\right] / \sigma_{\theta_T}, \quad (3)$$

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where $T_{b(0)}$ is the base temperature for rate of germination in water, $\theta_{T(50)}$ is the median thermal time to germination in water and m_b and m_T are the rates of change in T_b (°C MPa^{-1}) and $\theta_{T(50)}$ (°C d MPa^{-1}), respectively, due to water potential. σ_{θ_T} is the standard deviation of thermal times for germination in the seed population. It is important to note that equation (3) only describes the progress of germination; it does not predict final (maximum) germination and indeed assumes that the seed population will achieve 100% germination. This assumption is known to be invalid for some species, especially at the limits of the temperature range for germination or as water potential decreases (Ellis *et al*., 1987; Falleri, 1994; King and Oliver, 1994).

The ability to predict the amount of germination expected at any temperature and water potential has applications for both crops and weeds. For control of weeds such as *Orobanche*, predictions of infestation levels may enable farmers to devise a more rational control strategy. The purpose of this experiment was, therefore, to develop a model that would account for the effect of water stress and temperature on the final germination percentage of *O. aegyptiaca*.

Materials and methods

Orobanche aegyptiaca seeds were collected at the Newe-Yaar Research Centre in Israel in June 1995. The seeds were stored in black plastic containers and immediately dispatched to Reading where they were stored in the dark at 3 ± 2°C before use. Autoclaved, deionized water was used in all experiments. Filter paper and seeds were sterilized as described in Kebreab and Murdoch (1999a).

A moist pretreatment period known as 'conditioning' is a prerequisite for *Orobanche* germination during which the seeds become responsive to a germination stimulant (Joel *et al*., 1991). Seeds were conditioned by placement between glass fibre filter discs (Whatman GF/A, 9 mm diameter). These discs were incubated in 9 cm Petri dishes on top of two layers of filter paper (Whatman No. 1, 9 cm circles), which were moistened with 5 ml water for 2 weeks at 20°C to remove dormancy. The discs containing the seeds were then placed on a non-sterile filter paper to remove excess moisture before transfer to germination tests.

A range of osmotic potentials was produced using aqueous solutions of polyethylene glycol (PEG 6000, Merck). The solutions were originally prepared according to Michel and Kaufmann (1973) but later measured using a Dew Point Microvoltmeter (Wescor, model HR-33T). The values were in close agreement with the revised calculations of Michel (1983). A sample chamber (Wescor, model C-52-SF) was used to measure the water potential of the solutions at different temperatures. PEG 6000 solutions are relatively non-toxic to seeds, and any inhibition of seed germination should be due to the osmotic effect (Emmerich and Hardegree, 1990).

To ensure that all germination requirements other than temperature and water potential were satisfied, all germination tests included 3 ppm GR24 – an artificial germination stimulant. Storage and handling of this artificial stimulant are described in Kebreab and Murdoch (1999a). Germination tests were conducted on a temperature gradient plate (Murdoch *et al*., 1989) in an air-conditioned dark room. The plate operated in one direction and provided 13 constant-temperature regimes between 5 and 40°C. Polystyrene boxes (4.5 × 4.5 × 1.9 cm) were used for germinating seeds on the temperature gradient plate. Thermal conduction between the boxes and the plate was enhanced by placing the boxes on moist paper (kept moist by capillary action from a water trough around the perimeter of the working area of the plate). Convection currents across the plate were prevented by a 13 × 13 polystyrene matrix of cells (5.5 × 5.5 × 4.5 cm) each containing a single germination test. Heat losses above the plate were minimized by covering the matrix with chromatography paper, a sheet of black polythene and a triple-glazed lid. The temperature gradient across each cell was nominally 3°C, so specified temperatures are ± 1.5°C. The boxes were sterilized with 1% NaOCl solution for 10 min and rinsed thoroughly. The boxes were then dried and lined with two layers of filter paper (Whatman No. 1, 4.4 × 4.4 cm) and one upper layer of glass fibre filter (Whatman GF/A, 4.4 × 4.4 cm). Three millilitres of the appropriate solution of PEG with 3 ppm GR24 were added to each box. The boxes were left to stabilize for 2 h on the temperature gradient plate, after which the discs containing the seeds were placed on top of the glass fibre paper, and the boxes were covered with their lids. The boxes were sealed with parafilm to avoid moisture loss but were opened daily for aeration.

Treatments were replicated twice and lasted for up to 80 d. Germination was counted periodically. When counting, one box at a time was taken from the plate and examined under a microscope in an adjacent laboratory (*c*. 20°C). Germinated seeds, i.e. those with radicles, were counted and removed. The box was sealed again and immediately put back to its original place. Each count took less than 5 min per box.

Statistical analysis

For each water potential regime, a non-linear model was fitted to the observed data (comprising final germination of seeds at five water potentials and 11 temperatures) using GENSTAT (Genstat 5 Committee,

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1994). The model was constructed on the basis that all seeds have a minimum temperature requirement for germination and also a maximum temperature above which they cannot germinate. The effects of water potential on these requirements were then modelled using the non-linear procedure of GENSTAT (Genstat 5 Committee, 1994) which provides the amount of variation explained and standard errors of each of the model parameters estimated.

Results

Both water potential and temperature affected the final germination percentage. Final germination approached 100% at the higher water potentials and at temperatures between 14 and 26°C (Fig. 1). The optimum temperature for maximum germination decreased as the level of water stress increased, i.e. 26°C at 0 MPa and 20°C at −1.25 MPa. At supra-optimal temperatures, seeds incubated in lower water potentials had a lower temperature threshold for germination. For example, at 32°C more than 60% of seeds germinated at 0 MPa while no appreciable germination occurred at 26°C at −1.28 MPa (Fig. 1).

The maximum germination at any water potential increased with temperature up to an optimum and then decreased sharply at supra-optimal temperatures (Fig. 1). The observation that the increase at sub-optimal temperatures and the decrease at supra-optimal temperatures are not vertical (Fig. 1) demonstrates seed-to-seed variation in response to temperature. To describe this variation in response, an empirical model was developed with the following assumptions:

(a) individual seeds have a minimum temperature for germination and a maximum temperature above which they will not germinate;
(b) seed-to-seed variation in these two temperature thresholds is normally distributed in the seed population; and
(c) these two temperature thresholds operate independently in each seed.

Modelling the minimum temperature limit

Mathematically, the fraction of seeds whose minimum temperature requirement is satisfied (Φ_{min} in normal equivalent deviates (n.e.d.)) increases with temperature (T) as follows:

$$\Phi_{min} = [K_0 + bT], \quad (4)$$

where K_0 is the fraction of the seed population (in n.e.d.) whose minimum temperature requirement is met at 0°C and b is the temperature coefficient

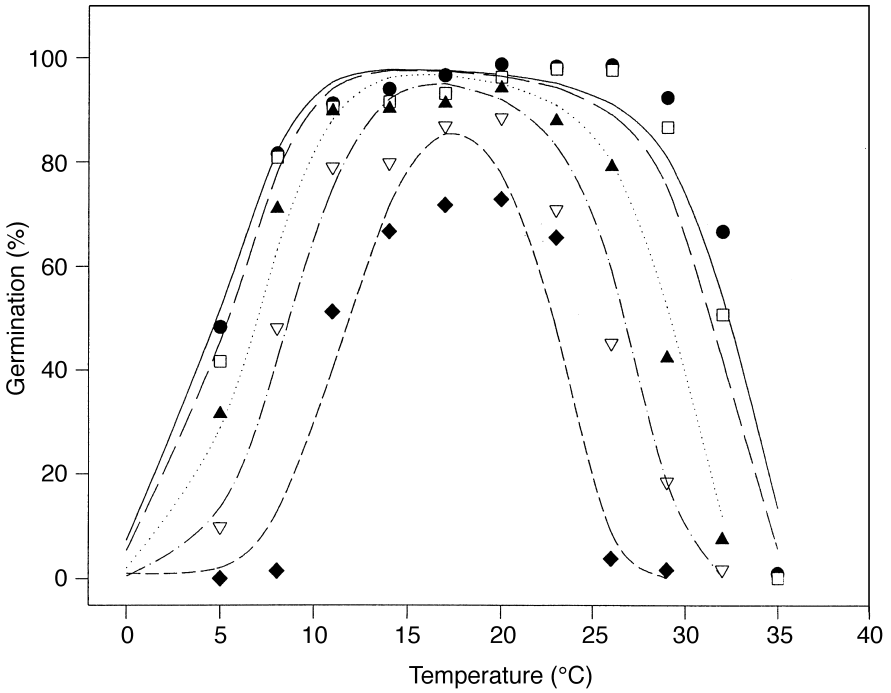

Figure 1. Germination percentages of *O. aegyptiaca* seeds incubated at various temperatures and water potentials. The lines were fitted according to equation (8) for the nominal water potentials at each temperature. The actual water potentials varied with temperature according to the ± values shown below. Water potentials are 0 (●, ——), −0.2 ± 0.04 (□, — —), −0.6 ± 0.06 (▲, ·····), −0.9 ± 0.1 (▽, · — · — ·) and −1.2 ± 0.13 MPa (◆, - - -).

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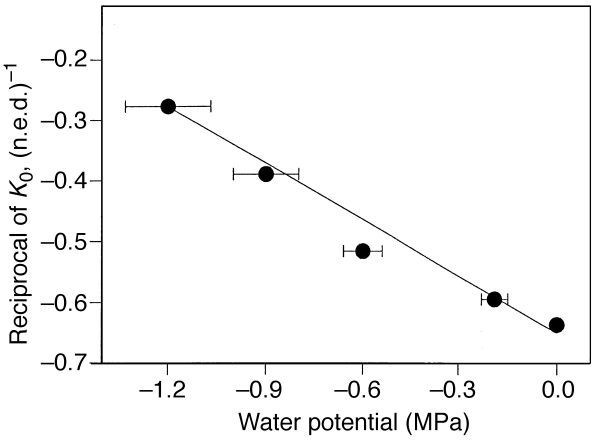

Figure 2. Relationship between the fraction of the seed population whose minimum temperature requirement is met at 0°C (K_0 in equation (4)) and water potential. Values at each water potential (●) relate to equation (4). The horizontal bars indicate the range of water potentials included in the analysis. The fitted line is $1/K_0 = -0.65 - 0.31\psi$ (Table 1) and $R^2 = 0.97$.

(n.e.d. °C^{-1}). The temperature coefficient is the reciprocal of the standard deviation of minimum temperature thresholds in the seed population.

When the model was run separately for the different water potentials, there was a systematic decrease in the estimated value of K_0 with decrease in water potential. However, the temperature coefficient (b) did not vary significantly ($P > 0.05$) between the different water potentials.

A linear effect of water potential on the reciprocal of the parameter K_0 (Fig. 2) accounted for the response. Incorporating this response in equation (4),

$$\Phi_{\min} = \left(K_w + a\psi\right)^{-1} + bT, \tag{5}$$

where K_w is the reciprocal of the fraction of the seed population (n.e.d.$^{-1}$) whose minimum temperature requirement is met at 0°C in water and a is the effect of water potential on K_w.

Modelling the maximum temperature limit

At supra-optimal temperatures, germinability declined according to a negative cumulative normal distribution and was an exponential function of maximum temperature (Kebreab and Murdoch, 1999c). Mathematically this can be expressed as follows:

$$\Phi_{\max} = \left[K_i + sr^T\right], \tag{6}$$

where Φ_{max} is the fraction of the seed population whose maximum temperature requirement for germination has not been exceeded (n.e.d.), K_i is the viability of seed lot (n.e.d.), s is the temperature coefficient for the decline of germinability with maximum temperature (n.e.d. ($\log_r$°C)$^{-1}$) and r is a constant. The value of r was estimated to be 1.17 as this value minimized the residual deviance in repeated analyses in which r was included as a constant. The model was run for all water potentials, and the initial viability was assumed not to vary because all the seeds used were from the same seed lot. The model explained over 93% of the variation in the data when analyzed separately for each water potential, and parameter estimates of s are shown in Fig. 3.

At supra-optimal temperatures, there was a linear effect of water potential on the reciprocal of the parameter s (Fig. 3). Equation (6) can, therefore, be rewritten as follows to include the effect of water stress:

$$\Phi_{\max} = \left[K_i + \left(c + d\psi\right)^{-1} r^T\right], \tag{7}$$

where c is the reciprocal of the parameter s in water ($\log_r$°C (n.e.d.)$^{-1}$) and d is the interaction of water potential and temperature, i.e. the effect of water potential on the value of $1/s$ ($\log_r$°C (n.e.d.)$^{-1}$ (MPa)$^{-1}$).

Assuming that the two relationships represented by equations (5) and (7) are independent, the actual proportion of seeds germinating is the product of these two functions after back-transformation of their respective n.e.d. values to probabilities. Using the

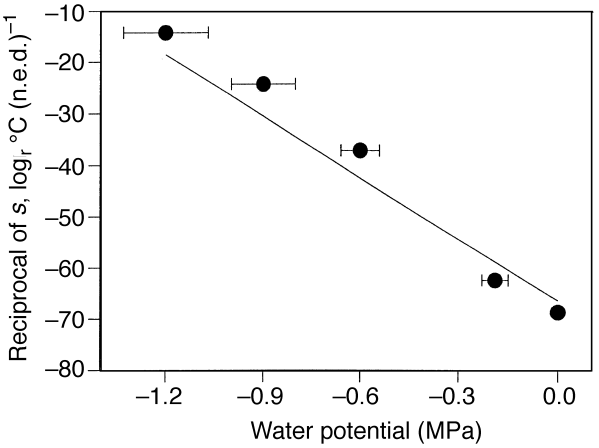

Figure 3. Relationship between water potential and the reciprocal of the temperature coefficient for decline of germinability with maximum temperature (s). Symbols representing the reciprocals of the estimated values of s relate to equation (6). The horizontal bars indicate the range of water potentials included in the analysis. The line uses parameter estimates in Table 1.

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symbol Φ^{-1} to indicate back-transformation, the maximum germination (G) at any temperature and water potential is given by:

$$G = (\Phi_{\min})^{-1}(\Phi_{\max})^{-1} = \Phi^{-1}\left[(K_w + a\psi)^{-1} + bT\right] \Phi^{-1}\left[K_i + (c + d\psi)^{-1} r^T\right]. \quad (8)$$

This model was used to analyze the raw data and estimate the parameters shown above directly from the data. The model explained 96% of the variation in final germination; the parameter estimates are given in Table 1. A comparison of the fitted model and the raw data is shown in Fig. 1.

Discussion

All treatments received an identical and optimal conditioning treatment (14 d at 20°C in water), so differences in subsequent germination when exposed to 3 ppm GR24 must be due to variability in water potential and temperature during the germination test. Longer conditioning periods are sub-optimal because secondary dormancy would be induced in the seeds (Kebreab and Murdoch, 1999a).

The observed final germination in water as a function of temperature was consistent with previous findings (Foy *et al*., 1991; Van Hezewijk *et al*., 1991; Weldeghiorghis and Murdoch, 1996). Apart from reducing the germination percentage, water potential also reduced the range of temperature over which highest germination occurs (e.g. from 11–26°C at 0 MPa to 17–21°C at −1.25 MPa) (Fig. 1).

Van Hezewijk *et al*. (1991) reported a similar pattern of the effect of temperature on final germination of *O. crenata* Forsk. in water. However, they did not quantify the relationship of temperature and germination, and their study was done only at one water potential. They reported an optimum temperature of 15–20°C in *O. crenata*. The slightly higher optimum reported here is very likely due to higher temperature tolerance of *O. aegyptiaca* seeds, as observed elsewhere (Kebreab and Murdoch, 1999a, b). Although Linke (1987) found that a reduction in water potential decreased the final germination of *O. ramosa* L., the effect was greater than reported here. For example, germination declined from 90 to 70% with a decrease in water potential from 0 to −0.2 MPa at room temperature (19–23°C) compared with a 2–3% reduction for *O. aegyptiaca* at such temperatures (Fig. 1), perhaps indicating a greater sensitivity to water stress in *O. ramosa*.

Attempts to account for germination as a function of temperature and moisture availability have mostly used empirical models such as quadratic, Weibull, logistic and Gompertz functions (e.g. Akanda *et al*., 1996; Gan *et al*., 1996). Although some of the models give a good fit to the data, this paper describes a model with parameters which have clearer biological meanings.

The model fitted in this paper adequately described the effects of water potential in reducing the maximum germination and also the temperature range for germination, although there was a tendency to reduce the upper temperature limit for highest germination (Fig. 1). With respect to the temperature range for germination, the model clearly defines seed-to-seed variation in both the minimum and maximum temperature limits. The variation in temperature range within the population is thus defined and may be calculated for any percentile. It is not, however, implied that there is a systematic link between the minimum and maximum temperature limits: the model assumes that the two limits are independent as far as individual seeds are concerned. The assumption of independence precludes inferences about the temperature ranges of individual seeds. A further possible consequence of independent temperature limits is that, at a given germination temperature, some seeds may not be above their minimum temperature and yet may have exceeded

Table 1. Parameter estimates and standard errors (SE) used in equation (8)

Parameter	Estimate	SE
Seeds whose minimum temperature requirement is met at 0°C in water (K_w)	−0.65	(0.08)
Effect of water potential on K_w (a)	−0.31	(0.01)
The temperature coefficient (minimum temperature threshold) (b)	0.31	(0.01)
Initial seed viability (K_i)	2.14	(0.16)
Reciprocal of temperature coefficient of maximum temperature threshold at 0 MPa (c)	−66.40	(5.63)
Interaction of temperature and water potential (d)	−39.90	(3.86)

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their maximum temperature limit. If true, the physiological mechanisms controlling the two limits must differ.

An objection to the model developed here may be that the parameters K_0, K_w and a relate to the theoretical behaviour of the seed lot at 0°C, a temperature at which the seeds are not expected to germinate. These three parameters relate directly to the median minimum temperature requirement in the seed population ($T_{min(50)}$, °C), i.e. the minimum temperature threshold for 50% of the seeds in the population, which is clearly not a theoretical parameter. In equation (4), (Φ_{min}) is by definition zero at the $T_{min(50)}$. Rearranging equation (4), the value of $T_{min(50)}$ at a given water potential is

$$T_{min(50)} = -K_0 / b. \quad (9)$$

Substituting for K_0 in equation (4),

$$\Phi_{min} = \left(T - T_{min(50)}\right)b. \quad (10)$$

In equation (5), the variation in K_0 with water potential (quantified by K_w and a) could then be interpreted by the variation in $T_{min\ (50)}$. A decrease in water potential gave rise to an exponential increase in $T_{min\ (50)}$ (Fig. 4).

Further work is needed to validate the model on other species and seed lots and to determine how parameter values vary between seed lots. Consequences of sub-optimal conditioning treatments (with respect to duration, temperature and water potential during conditioning) on parameter estimates also merit further study. In terms of general applicability of responses, Grundy (1997) found that the temperature range for maximum germination, at a given water potential, did not vary between seed lots of *Stellaria media* L.

For practical applications, in which it is intended to predict germination, equation (3) must be used in conjunction with equation (8). The final germination at a given temperature and water potential must first be predicted from equation (8). The progress of germination towards that maximum percentage may then be predicted from equation (3).

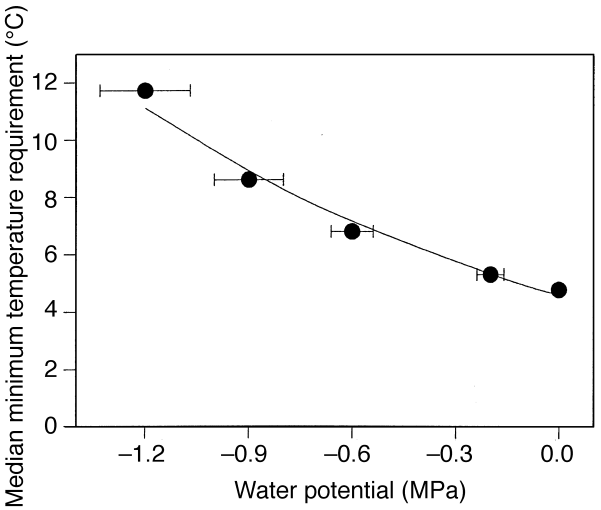

Figure 4. The effect of water potential on the median minimum temperature requirement for germination ($T_{min\ (50)}$). Values at each water potential (●) relate to equation (9). The horizontal bars indicate the range of water potentials included in the analysis. The fitted line is $T_{min\ (50)} = 4.6\ e^{-0.68\psi}$ ($R^2 = 0.98$).

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