

## Modelling Effects of Prolonged Conditioning on Dormancy and Germination of *Striga hermonthica*

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**Abstract:** The impact of environment on the germination biology of the parasite was studied in the laboratory with seeds conditioned at various water potentials, urea concentrations and at 17.5 to 37.5°C for up to 133 days. Maximum germination was observed at 20 to 25°C. Water stress and urea suppressed maximum germination. The final percentage germination response to period of conditioning showed a non-linear relationship and suggests the release of seeds from dormancy during the initial period and later on dormancy induction. Germination percentage increased with increase in conditioning period to a threshold and remained stable for variable periods followed by a decline with further extension of conditioning time. The decline in germination finally terminated in zero germination in most treatments before the end of experimentation. The investigated factors of temperature, water potential and urea showed clear effects on the expression of dormancy pattern of the parasite. The effects of water potential and urea were viewed as modifying a primary response of seeds to temperature during conditioning. The changes in germinability potential during conditioning were consistent with the hypothesis that dormancy periods are normally distributed within seed populations and that loss of primary dormancy precedes induction of secondary dormancy. Hence an additive mathematical model of loss of primary dormancy and induction of secondary as affected by environment was developed as:

$$G = \{[\Phi^{-1}(K_p + (p_o + p_n N + p_w W)(T - T_b) t)] - [\Phi^{-1}(K_s + ((s_w W + s_a) + s_r r^T) t)]\} [\Phi^{-1}(aT^2 + bT + c + c_w W)].$$

**Key words:** Germination, dormancy, modelling, factors, *Striga hermonthica*

### INTRODUCTION

Dormancy and germination generally are important phenological events that influence the success or failure of a plant and may be subject to precise regulation by external factors and characteristics within the seed (Forcella *et al.*, 2000). When seeds do not germinate or germinate poorly under favourable growth conditions, they are considered dormant. Primary dormancy in parasitic weed seeds sets in during seed development on the mother plant (Baskin and Baskin, 1998); whilst secondary dormancy usually develops under conditions which do not permit germination of seeds (Karssen, 1980/1981).

Conditions of imbibed storage environment are expected to influence the expression of dormancy and consequently the pattern of germination and subsequent emergence of weed seeds. Temperature has been identified as the main factor controlling changes in the degree of dormancy in temperate environments where

water is not seasonally restricted (Benech-Arnold *et al.*, 2000). The effect of temperature on dormancy release may however, be modified by other factors such as soil moisture (Reisman-Berman *et al.*, 1991; Christensen *et al.*, 1996; Benech-Arnold *et al.*, 2000; Forcella *et al.*, 2000). Progressive loss of dormancy in seed populations may be related to a progressive decrease in mean water potential (Bradford, 1995; Christensen *et al.*, 1996). Light, nitrate, smoke and other factors determine the dormancy status of a seed (Hilhorst, 1990; Bewley and Black, 1994; Baskin and Baskin, 1998; Forcella *et al.*, 2000).

*Striga hermonthica* is a root parasite of cultivated cereals that determines the food security pattern of the rural farming community in sub-Saharan Africa (Parker and Riches, 1993). During imbibed storage of seeds of the parasite, germination occurs in response to specific stimulatory action derived from root exudates of the hosts and sometimes non-hosts. When the transfer of seeds from the conditioning medium to a suitable stimulant is delayed beyond the optimum time, the final germination

percentage may reduce progressively to zero due to induction of secondary dormancy (Vallance, 1950; Reid and Parker, 1979; Sonko, 1998).

It is speculated that in the field secondary dormancy might determine the extent of field emergence of *Striga* as affected by delayed sowing (i.e., relative to the onset of major rains) (Parker and Riches, 1993; Pieterse and Verkleij, 1994). This trait could therefore lend support to realistic modelling of how long seeds of the parasite undergo imbibed storage for maximum germination in a given environment (Murdoch *et al.*, 2000). The few models on parasitic weeds are based on the assumptions put forward for *Rumex* spp. (Totterdell and Roberts, 1979). In their model, Totterdell and Roberts (1979) attributed the optimum period for stratification required at 1.5 to 15°C to the physiological processes of loss of primary dormancy and induction of secondary dormancy. It is reasonable to assume a close relationship between the behavior of *Rumex* spp. (Totterdell and Roberts, 1979) during prechilling and that of *S. hermonthica* during imbibed storage. The main difference in the germination responses of the seeds is that the stimulation of *Rumex* seeds is provided by a shift to warmer temperature, whereas that of *S. hermonthica* comes from host exudates or synthetic analogues.

It was suggested that empirical modelling focus on integration of important soil factors for enhanced prediction of the direct and interactive effects on dormancy release and induction and subsequent influence on seed germination (Forcella *et al.*, 2000). However, information on the relationship between extended conditioning periods (as pertains in fields of *S. hermonthica*) and seed dormancy and germination, due to temperature is limited to 20 to 35°C and non-existent in the literature with respect to water potential and urea concentrations. Due to the ecological niche of the parasite, this paper attempted to widen the temperature range from 17.5 to 37.5°C and also examine variation in water potentials and urea concentrations on expression of dormancy and germination.

The objectives of this research were to examine the dormancy and germination response of *S. hermonthica* over a wide range of conditioning environments including temperature, water potential and urea as variables and thereby provide a model for conditioning and secondary dormancy of *S. hermonthica* seeds so that planting date effects on *Striga* infestation in the field can be predicted.

The investigations were based on the hypotheses that seed-to-seed variation with respect to periods for loss of primary dormancy and induction of secondary dormancy are normally distributed in populations of imbibed seeds and these processes occur sequentially and the secondary process is dependent on the primary

process in each individual seed and are determined by temperature, water potential and nitrogen during conditioning.

## MATERIALS AND METHODS

Seeds of the Sudanese seed lot of *S. hermonthica* (Wad Merki strain) were utilized in the two experiments carried out in 2002 in the Seed Science Laboratory of the School of Agriculture at the University of Reading, UK. *Striga* seeds were collected on sorghum by Dr. A.G.T. Babiker and stored at the University of Reading in 1996 by Dr. Drennan and later on moved to the Seed Science Laboratory by Dr. A.J. Murdoch and stored at 3±2°C.

All non-sterile materials and equipment used in the experiments were sterilised by autoclaving to get rid of microbial contaminants such as bacteria and fungi during the processes of conditioning and germination following the procedure of Kebeab and Murdoch (1999).

In addition to temperature and water potential, other germination requirements were satisfied. The artificial germination stimulant-GR24, at 3 ppm was used. The procedure of Michel and Kaufmann (1973) was used in the preparation of all osmotic potentials using aqueous solutions of polyethylene glycol (PEG 6000, Merck). However, the empirical equation for polyethylene glycol 8000 (PEG) (Michel, 1983) was used in the calculations for preparation of water potential solutions as follows:

$$\Psi = 1.29 [\text{PEG}]^2 T - 140 [\text{PEG}]^2 - 4.0 [\text{PEG}] \quad (1)$$

Where  $\Psi$  is the required osmotic potential (bars), converted to Mega Pascal (bars/10), [PEG] is the concentration of polythene glycol 8000 (g PEG/g H<sub>2</sub>O) and T is the temperature (°C). Osmotic potentials of -2.25, -1.5, -0.75, -0.25 and 0 MPa were prepared.

**Experiment 1:** To examine the effects of loss of primary dormancy and induction of secondary dormancy in *S. hermonthica*, seeds were conditioned at constant temperatures of 17.5, 20, 25, 30, 35 and 37.5°C, water potentials of 0, -0.25, -0.75, -1.5 MPa and in 0, 316 and 3.16 mM urea factorially combined in various incubators.

The preparation of the PEG solutions containing the desired urea N concentrations for each temperature, the seed conditioning and germination procedure were reported in an earlier paper (Dzomeku and Murdoch, 2007).

**Experiment 2:** Experiment 2 was designed using a more limited range of treatments to confirm the results of experiment 1 on dormancy and germination responses of

*S. hermonthica* seeds to imbibed storage conditions of temperature, water potential and urea. *S. hermonthica*, seeds were conditioned according to procedures used for experiment 1 at constant temperatures of 20, 30 and 35°C, water potentials of 0,-0.25,-0.75,-2.25 MPa and in 0 and 0.083 mM urea in various incubators. Due to the high germination after conditioning at 1.5 MPa in experiment 1, it was decided to increase the water stress treatment in this experiment to -2.25 MPa.

**Approach to model development:** Development of the composite model was carried out by first examining the effects of temperature and then the simultaneous influences of water potential and urea on the rate of loss of primary dormancy in both experiments 1 and 2. This approach was used to determine and select the factor most consistently influencing the rate. This became necessary to justify the development of the model on temperature before description of the effects of water potential and urea on the temperature model. Temperature is, however, the basis of most conditioning models presented in the literature (Ibrahim and Roberts, 1983; Washitani, 1987; ZebtabSamasi, 2006). For the sake of comparison of the results with the existing literature on parasitic weeds therefore, it is rational to use temperature as the base of quantifying the present data. The conditioning model was based on the results of experiment 1 and the model fitted to the data of experiment 2 for validation purposes.

**Statistical handling of data:** Non-linear modelling was carried out using the fitnonlinear directive to analyse proportions of seed germination along the lines of probit analysis in Genstat (Anonymous, 2002) of seed conditioning data. Composite non-linear models were fitted. Final seed Germination (G) of the parasite was modelled as the difference between number of seeds which have lost primary dormancy ( $\Phi^{-1}_p$ ) and the number that have induced secondary dormancy ( $\Phi^{-1}_s$ ) multiplied by the potential germinability of the seed population in a given environment  $\Phi^{-1} K_g$ , using:

$$G = [\Phi^{-1}(K_p + pt)] - [\Phi^{-1}(K_s + st)] [\Phi^{-1} K_g] \quad (2)$$

as the separate line model. This equation was analysed based on the assumption that the intercept  $K_p$  was common to both the primary and secondary functions such that  $K_p = K_s = -3$  ned and  $s \leq p$ ,  $p$  estimates the rate of loss of primary dormancy during conditioning (ned day<sup>-1</sup>) for  $t$  days and  $s$  estimates the rate of induction of secondary dormancy during conditioning (ned day<sup>-1</sup>). By employing probit analysis, it was

assumed that the error variance has binomial distribution within the seed population. Mead and Gray (2002) developed the method of weighting for the binomial error distribution used in this study when using the Genstat directive fitnonlinear to analyze proportions along the lines of probit analyses.

A comparison and selection of the best regression model was carried out based on two criteria: (a) their residual sum of squares and their corresponding variance degrees of freedom where appropriate and (b) the precision of the fitted curve relative to the observed data. Parameter estimates were substituted in the equations for respective models and fitted to the observed data. The observed germination was transformed into normal equivalent deviates (ned) and back transformed into percentages before plotting. Since the probit analyses cannot handle zeros, germination data was adjusted before analysis to 0.5% (i.e., for 100 seeds per replicate, zero germination is equivalent to 0.5 seed germination divided by the total number of seeds (0.5+99.5) multiplied by 100%.

The effect on final percentage seed germination of the period of conditioning in forty out of the seventy-two environments have been described by the additive probability model. The model was based on data collected from 17.5 to 35°C, 0 to -1.5 MPa and 0 to 0.316 mM urea. The data on the effects of conditioning in 3.16 mM urea at all temperatures and water potentials were not included in the model. Similarly data at 37.5°C in the other environments examined were also not modelled. With the exception of the effect of 3.16 mM urea at 0 MPa and 17.5 to 35°C, the rest of the data at 3.16 mM urea could not be fitted to the model using GENSTAT. It appears that in most of these environments, rates of both loss of primary dormancy and induction of secondary dormancy were very rapid.

## RESULTS

**Modelling loss of primary dormancy:** Seed germination was modelled based on the separate line model of Eq. 2. For temperatures of 17.5-35°C the rates of loss of primary dormancy increased approximately linearly with increase in the conditioning temperature. As such Eq. 2 was rewritten as,

$$G = [\Phi^{-1}(K_p + (p_0 + p_T T)t)] - [\Phi^{-1}(K_s + s t)] [\Phi^{-1} K_g] \quad (3)$$

Where  $p_0$  is the rate of loss of primary dormancy during conditioning at 0°C and  $p_T$  is the temperature coefficient.

Given a linear model, there is clearly a base temperature ( $T_0$ ) for conditioning at which the loss of

primary dormancy in the population per unit time ( $P_0 = -P_T T_b$ ) is zero. As such  $pp_0 = -p_T T_b$ . Eq. 3 can therefore, be rewritten as follows:

$$G = [\Phi^{-1}(K_p + (p_T(T - T_b))t)] - [\Phi^{-1}(K_s + s t)] [\Phi^{-1} K_g] \quad (4)$$

The analyses of deviance of the linear model of Eq. 4, however, showed significant increases in residual deviance compared with the separate line model. The deviance ratios for seeds conditioned without urea at 0, -0.25, -0.75 and -1.5 MPa were, respectively  $F = 19$  on 3 and 1049 df,  $p < 0.0001$ ,  $F = 7.3$  on 3 and 449 df,  $p < 0.001$ ,  $F = 14.7$  on 3 and 405 df,  $p < 0.001$  and  $F = 17$  on 3 and 425 df,  $p < 0.001$ . For seeds conditioned in 0.316 mM urea, the deviance ratios at 0, -0.25, -0.75 and -1.5 MPa were, respectively  $F = 19.67$  on 3 and 473 df,  $p < 0.001$ ,  $F = 17.67$  on 3 and 445 df,  $p < 0.001$ ,  $F = 23.67$  on 3 and 411 df,  $p < 0.001$  and  $F = 6.3$  on 3 and 400 df,  $p < 0.001$ .

The variable (i.e., different  $T_b$  for each water potential and urea treatment combination) base linear temperature model of Eq. (4) nevertheless explained more than 91% of the variance in all the conditioning environments (0 MPa, 97%, -0.25 MPa, 97%, -0.75 MPa, 94%, -1.5 MPa, 93% and in the presence of 0.316 mM N at 0 MPa, 95%, -0.25 MPa, 97%, -0.75 MPa, 93% and -1.5 MPa, 92%). The implication of these correlations is that the rate of relief of primary dormancy generally increases with increase in conditioning temperature in a way, which is fairly well described by a linear model.

In order to get a usable model, there was the need to reduce further the number of parameters. For a seed lot, it is reasonable to assume a common value for  $T_b$  irrespective of the conditioning environment. This was estimated by analysing the results from the different treatments together. Within Eq. 4, the common base temperature model was similar to the linear model in some of the conditioning environments being at 0 MPa ( $F = 1$  on 1 and 1952 df,  $p > 0.05$ ), -0.25 MPa ( $F = 1$  on 1 and 452 df,  $p > 0.05$ ), -0.75 MPa ( $F = 6$  on 1 and 408 df,  $p > 0.05$ ), -1.5 MPa ( $F = 28$  on 1 and 452 df,  $p < 0.001$ ) and in 0.316 mM urea at 0 MPa ( $F = 1$  on 1 and 476 df,

$p > 0.05$ ), -1.5 MPa ( $F = 1$  on 1 and 403 df,  $p > 0.05$ ). Parameter estimates and standard errors are given in Table 1.

The common base temperature model (Eq. 4) on loss of primary dormancy (Fig. 9) also accounted for more than 91% of the variance in all the conditioning environments (0 MPa, 97%; -0.25 MPa, 97%; -0.75 MPa, 94%; -0.5 MPa, 93% and in the presence of 0.31 mM N at 0 MPa, 95%; -0.25 MPa, 97%; -0.75 MPa, 93% and -1.5 MPa, 92%).

The quadratic model was tested on the rate of loss of primary dormancy to confirm the linearity of the rate response to temperature. The model reduced the residual deviance significantly ( $F = 9$  on 2 and 4166 df,  $p < 0.01$ ) compared with the common  $T_b$  linear model. However, at conditioning temperatures of 25-35°C and water potentials of -0.75 and -1.5 MPa, the increase in  $p$  with increase in temperature was higher than at lower temperatures (Fig. 1C and D). The reverse was the case with  $p$  at same temperatures in -0.75 MPa (Fig. 1G). Overall, the linear model should therefore give a better fit to the data than the quadratic when modelling the forty environments. This was confirmed by the inability to fit the quadratic model in Genstat when accounting for the effects of water potential and urea in the composite model.

In Table 1 the estimated theoretical base temperature for loss of primary dormancy was c. 11.2°C. Parameter  $K_p$  was fixed at -3 ned equivalent to 0.2% germination, which supports the hypothesis of an absolute requirement for conditioning of *Striga* seeds prior to exposure to stimulants for germination.

The effect of temperature on the rate of loss of primary dormancy varied with the conditioning water potentials and urea concentrations (Fig. 1 and Table 1). Except for the conditioning treatment at -0.75 MPa, the rate of loss of primary dormancy decreased with increase in water potential ( $p < 0.001$ ). The rate of loss of primary dormancy decreased and was lowest with increase in urea concentration from 0 to 0.316 mM (Fig. 1E and Table 1). Exclusion of -0.75 MPa, the rate of loss of primary dormancy decreased with increase in water potential in the presence of 0.316 mM urea. As such seeds conditioned at -1.5 MPa without (Fig. 1D and Table 1) and with 0.316 mM urea (Fig. 1H; Table 1) were the most sensitive to changes in conditioning temperature.

Table 1: Parameter estimates and standard errors (in brackets) for loss of primary dormancy in Eq. 4 for seeds conditioned in different water potentials and urea. Note that the value of  $K_p$  was fixed arbitrarily.  $K_p$  and  $T_b$  are common to both urea levels

Parameter	0 MPa	-0.25 MPa	-0.75 MPa	-1.5 MPa
A Without urea				
p	0.0432 (0.0004)	0.0499 (0.0007)	0.0441 (0.0008)	0.0577 (0.0013)
$T_b$	11.201 (0.138)			
$K_p$	-3 (N/A)			
B. With 0.316 mM urea				
p	0.0397 (0.0006)	0.0482 (0.0007)	0.0453 (0.0009)	0.0586 (0.0016)

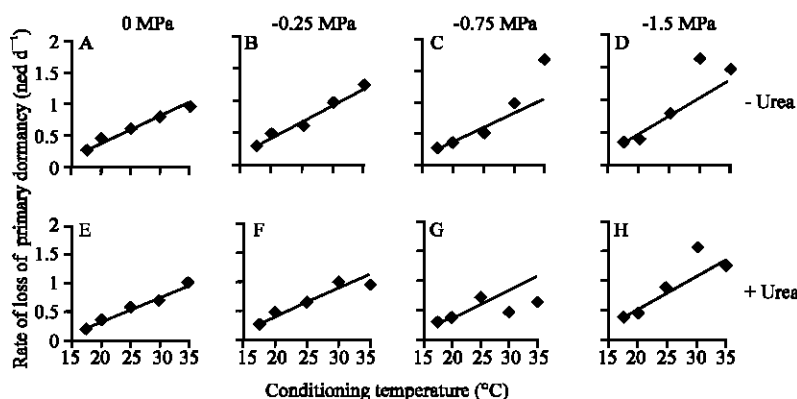


Fig. 1: Rate of loss of primary dormancy during conditioning in seeds of *Striga hermonthica* as a function of conditioning temperature without urea in water potentials of (A) 0 MPa, (B) -0.25 MPa, (C) -0.75 MPa and (D) -1.5 MPa and with 0.316 mM urea at (E) 0 MPa, (F) -0.25 MPa, (G) -0.75 MPa and (H) -1.5 MPa. The symbol (◆) represent values of the parameter p in Eq. 2 derived independently for each temperature or lines were fitted according to Eq. 4 with a common base temperature for parameter p. Parameter estimates and standard errors are given in Table 1

**Interaction of water potential and urea on the effect of temperature on loss of primary dormancy of *Striga hermonthica* seeds:**

The effect of water potential on the temperature coefficient for loss of primary dormancy could be approximately described by an inversely linear function. This influence on  $p_T$ , was accounted for in the model by revising Eq. 4. Since only two levels of urea was included in the model, it was assumed to have linear effect on the intercept of the water potential effect. To take account of these interactions with temperature, Eq. 4 can be rewritten as:

$$G = \{[\Phi^{-1}(K_p + ((p_{T_0} + p_n N + p_w W)(T - T_b))t)] - [\Phi^{-1}(K_s + s t)]\} [\Phi^{-1}(K_g)] \quad (5)$$

Where  $p_{T_0}$  is the value of  $p_T$ (Eq. 3) at 0MPa without urea,  $p_n$  is the interaction of urea and temperature coefficient, N is urea concentration (0.316 mM),  $p_w$  is the interaction of water potential and temperature coefficient and W is water potential (MPa).

Including these effects of water potential and urea on the rate of loss of primary dormancy reduced the residual deviance significantly (F = 90.5 on 2 and 4166 df,  $p < 0.001$ ). The parameter estimates and standard errors for Eq. 5 are given in Table 2. The model explained 93.6% of the variation in the data set.

The analysis was carried out by dropping the nitrogen term ( $p_n$ ) in Eq. 5 to confirm the influence of urea on loss of primary dormancy. The results increased the residual deviance significantly (F = 41 on 1 and 4164 df,  $p < 0.001$ ) compared with Eq. 5 indicating that urea influenced the rate of loss of primary dormancy.

Likewise to test the hypothesis that water potential does not affect the process of loss of primary dormancy Eq. 5 was mathematically revised as:

Table 2: Parameter estimates and standard errors (in brackets) after including the effects of water potential and urea on the temperature model on loss of primary dormancy in Eq. 5 of *S. hermonthica* seeds conditioned in different water potentials, urea concentrations and temperature regimes, derived from experiment 1

Parameter	Estimate	Parameter	Estimate
$K_p$	-3 (N/A)	$p_n$	-0.0102 (0.0015)
$T_b$	11.201 (0.138)	$p_w$	-0.005 (0.0004)
$p_{T_0}$	0.0506 (0.0004)		

$$G = \{[\Phi^{-1}(K_p + ((p_{T_0} + p_n N)(T - T_b))t)] - [\Phi^{-1}(K_s + s t)]\} [\Phi^{-1} K_g] \quad (6)$$

Quantifying the effect of urea concentration ( $p_n$ ) alone on loss of primary dormancy in Eq. 6 to confirm the influence of water potential on the primary process resulted in an increased residual deviance (F = 127 on 1 and 4164 df.,  $p < 0.001$ ) compared with Eq. 5. This result implies that water potential has a more profound influence than urea on rate of loss of primary dormancy.

**Modelling induction of secondary dormancy:**

The relationship between the rate of induction of secondary dormancy as a function of temperature showed that as temperature increases, the increase in this rate tended towards an asymptote and was maximised at about 25°C (Fig. 2). Equation 5 was therefore modified to account for this exponential response of the rate of induction of secondary dormancy to temperature such that:

$$G = \{[\Phi^{-1}(K_p + ((p_{T_0} + p_n N + p_w W)(T - T_b))t)] - [\Phi^{-1}(K_s + s_a + s_r T^T) t]\} [\Phi^{-1} K_g] \quad (7)$$

Where  $s_a$  is the asymptotic rate of induction of secondary dormancy as temperature increases,  $s_r$  is the range of the

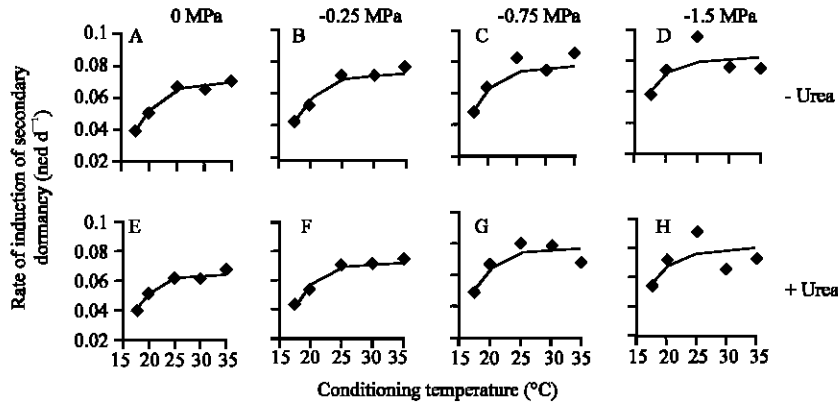


Fig. 2: The rate of induction of secondary dormancy of *S. hermonthica* seeds during conditioning as a function of conditioning temperature without (A-D) and with (E-H) 0.316 mM urea at water potentials of 0 MPa (A,E), -0.25 MPa (B,F), -0.75 MPa (C,G) and -1.5 MPa (D,E) in experiment 1. The numbers were derived independently for each temperature (symbols) using Eq. 2 or lines were fitted according to Eq. 7. Parameter estimates and standard errors are given in Table 3

Table 3: Parameter estimates and standard errors (in brackets) for induction of secondary dormancy in Eq. 7 for seeds conditioned in different water potentials and urea concentrations derived from experiment 1. Note that  $s_a$  had to be common for all water potentials and both levels of urea to enable the fitting of the data in Genstat

Parameter	0 MPa	-0.25 MPa	-0.75 MPa	-1.5 MPa
A. With 0 mM urea				
$s_a$	0.0678 (0.0006)	0.0721 (0.0009)	0.0804 (0.0013)	0.0811 (0.0013)
r	0.7622 (0.0012)	0.7631 (0.0019)	0.7656 (0.0026)	0.7483 (0.0045)
$s_b$	-3.4607 (7.58)			
B. With 0.316 mM urea				
$s_a$	0.0639 (0.0008)	0.0716 (0.0009)	0.0751 (0.0015)	0.0785 (0.0016)
r	0.7546 (0.0019)	0.7632 (0.0019)	0.7555 (0.0034)	0.7503 (0.0048)

curve between the rate of induction at 0°C and the asymptote and r defines the rate of exponential increase. Table 2 shows the parameter estimates and standard errors.

The asymptotic exponential model of temperature (Eq. 7) on the rate of induction of secondary dormancy increased the residual deviance (F = 31.33 on 3 and 4164, p<0.001) compared with the model on loss of primary dormancy (Eq. 5).

Within the range of temperature tested, the predicted lowest rate of induction of secondary dormancy was at 17.5°C. The highest rates generally occurred at 25 to 35°C. The exponential model of temperature explained 93.5% of the variance in the rate of induction of secondary dormancy. The quadratic relationship between the rate of induction of secondary dormancy and temperature was tested. The model increased the residual deviance (F = 114 on 1 and 4068 df, p<0.001) compared with the asymptotic exponential model (Eq. 7).

The asymptotic rate ( $s_a$ ) of induction of secondary dormancy significantly (p<0.05) increased with increasing water potential between tested range of 0 and -0.75 MPa (Table 3). Conditioning in urea resulted in a lower mean asymptotic rate of induction of secondary dormancy. The parameter increased with increase in water potential within the full range of the factor in 0.316 mM urea.

The rate of exponential increase (r) in induction of secondary dormancy remained constant over the range of water potential of 0 to -0.75 MPa but decreased with an additional decrease in water potential to -1.5 MPa (Table 3). However, in 0.316 mM urea, the estimated r increased with decrease in water potential within the full range of the factor tested.

**Interaction of water potential and urea on the effect of temperature on induction of secondary dormancy of *Striga hermonthica* seeds:**

The effect of water potential on the asymptote ( $s_a$ ) of the exponential rate of induction of secondary dormancy was modelled on the hypothesis of a quadratic increase in  $s_a$  with increase in water potential (Table 4). To achieve this Eq. 7 was rewritten as:

$$G = \{[\Phi^{-1}(K_p + ((p_{T_0} + p_n N + p_w W) (T - T_b)))t] - [\Phi^{-1}((K_s + ((s_q W^2 + s_w W + s_a) + s_r T)))] [\Phi^{-1}K_g] \} \quad (8)$$

Where  $s_q$  and  $s_w$  are quadratic and linear water potential coefficients, respectively. The quadratic effect of water potential on the parameter significantly reduced the residual deviance (F = 1915 on 2 and 4068 df, p<0.001) compared with Eq. 7.

Table 4: Parameter estimates and standard errors (in brackets) after including the effects of water potential and urea on the temperature model of induction of dormancy in Eq. 9 of *S. hermonthica* seeds conditioned in different water potentials, urea concentrations and temperature regimes, derived from experiment 1

Parameter	Estimate	Parameter	Estimate
K <sub>d</sub>	-3 (N/A)	sw	-0.0232 (0.0004)
T <sub>b</sub>	11.201 (0.138)	sa	0.0638 (0.0004)
p <sub>to</sub>	0.0489 (0.0004)	so	-4.33 (1.04)
p <sub>n</sub>	-0.0101 (0.0014)	r	0.751 (0.0106)
p <sub>w</sub>	0.005 (0.0004)		

The linear effect of water potential on the parameter on (s<sub>a</sub>) was also tested by revising Eq. 8 as follows:

$$G = \{[\Phi^{-1} (K_p + ((p_{to} + p_n N + p_w W) (T - T_b)))t] - [\Phi^{-1}((K_s + ((s_w * W + s_a) + s_r r^T)t)]\} [\Phi^{-1} K_g] \quad (9)$$

The model of a linear decrease in s<sub>a</sub> with increase in water potential gave a slight increase in residual deviance (F = 5 on 1 and 4065 df, p<0.05) relative to the quadratic model of water potential (Eq. 8). Nevertheless the inclusion of Eq. 9 in the final composite model gave a better fit to the experimental data compared with using Eq. 8.

The interaction effect of water potential and urea on (s<sub>a</sub>) was also quantified on the assumption of a linear effect of water potential on parameter s<sub>a</sub> and urea modifying the intercept of the water potential curves (Eq. 10).

$$G = \{[\Phi^{-1} (K_p + ((p_{to} + p_n N + p_w W) (T - T_b)))t] - [\Phi^{-1} ((K_s + ((s_a + s_n N + s_w W) + s_r r^T)t)]\} [\Phi^{-1} K_g] \quad (10)$$

Where s<sub>n</sub> is the urea coefficient, N is urea concentration, s<sub>w</sub> is the water coefficient and W is water potential.

However, modelling the interaction effects of water potential and urea on induction of secondary dormancy showed that the presence of urea did not alter the residual deviance (F = 1 on 1 and 4166 d.f., p>0.05) compared with Eq. 9. Therefore, Eq. 9 was selected as the best among the models evaluated based on the ability to fit the experimental data.

**Modelling the potential germinability of the seed lot:** By the use of the additive model, it was necessary to modify parameter K<sub>g</sub> that was used in the previous models on parasitic weeds to quantify the proportion of viable seeds (Sonko, 1998; Kebreab and Murdoch, 1999). The potential germinability K<sub>g</sub> by the additive model assumes that the germinability in any given environment is the combination of the proportion of viable seeds and the reduction in maximum germination due to treatment in the given

conditioning environment. Inspection of the relationship of K<sub>g</sub> with temperature after modelling the effects of the factors on primary and secondary dormancy suggested that a quadratic function might account for much of the variation such that Eq. 9 was revised as:

$$G = \{[\Phi^{-1} (K_p + (p_o + p_n N + p_w W) (T - T_b)t)] - [\Phi^{-1} (K_s + ((s_w W + s_a) + s_r r^T)t)]\} [\Phi^{-1} (aT^2 + bT + c)] \quad (11)$$

Where T is temperature in °C, a and b are quadratic and linear temperature coefficients, respectively. The hypothetical potential germinability at 0°C is quantified by the constant c.

The estimated value of the constants a remained similar at all water potentials in the absence of urea (Table 5). However, the value of b decreased significantly (p<0.05) with decrease in water potential without urea. The theoretical potential germinability at 0°C (parameter c) was similar at 0 and -0.25 MPa but decreased with further decrease in water potential below -0.25 MPa without and with urea. In urea, a and b did not show a consistent trend of variation with water potential. The mean value and standard errors in brackets of parameter c in water and urea were -1.877 (0.112) respectively -1.599 (0.134) and were statistically similar.

Ultimately, if loss of primary dormancy and induction secondary dormancy are dependent, then the number of seeds Germinating (G) is most simply modelled according to Eq. 11 which describes (a) the probability or the proportion of seeds which have lost primary dormancy and (b) the probability or the proportion of seeds which have got secondary dormancy induced and their product with the (C) the proportion of germinable seeds (the potential germinability) of the seeds in a given environment. Based on the assumption of binomial error distribution, a weighted regression was carried out since there was no loss of seed viability (data not shown) during conditioning.

The model (Eq. 11) explained over 90% of the variance in seed germination (0 MPa, 96.6%; -0.25 MPa, 96.8%, -0.75 MPa, 93% and -1.5 MPa, 93%; 0.316 mM N, 95%; -0.25 MPa and 0.316 mM N, 97%; -0.75 MPa and 0.316 mM N, 91%; -1.5 MPa and 0.316 mM N, 91%).

**Interaction effects of water potential and urea on potential germinability of *S. hermonthica*:** The relationship between water potential and the theoretical potential germinability at 0°C indicated a quadratic association. It was therefore hypothesised that an increase in water potential during seed conditioning results in quadratic increases in potential germinability at

zero degree Celcius. Equation 11 was therefore rewritten to test the quadratic effects of water potential on parameter c.

$$G = \{[\Phi^{-1}(K_p + (p_o + p_n N + p_w W)(T - T_b)t)] - [\Phi^{-1}(K_s + ((s_w W + s_a) + s_o r^T)t)]\} / [\Phi^{-1}(aT^2 + bT + (c + c_q W + c_w W^2))] \quad (12)$$

The model Eq. 12 further reduced the residual deviance (F = 1694 on 2 and 4164 df, p < 0.001) compared with Eq. 11, but could not fit the data well.

To test the interaction of linear effects of water potential and urea on parameter c, Eq. 12 was rewritten as:

$$G = \{[\Phi^{-1}(K_p + (p_o + p_n N + p_w W)(T - T_b)t)] - [\Phi^{-1}(K_s + ((s_w W + s_a) + s_o r^T)t)]\} / [\Phi^{-1}(aT^2 + bT + c + c_n N + c_w W)] \quad (13)$$

Where c is the potential germinability at 0°C, 0 MPa without urea and c<sub>n</sub> and c<sub>w</sub> are respectively the coefficients for the effects of urea and water potential on c.

The resultant model of Eq. 13 could not be compared statistically to model Eq. 12 because of equivalent degrees of freedom. The model also did not fit the observe data well especially, the urea treatments. Equation 13 was simplified to test the linear effect of water potential on c as:

$$G = [\Phi^{-1}(K_p + (p_o + p_n N + p_w W)(T - T_b)t)] - [\Phi^{-1}(K_s + ((s_w W + s_a) + s_o r^T)t)] / [\Phi^{-1}(aT^2 + bT + c + c_w W)] \quad (14)$$

The composite model Eq. 14 increased the residual deviance (F = 364 on 1 and 4162 df, p < 0.001) relative to Eq. 12. The model Eq. 14 however, gave a better fit to the observed data compared with Eq. 12 and 13.

The composite model Eq. 14 resulted in an increase in residual deviance compared with the separate line model Eq. 2 (Table 6). The conditioning composite model nevertheless explained 95.3% of the variation in the population of *S. hermonthica* seeds stored under imbibed conditions in the forty environments modelled.

**Laboratory validation of the conditioning model:** Predicted changes in the final percentage germination due to conditioning effects of temperature, water potential and urea of model Eq. 14 were generally close to those determined from germination time course curves of seeds of the same seed lot in most of the environments tested in experiment 2 (Fig. 5).

## DISCUSSION

### Final percentage germination response of *Striga hermonthica* seeds to prolonged conditioning:

The final percentage germination response to period of conditioning showed a non-linear relationship and suggests the release of seeds from dormancy during the initial period and later on dormancy induction (Fig. 3 and 4). As such germination percentage increased with increase in conditioning period to a threshold and remained stable for variable periods followed by a decline with further extension of conditioning time. The investigated factors of temperature, water potential and urea concentration therefore showed clear effects on the expression of dormancy pattern of the parasite. The effects of water potential and urea were viewed as modifying a primary response of seeds to temperature during conditioning. As in the previous analyses on the relationship of the germination of *S. hermonthica* (Sonko, 1998) and *Orobanch*e species (Kebreab and Murdoch, 1999) with temperature, it was easy to differentiate between the loss of primary dormancy and induction of secondary dormancy in the present experiments. Seeds that germinated after the conditioning process and on exposure to 3 ppm of GR24 at 35°C were considered to have undergone loss of primary dormancy (Murdoch *et al.*, 2000) and did not have secondary dormancy induced in them. After the stimulation period, non-germinated but viable seeds (determined by tetrazolium test, data not shown) were considered to have developed secondary dormancy or wet dormancy as first stated by Vallance (1950). The pattern of response reported in this thesis on loss of primary dormancy and induction of secondary dormancy agrees with those earlier reported for *S. hermonthica* (Vallance, 1950; Reid and Parker, 1979; Sonko, 1998).

The findings of the present experiment confirm the hypothesis that seed germination can be quantified by the net result of two sub-processes in *S. hermonthica* (Sonko, 1998) as in *Rumex* sp. (Totterdell and Roberts, 1979) and in three *Orobanch*e sp. (Kebreab and Murdoch, 1999). One notable difference between the current and the previous models, however, is the use of the additive model rather than the multiplicative probability model to quantify the net final germination. In addition the earlier multiplicative model on *S. hermonthica* (Sonko, 1998) was limited to conditioning in water at 20 to 35°C. The use of the additive (or more strictly subtractive) model suggests that the processes of loss of primary dormancy and induction of secondary dormancy are dependent and sequential. In addition, because germination is a binary response (Murdoch *et al.*, 2000), the net germination was



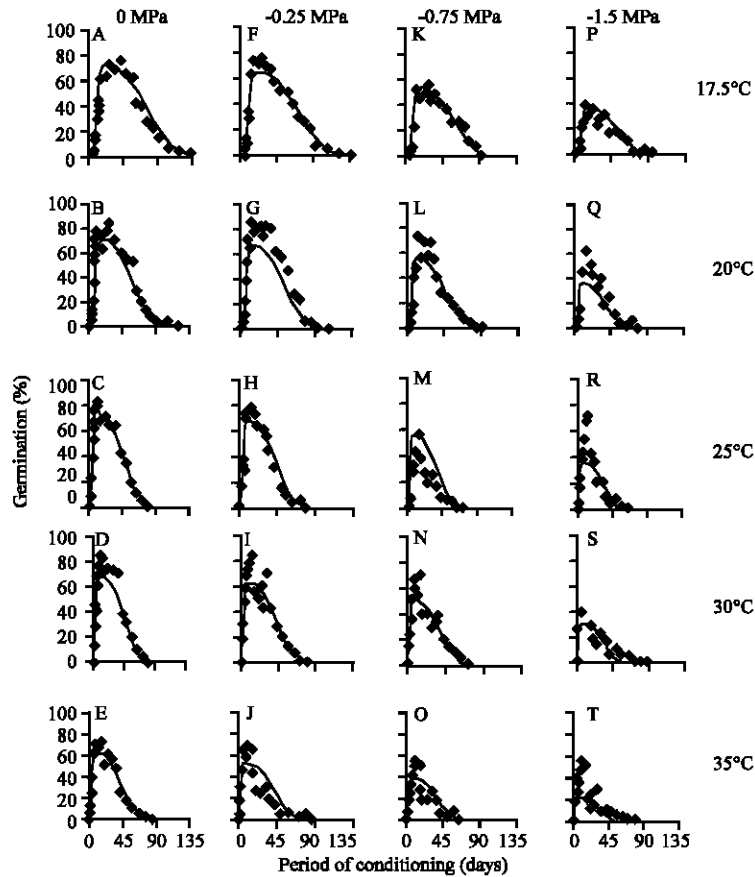


Fig. 3: Final percentage germination of *Striga hermonthica* seeds after conditioning at temperatures of 17.5 (A,F,K,P), 20 (B,G,L,Q), 25 (C,H,M,R), 30 (D,I,N,S) and 35°C (E,J,O,T) at water potentials of 0 (A-E), -0.25 (F-J), -0.75 (L,M,N,P,Q) and -1.5 MPa (P-T) for up to 19 weeks in experiment 1. Lines were fitted by Eq. 14 with composite lines fitted. Parameter estimates (and standard errors) of fitted lines are shown in Table 7

assumed to have binomial error distributions. Murdoch *et al.* (2000) suggested that assumptions of models have physiological implications. In the case of the multiplicative model, where the underlying processes are assumed to occur independently, the component physiological processes have different mechanisms. As a consequence of the use of the additive model it is possible that the component processes have the same physiological mechanisms.

In the present studies, temperature had a more consistent influence on loss of primary dormancy and induction of secondary dormancy (Fig. 2) and also the potential germinability of the parasite than water potential and urea. The processes were successfully modelled based on the effects of conditioning temperatures of 17.5 to 35°C and where necessary modified by the effects of water potentials of 0 to -1.5 MPa and 0 and 0.316 mM urea environments confirming the suggestion of Forcella *et al.* (2000) empirical models should incorporate interaction of soil factors. In contrast to the rapid loss of primary

dormancy which took c. 5-23 days to completion, the rate of induction of secondary dormancy occurred quite slowly requiring periods of c. 59 to 133 days depending on the conditioning environment. Despite several other studies on seed dormancy of *S. hermonthica* (Vallance, 1950; Reid and Parker, 1979; Gbehounou *et al.*, 1994), only one attempt has been made previously to quantify the effect of environmental factors on these physiological processes during conditioning (Sonko, 1998). The conditioning model of Sonko (1998) was limited to effects of temperatures of 20 to 35°C. An ideal model for prediction of the likely *S. hermonthica* infestation in the field probably needs to account for effects of most of the important environmental variables on seed germination as emphasized by the recent review of Forcella *et al.* (2000). This study has contributed to this objective in terms of *S. hermonthica* seed conditioning process.

**Justification for accepting the composite model:** The present model gave rise to higher residual deviance

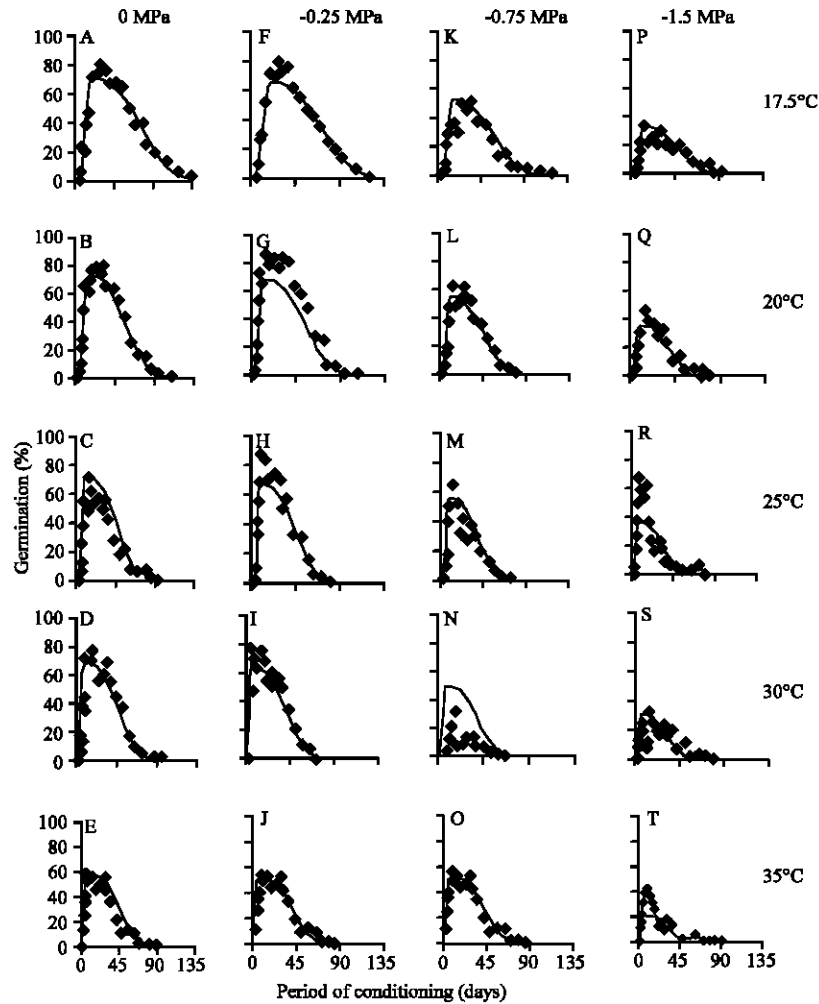


Fig. 4: Final percentage germination of *Striga hermonthica* seeds after conditioning at temperatures of 17.5 (A,F,K,P), 20 (B,G,L,Q), 25 (C,H,M,R), 30 (D,I,P,N) and 35°C (E,J,O,T) at water potentials of 0 (A-E), -0.25 (F-J), -0.75 (K-O) and -1.5 MPa (P-T) for up to 19 weeks in experiment 1. Lines were fitted by Eq. 14 with composite lines fitted. Parameter estimates (and standard errors) of fitted lines are shown in Table 7

compared with the separate line model despite the use of several approaches to minimize the residual. The good model predictions especially after 42 days of conditioning satisfies the main objective of this paper of prediction of likely *S. hermonthica* infestation of late planted host crops. The model Eq. 14 also fitted quite well a second independent experimental data set on the same seed lot (Fig. 5).

**Effect of temperature on the rate of loss of primary dormancy:** The effect of conditioning temperature on primary dormancy has been quantified by considering temperatures from 17.5 to 35°C. The rate of loss of primary dormancy increased approximately linearly with increase in temperature (Eq. 4) in *S. hermonthica* (Fig. 1). In

contrast to the present results, the rate of loss primary dormancy in a Gambian seed lot of *S. hermonthica*, did not depend on the conditioning temperature between 20 and 35°C (Sonko, 1998). Nevertheless, conditioning temperatures between 10 and 30°C in *O. aegyptiaca* and *O. cernua* and between 10 and 25°C in *O. crenata* during conditioning has a strong linear relationship with the rate of loss of primary dormancy (Kebreab and Murdoch, 1999). The results obtained here using a wider range of temperatures would therefore suggest a significant effect of temperature on the rate of loss of primary dormancy, which is comparable to that in *Orobanchae* species. The absence of a significant effect of temperature in Sonko's (1998) work may be due to the difference in the approach of modelling the rate of loss of primary dormancy. In the

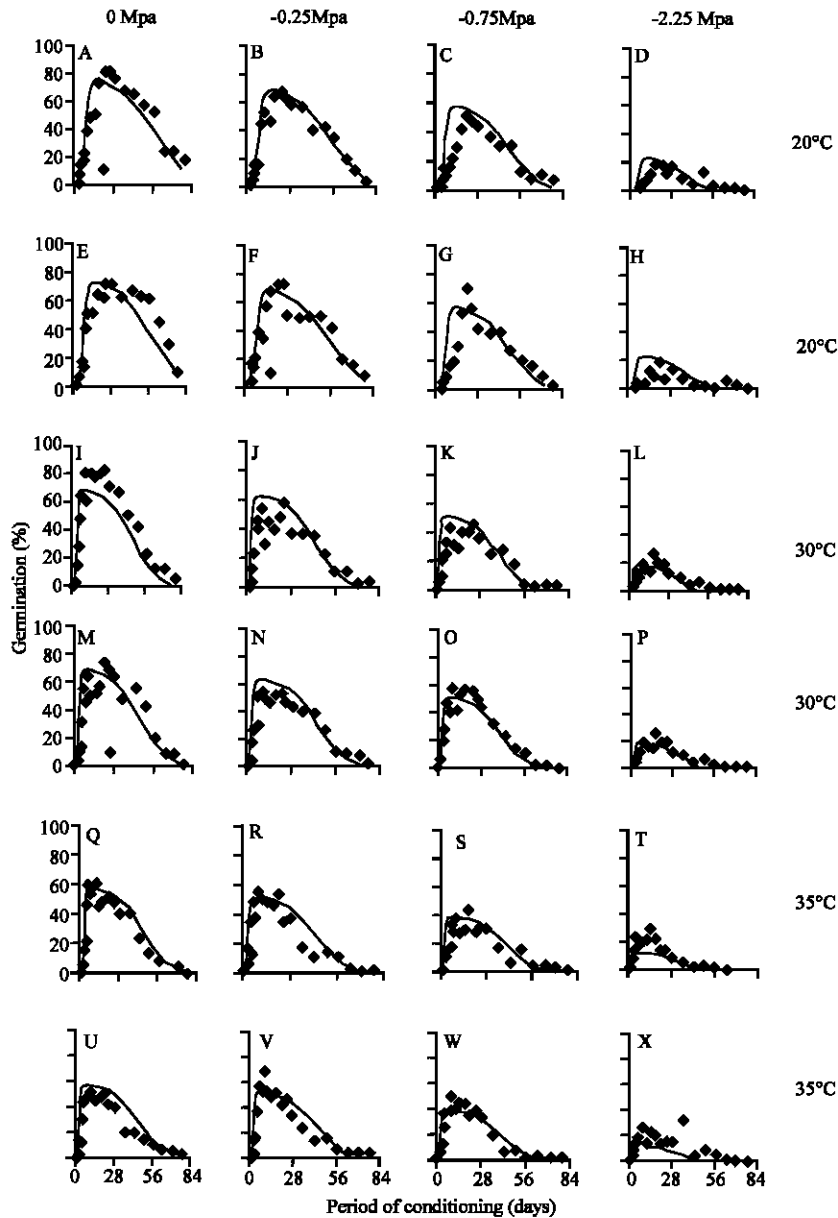


Fig. 5: Validation of sequential model (Eq. 14). Observed percentage germination (◆) of *Striga hermonthica* seeds in experiment 2 compared with predicted lines according to Eq. 14 using parameter estimates derived from experiment 1 (Table 7). Seeds were conditioned at temperatures of 20 (A-H), 30 (I-P) and 35°C (Q,X) at water potentials of 0 (A,E,I,M,Q,U), -0.25 (B,F,J,N,R,V), -0.75 (C,G,L,Q,U,Y) and -2.25 MPa (D,H,M,R,V,Z), without urea (A,B,C,D,I,J,K,L,Q,R,S,T) and in 0.083 mM urea (E,F,G,H,M,N,O,P,U,V,W,X) for up to 10 weeks in experiment 2

present model, a common base temperature and variable  $p_T$  was adopted which has not been examined by Sonko (1998). One difference between the linear models of *Orobanche* and *S. hermonthica* is that the model for the latter species was to absolutely test for a common base temperature for loss of primary dormancy in a range of environments. The base temperature of a crop species reflects its ability to tolerate cold temperatures. The base

temperature for conditioning for *S. hermonthica* reported here 11.2°C (Table 4) is actually very close to the lowest conditioning temperature of 12°C reported for the species (Vallance, 1950).

**Interactions of temperature, water potential and urea on the rate of loss of primary dormancy:** The dependence of the rate of loss of primary dormancy on temperature was

modified by water potential and urea conditioning environments (Eq. 5). The rate of loss of primary dormancy was fastest during conditioning in experiment 1 in the highest water stress of -1.5 MPa without and with 0.316 mM urea and the lowest was in 0.316 mM urea (Table 1), suggesting the overriding influence of water stress on  $p$  rather than urea concentration up to 0.316 mM. The faster rate of loss of primary dormancy at low water potentials explains why optimum conditioning periods are much shorter in such conditioning environments (Fig. 3 and 4). The effect of urea in lowering the rate of loss of primary dormancy is in line with the observation that the presence of ammonium-N during *in vitro* conditioning inhibits *S. hermonthica* germination (Bebawi *et al.*, 1991; Pieterse, 1991; Okonkwo, 1991; Sonko, 1998). Water potential promoted to a great extent the suppressive effect of urea on the rate of loss of primary dormancy at all temperatures (Table 1), probably by affecting the degree of hydrolyzation of urea to ammonium-N. This perhaps explains why urea and other ammonium sources of nitrogen give variable results in suppression of *Striga* infestation under varying field conditions (Pieterse and Verkleij, 1991; Osman *et al.*, 1991; Odhiambo and Ransom, 1994). Pieterse (1991) also attributed the inconsistent influence of ammonium-N on field emergence of *S. hermonthica* to the dilution effect of rainfall on the concentration of N-fertilizers. Sonko (1998) observed that conditioning of *S. hermonthica* seeds in 10mM of urea was harmful to germination. Bebawi *et al.* (1991) suggested that in the absence of urea the germination capacity of the seed determines its ability to germinate. It cannot be deduced from the model (Eq. 14) that urea reduces *Striga* seed germination by reducing the proportion of seeds in the seed population capable of being conditioned (kg). It was, however, clear from the results obtained at 3.16 mM and also from Sonko's (1998) results that such a reduction may occur at 3.16 mM urea.

**Effects of temperature on the rate of induction of secondary dormancy:** Temperature also influenced the rate of induction of secondary dormancy in the seeds (Fig. 2). The rate of induction of secondary dormancy increased with increase in temperature up to 25°C and then remained stable up to 30°C. There was only a very slight increase in the rate with an increase in temperatures between 30 and 35°C. As such, an exponential (asymptotic) relationship between the rate of induction of secondary dormancy and temperature was used to describe the data (Fig. 2). Totterdell and Roberts (1979) model on *Rumex* established a linear relationship between temperature and the rate of induction of secondary dormancy, such that the higher the temperature, the more

rapid the rate, while the present asymptotic model for *S. hermonthica* clearly differs; the basic conclusion of an increase in the rate with temperature is similar. Sonko's (1998) model of a decrease in the rate of induction of secondary dormancy with increase in temperature within the range of 20 to 30°C on *S. hermonthica* is in contrast with our exponential (asymptotic) relationship. However, his suggested increase in rate of induction of secondary dormancy between 30 to 35°C (Sonko, 1998) agrees with the present model. Despite the recommended exponential (asymptotic) model for induction of secondary dormancy in both *Orobancha* species (Kebreab and Murdoch, 1999) and the current data on *S. hermonthica*, remarkable differences occur in the trend of the response to temperature. In *Orobancha* (Kebreab and Murdoch, 1999) the rate of induction of secondary dormancy decreased to an asymptote with increase in temperature. In contrast, the rate of induction of secondary dormancy increased with increase in temperature to an asymptote in *S. hermonthica* probably due to the regional difference of occurrence of the parasites.

**Interactions of temperature, water potential and urea on the rate of induction of secondary dormancy:** The asymptotic rate  $s_a$  of induction of secondary dormancy on temperature was modified by water potential during conditioning (Eq. 9). This rate increased with water stress and was fastest during conditioning at -0.75 MPa without and with 0.316 mM urea and the lowest in 0.316 mM urea at -0 MPa (Fig. 1 and 2 Table 3). The suppressive effect of urea on the asymptotic rate of induction of secondary dormancy was alleviated by decreasing water potential to -0.75 MPa; suggesting a greater influence of water stress on  $s_a$  than urea concentration. The lowering effect of 0.316 mM urea on parameter  $s_a$  did not however, clearly reflect on the conditioning time required to terminate germination. Nevertheless, the faster asymptotic rate of induction of secondary dormancy attained with increased water stress might explain the progressive shortening of conditioning time required for germination to reach zero. With the high level of seed viability maintained during such periods, it could be concluded that water stress promotes induction of secondary dormancy and the process was responsible for the decrease in germination with reduced water availability. Field reports on effects of water potential on the emergence and growth of the parasite are very inconsistent but in general heavy irrigation inhibits whilst light irrigation promotes germination (Patterson, 1987). Since by the present results water stress promoted both rates of loss of primary dormancy and induction of secondary dormancy, it is reasonable to postulate the proportion of seeds germinating in any growth environment will depend on

Table 5: Parameter estimates and standard errors (in brackets) for potential germinability in Eq. 11 for seeds conditioned in different water potentials and urea concentrations derived from experiment 1

Parameter	0 MPa	-0.25 MPa	-0.75 MPa	-1.5 MPa
<b>A. Without urea</b>				
a	-0.0038(0.0004)	-0.0042 (0.0005)	-0.0004 (0.0005)	-0.0043 (0.0005)
b	0.0569 (0.0068)	0.0315 (0.0103)	-0.0148 (0.0099)	-0.0719 (0.0095)
c	0.525 (0.0268)	0.5250 (0.0397)	0.1145 (0.0378)	-0.3960 (0.0366)
<b>B. With 0.316 mM urea</b>				
a	-0.0010(0.0005)	-0.0065 (0.0006)	0.0015 (0.0005)	-0.0033 (0.0005)
b	-0.0158(0.0105)	0.0739 (0.0105)	-0.0779 (0.0101)	0.0523 (0.0102)
c	0.6206 (0.041)	0.6049 (0.0400)	0.1465 (0.0391)	-0.5357 (0.0368)

Table 6: Analysis of deviance for comparing models for the rate of loss of primary dormancy, induction of secondary dormancy and potential germinability of *Striga hermonthica* seeds during *in vitro* conditioning in 0 and 0.316 mM urea nitrogen at water potentials of 0, -0.25, -0.75 and -1.5MPa and temperatures of 17.5, 20, 25, 30 and 35°C

Model	Sum of squares	Degrees of freedom	F-ratio (approximation)
(1) Separate lines* Eq. 2	13568	3977	
(2) Composite model Eq. 14	17192	4163	
Difference (1)-(2)	3624	186	19.5** on 186 and 3977 d.f.

\*Fitted independently for each of the forty environments tested

Table 7: Parameter estimates for Eq. 14 and standard error (in brackets) for loss of primary dormancy, induction of secondary dormancy and potential germinability of *S. hermonthica* seeds as influenced by forty conditioning environments

Parameter	Estimate	Parameter	Estimate
$K_p$	-3 (N/A)	$s_a$	-0.0665 (0.0004)
$p_o$	0.0471 (0.0004)	$s_o$	-3.4607 (0.12)
$p_a$	-0.0262(0.0041)	$r$	0.7592 (0.0007)
$p_w$	-0.0086 (0.0006)	$a$	-0.0028 (0.0002)
$T_b$	11.201 (0.138)	$b$	0.1215 (0.0093)
$K_g$	-3 (N/A)	$c$	-0.671 (0.119)
$s_w$	-0.0128(0.0004)	$c_w$	0.6173 (0.0108)

the balance in soil water potential. There was no significant difference in the rate of exponential increase ( $r$ ) in the rate of induction of secondary dormancy in all the conditioning environments (Table 3).

**The Potential germinability of *Striga hermonthica* seeds:**

The potential germinability of the parasite varied with the conditioning temperature. The parameter  $K_g$  increased with increased in temperature up to about 20°C in all conditioning environments (Eq. 11). This temperature lies within the optimum temperature reported for conditioning of *S. hermonthica* (Parker and Riches, 1993). At higher temperatures, the potential germinability decreased in such a manner that a quadratic model explained the data better.

The model, however, does not support the models on fully imbedded seeds of Sitka spruce seeds (Jones *et al.*, 1997) and conditioning of three *Orobanch* species at 30°C (Kebreab and Murdoch, 1999). However, by the additive model, this study has shown that the potential germinability of the seed is controlled by not only by the seed viability but also treatment effects in any given environment.

**Interactions of temperature, water potential and urea on the potential germinability of *Striga hermonthica* seeds:**

The value of the constant a was very close to zero and did not change appreciably with changes in water potential (Table 5), but decreased with decrease in water potential in the presence of urea (Table 5). The constant b decreased with an increase in water potential but did not show any consistent trend in urea (Table 5). The value of c decreased with decrease in water potential and did not appear to be affected by the interaction effect of water potential and urea (Table 5). The intercept c of the quadratic model on potential germinability was modified by water potential.

In the development of the composite model, the effects of temperature and water potential were quantified on loss of primary dormancy, induction of secondary dormancy and potential germinability. It was feasible to account for the effect of urea concentration only on loss of primary dormancy. The composite model explained 95% of the variation in the dormancy and germination behavior of *S. hermonthica* seeds.

**Period of constant germinability of *Striga hermonthica* seeds:**

The seed germination time-course response curves showed that the period after the maximum loss of primary dormancy was characterized by a steady period of germinability being longest at 17.5 and 20°C but decreasing with increase in temperature and also decreasing water potential. This resistance to decline in germinability could be explained by hypothesizing that (1) the two processes of loss and induction of dormancy are dependent on each other and that (2) a lag phase occurs between the onsets of the processes. Similar dormancy stabilization periods were reported for seeds of Sitka spruce (Jones *et al.*, 1997) and *Orobanch* species (Kebreab and Murdoch, 1999). The occurrence of annual dormancy cycles in which a seed, which has developed secondary, could undergo cycles of relief and re-induction of secondary dormancy in a normal distribution function in the seed population was reported (Murdoch and Ellis, 1992).

We speculate that in *S. hermonthica* this stable germinability period could be an ecological adaptation of the parasite to perpetuate its germinability in an

environment within a threshold period, the duration of this period being defined by the suitability of the prevailing growth conditions.

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