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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 *Striga hermonthica* was studied in the laboratory by conditioning seeds at various water potentials and urea concentrations at 17.5 to 37.5°C for up to 133 days. The experimental results presented in this research are related to the effects of temperature, water potential and urea nitrogen concentration during conditioning on subsequent germination percentage of *S. hermonthica*. Maximum germination in *S. hermonthica* seeds was observed at conditioning temperatures of 20 to 25°C within the range investigated of 17.5 to 37.5°C. Water stress and also urea during conditioning suppressed maximum germination. However, the conditioning temperature ranges at which maximum germination percentages occur vary with water stress and also urea concentration. In the presence of a high concentration of urea (3.16 mM), temperatures required for maximum germination narrowed to between 17.5 to 20°C. The optimum period of conditioning decreased with increase in water stress and also urea concentration similar to previous reports. The implications of these findings on *Striga hermonthica* field infestations have been investigated and being reported in another paper. Germination was greatly suppressed by conditioning environments including 3.16 mM urea and at 37.5°C. At the high concentration of 3.16 mM, temperatures required for maximum germination narrowed to between 17.5 and 20°C. Optimum conditioning period decreased with water stress and with increase in urea concentration.

Key words: *Striga hermonthica*, germination, temperature, water potential, urea nitrogen

INTRODUCTION

Striga (witchweed) is a root parasitic weed devastating crop production in much of Africa and parts of Asia (Anonymous, 2006). In particular, *Striga hermonthica* infests the major cereal grains and average yield losses of 25-40% could occur but total crop failure under drought is not uncommon (Hess *et al*., 2001).

The germination of *S. hermonthica* seeds is such that, fully after-ripened seeds of the parasite must first undergo a period of imbibed storage in a warm environment to become sensitive to stimulants produced by host roots or applied experimentally (Logan and Stewart, 1992; Mangnus *et al*., 1992; Parker and Riches, 1993; Jones *et al*., 1997). This process of sensitization of *S. hermonthica* seeds in readiness for germination was generally called conditioning (Logan and Stewart, 1992; Mangnus *et al*., 1992).

Besides, the period of conditioning, the conditioning environment itself affects germination of *S. hermonthica* seeds such that temperature, water potential and nitrogen have been identified as key factors (Parker and Riches, 1993; Pieterse *et al*., 1993; Baskin and Baskin, 1998). Seed germination percentage increases with period of conditioning and then decreases when the time is extended beyond a few weeks (Pieterse *et al*., 1993; Murdoch *et al*., 2000). Vallancce (1950) found that maximum germination was attained after 6 days but after 30-33 days of conditioning the germination of *S. hermonthica* decreased to only 5-10%. The optimum period of conditioning of *S. hermonthica* seeds varied with temperature such that at 23°C it required 10 days (Dawoud and Sauerborn, 1994) but at 25and 30°C, it took 21 to 28 days and 21 days, respectively (Pieterse *et al*., 1993). Parker and Riches (1993) reported that the optimum temperature for conditioning of seeds of *S. hermonthica* ranges between 20 to 35°C. High temperatures usually above 33°C accelerated the conditioning process but did not give rise to increased germination percentage (Reid and Parker 1979), whilst seeds took a longer time to condition at a lower temperature of 12°C; but resulted in high germination percentage (Vallancce, 1950).

The potential of conditioning *S. hermonthica* seeds at low osmotic potential *in vitro* has received little

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attention. Water potential generally affects the conditioning of seeds such that water stress reduces the percentage (Bewley and Black, 1994) but the seeds of *S. hermonthica* could germinate at -1.5 MPa (Dawoud and Sauerborn, 1994).

Generally the effect of nitrogen during conditioning depended on the source, but urea most consistently suppressed germination of *S. hermonthica* seeds when applied during conditioning and/or germination (Bebawi *et al*., 1991; Sonko, 1998; Baskin and Baskin, 1998). When urea was applied at low concentrations during conditioning, it enhanced seed germination of the parasite, but increasing the rate of application above a threshold inhibited the process (Bebawi *et al*., 1991; Sonko, 1998). The relationship between urea concentrations of 4 to 8 mM (Pieterse, 1991) and 0.316 to 10 mM (Sonko, 1998) and germination of *S. hermonthica* seeds was negative and linear.

It is evident that temperature, water potential and urea of the conditioning medium of *S. hermonthica* seeds during short periods of imbibed storage affects loss of primary dormancy and its subsequent germination. However, no work has been reported on the interaction effect of temperature, water potential and urea neither during short nor extended periods of conditioning of *S. hermonthica* seeds on subsequent germination as it might obtain in the field environment. The objective of this paper therefore was to determine the combined influence of temperature, water potential and urea during extended periods of conditioning *in vitro* on subsequent germination of *S. hermonthica* seeds and widen temperature and water potential range for which *Striga* seeds could germinate.

MATERIALS AND METHODS

The study was conducted at the Seed Science Laboratory of the school of Agriculture of The University of Reading in 2002. Seeds of the Sudanese seed lot of *S. hermonthica* (Wad Merki strain) were utilized in the two experiments. *Striga* were collected on sorghum by Dr. A. G.T. Babiker and stored at The University of Reading by Dr. Drennan and later stored at the Seed Science Laboratory by Dr. A. J. Murdoch in 1998 at 3+2°C.

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

Striga seeds were surface sterilized for 5 min in 1% sodium hypochlorite solution (prepared from a solution with 12% available chlorine, supplied by Merck, UK). During the period of sterilization, the solutions were continuously stirred to ensure effective seed-solution contact. The seeds were then thoroughly washed with 150 mL of sterile deionised water on a Buchner funnel lined with two 9 cm Whatman No. 1 filter papers and powered by a suction pump system to ensure rapid and efficient rinsing and surface drying of seeds. The seeds on the filter papers were transferred to a Petri dish and dried overnight at 20+2°C.

The procedure of Michel and Kaufmann (1973) was used in the preparation of the osmotic potentials used in the experiments, 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:

$$\Psi = 1.29\,[PEG]^2T - 4.0[PEG] \quad (1)$$

Where Ψ is the required osmotic potential (bars), converted to Mega Pascal (bars/10), [PEG] is the concentration of polythene glycol 8000 (g PEG/g H_2O) and T is the temperature (°C). Osmotic potentials of -2.25, -1.5, -0.75, -0.25 and 0 MPa were prepared. The artificial germination stimulant -GR24, at 3 ppm was used and all germination requirements were satisfied. The Petri dishes containing seeds were opened periodically during conditioning to recover seeds for germination and to maintain oxygen supply.

Experiment 1: *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, -1.5MPa and in 0, 0.316 and 3.16 mM urea factorially combined in various incubators.

The PEG solutions containing the desired urea N concentrations for each temperature were prepared by the addition of 0.1 mL each of 0.316 and 3.16 M urea N solutions to 99.9 mL PEG solution in volumetric flasks to obtain 0.316 and 3.16 mM urea N, respectively. It was assumed that the very small quantities of urea would not alter the water potential substantially. Nine milliliters of PEG solution was added to 9 cm diameter sterilized Petri dishes previously lined with three circles of Whatman No.1 paper and one circle of Whatman GF/A glass fibre filter (9 cm diameter). Fifteen Whatman GF/A glass fibre filter discs (0.9 cm diameter) were placed on top and approximately 25-32 seeds were evenly spread on each disc with a paintbrush. Each disc with seeds was then covered with a further whatman GF/A glass fibre filter disc of 0.9 cm. Two of such Petri dishes with fifteen pairs of discs made up one replication.

Conditioning to remove dormancy: Eight replications were used for the water control conditioning treatments, whilst all other treatments were replicated four times. The greater number of replicates in the water control was because of the greater accuracy required in that treatment. Petri dishes with the same urea concentration and osmotic potential were stacked together and sealed with aluminium foil to exclude light. They were then wrapped in wet paper towels before placement in transparent polythene bags to reduce evaporative losses. The polythene bags were sealed before placement in an incubator at the appropriate temperature for seeds to condition for a maximum period of 19 weeks. The Petri dishes were opened to remove one sandwich disc of 25-32 seeds per recovery per replicate for transfer into the germinator.

Germination tests: To set conditioned seeds to germinate each sandwiched disc with seeds was rinsed for 1 min with 150 mL of sterilized, deionised water to remove urea and PEG so that they would not modify germination. The sandwich discs containing seeds from the conditioning medium were then placed on a non-sterile paper towel to remove excess moisture. Six discs containing seeds from the six conditioning temperatures and having the same osmotic potential and urea concentration were then placed in a fresh Petri dish containing two layers of 9 cm filter papers. The dishes were moistened with 5 mL of 3 ppm GR24 and then incubated for 7 days in the dark at 35°C. Germinated and ungerminated seeds were counted in the laboratory under a binocular microscope. A seed with an emerged radicle was considered germinated.

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. Procedures for sterilization and preparations of osmotic potentials (PEG solutions), conditioning and germination of seeds were as described for experiment 1. *S. hermonthica* seeds were conditioned 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. 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. The concentration of urea in experiment 2 was reduced to quantify the effect of very small rates of urea as pertains in fields of peasant farmers. The maximum conditioning period was 10 weeks and treatments were replicated four times.

Statistical handling of data: As a preliminary step, analyses of variance were carried out on the maximum percentage germination and optimum period of conditioning observed in the two experiments. Maximum percentage germination and optimum period of conditioning were determined by inspection of the experimental data to select the time of conditioning at which germination percentage was at a maximum. Before analysis with Genstat (Anonymous, 2000), an angular transformation of the maximum percentage germination data was carried out to standardize the variation based on the first four replicates of experiment 1 and the four replicates of experiment 2 to standardize the variation within each treatment:

$$x = \text{arcsinev}\sqrt{(\%\ \text{germination}/100)}\ \text{in degrees}$$

Comparison of the data was based on the transformed scale. For the control treatment in Experiment 1 only four of the eight replicates were included to reserve an orthogonal design.

RESULTS

Effects of conditioning on maximum percentage germination and optimum period: Conditioning of *S. hermonthica* seeds in the 72 and 24 environments studied for various periods in experiments 1 and 2, respectively resulted in different responses in terms of maximum and optimum period of conditioning (Fig. 1-9). Seed viability tests were carried out on non-germinated seeds at the end of each conditioning treatment in both experiments 1 and 2 by tetrazolium. The test confirmed the viability of the seeds and that changes in germination after conditioning were associated with changes in dormancy rather than loss of viability. The behavior of the seeds shown by the maximum percentage germination and optimum period of conditioning are described in turn.

Effect of the different conditioning environments on maximum germination: In both experiments 1 and 2 the second order interaction of temperature, water potential and urea on maximum percentage germination was not significant. In experiment 1, the main effects and the first order interactions were all significant ($p<0.001$). Temperature affected the maximum germination of *Striga* seeds such that germination was optimum at 20-25°C but remained stable over the temperature range of 17.5 to 35°C, after which further increases in temperature to 37.5°C depressed the parameter (Fig. 1). Water stress modified the effect of temperature such that maximum germinations at 0 and -0.25 MPa were similar. Except at -1.5MPa and 25°C water stress of -0.75MPa or more reduced maximum germination (Fig. 1).

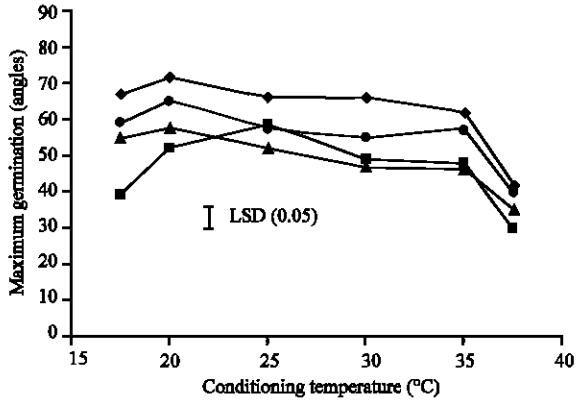

Fig. 1: Maximum percentage germination of *Striga hermonthica* seeds in response to conditioning temperatures in experiment 1 at water potentials of 0 (♦), -0.25 (●), -0.75 (▲) and -1.5 MPa (■). Results are means of germination at three different urea concentrations of 0, 0.316 and 3.16 mM

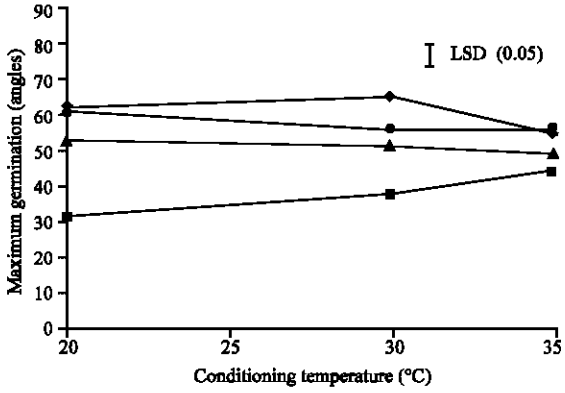

Fig. 2: Response of maximum germination of *Striga hermonthica* seeds to conditioning temperature at water potentials of 0 (◆), -0.25 (●), -0.75 (▲) and -2.25 MPa (■) in experiment 2. Results are means of urea concentrations of 0 and 0.083 mM

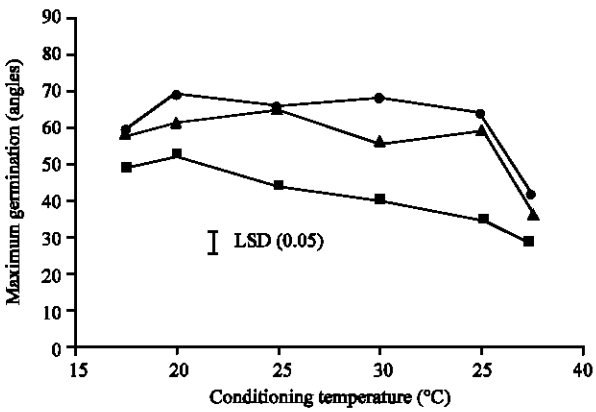

Fig. 3: Maximum germination of *Striga hermonthica* seeds in response to conditioning temperatures and urea in experiment 1. The urea concentrations were 0 (●), 0.316 (▲) and 3.16 mM (■) urea. Results are means of germination at different water potentials of 0 to -1.5 MPa

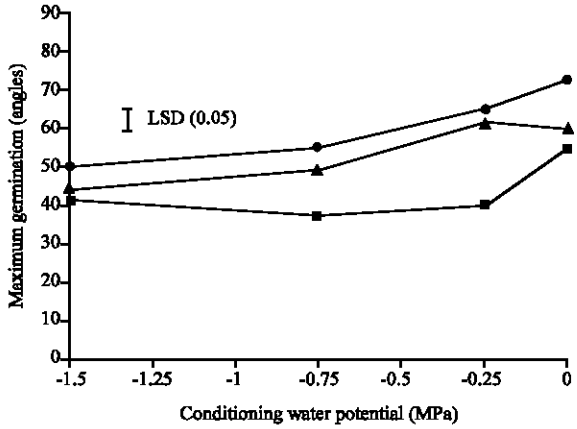

Fig. 4: Maximum germination of *Striga hermonthica* seeds in response to conditioning water potential at urea concentrations of 0 (●), 0.316 (▲) and 3.16 mM (■) in experiment 1. Results are means of germination at temperatures of 17.5 to 37.5°C

In experiment 2, maximum percentage germination was not a function of temperature and urea and their first order interaction ($p>0.05$). Similar to experiment 1, however significant first order interaction of temperature and water potential ($p<0.001$) and water potential and urea ($p<0.05$) and main effect of water potential ($p>0.001$) were observed. The main effect of water potential ($p<0.001$) depressed maximum germination, which was evident at -0.75 and -2.25 MPa where the mean germination (Fig. 2) was 57 and 33%, respectively compared to 76 and 70% at 0 and -0.25 MPa, respectively. The interaction of temperature and water potential on maximum germination was a result of the positive response to increase in temperature from 20-35°C at -2.25 MPa compared, respectively with the negative and zero germination responses at higher water potentials of 0 MPa and -0.75 to -0.25 MPa (Fig. 2).

Effects of temperature and urea on maximum germination: The main effect of temperature on maximum germination can be seen in Fig. 1 is again evident in Fig. 3. The main effect of urea during conditioning suppressed maximum germination from 75% without urea to 43% with 3.16 mM urea (Fig. 3). The significant

($p<0.001$) interaction of temperature with urea resulted in the relative suppression of maximum germination by 3.16 mM urea was greater at 25 to 35°C than at 17.5 to 20°C or at 37.5°C.

Effects of water potential and urea on maximum percentage germination: Water stress depressed maximum germination such that increasing water potential from -1.5 to 0 MPa increased maximum percentage germination of *S. hermonthica* seeds (Fig. 4). The interaction of water potential with urea during conditioning was observed mainly by the relatively greater suppression of maximum germination by 3.16 mM at -0.25 and -0.75 Mpa compared to 0 and -1.5 MPa (Fig. 4).

Similar to the results in experiment 1, water stress reduced maximum percentage germination as the parameter increased with increase in water potential from -2.25 to 0 MPa in experiment 2 (Fig. 5). In experiment 2, the interaction of water potential and urea on maximum germination showed an increased germination with 0.083 M urea at -0.75 MPa but not at -2.25 MPa and -0.25 to 0 MPa based in LSD comparison for each water potential (Fig. 5).

Effect of different environment on optimum conditioning period: In experiment 1, the optimum time required to maximize germination was affected significantly by the main effects of temperature and urea ($p<0.001$) and water potential ($p<0.01$). First and second order interactions of these factors on the optimum period were not, however, significant. In experiment 2, only the main effect of temperature significantly ($F = 24.03$ on 2 and 69 df, $p<0.001$) determined the optimum period of conditioning.

Effect of temperature on optimum time to maximize germination: Period of conditioning to maximum germination decreased from 25 to 11 days with increases in temperatures between 17.5 to 25°C. Optimum conditioning period to attain maximum germination remained similar with further increases in the conditioning temperature (Fig. 6).

The optimum conditioning period required to maximize germination profoundly decreased with increase in temperature within the range of 20 to 35°C in experiment 2 (Fig. 7). It required 24 days to optimize conditioning at 20°C while only 17 and 13 days were sufficient at respective temperatures of 30 and 35°C.

Effect of water potential on optimum period to maximum percent germination: Seed conditioning proceeded more rapidly ($p<0.01$) with a decrease in water potential (Fig. 8). Water stress of -1.5 MPa sped up the process of conditioning such that 12 days was enough to optimize conditioning. Thus a significant difference in the effect of water potential on optimum period for maximising germination was primarily due to the -1.5 MPa treatment in this experiment.

Effect of urea on optimum period to maximum percent germination: The optimum period to maximum germination was increased by a small amount of urea at 0.316 mM whilst a high amount of 3.16 mM urea

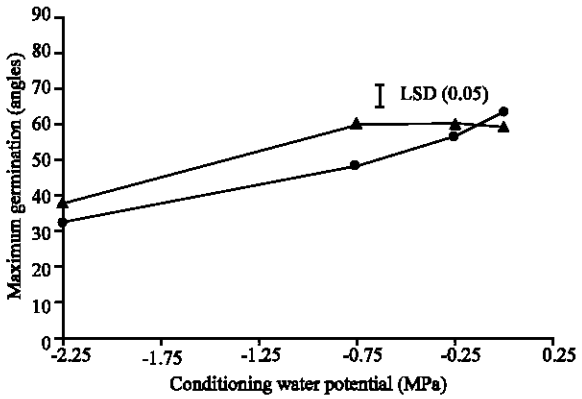

Fig. 5: Maximum percentage germination of *Striga hermonthica* seeds as affected by conditioning water potential at urea concentrations of 0 (●), 0.83 mM (▲) urea in experiment 2. Results are means of conditioning temperatures of 20, 30 and 35°C

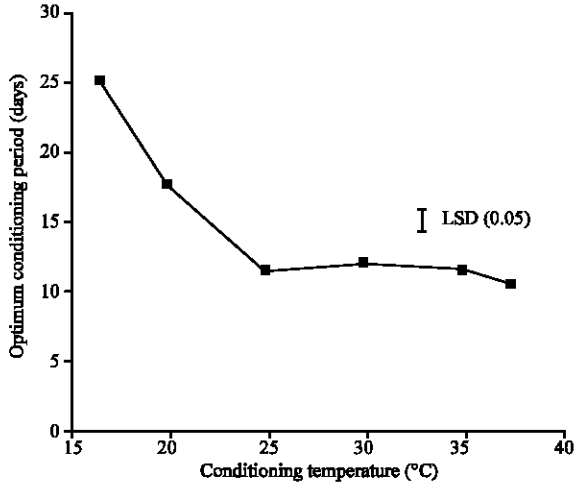

Fig. 6: Relationship between temperature and optimum conditioning period required for *Striga hermonthica* seeds in experiment 1. Results are means of optimum conditioning period at water potentials of 0, -0.25, -0.75 and -1.5 MPa and at urea concentrations of 0.0.316 and 3.16 mM

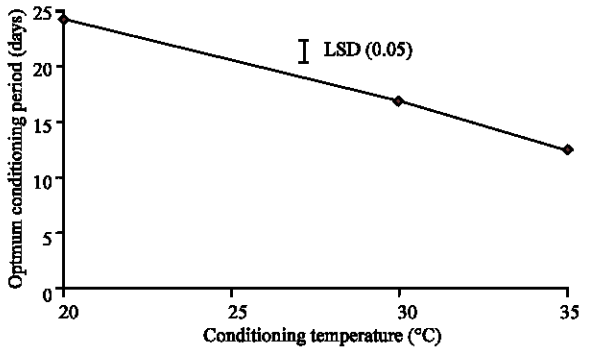

Fig. 7: Effect of temperature on optimum conditioning period of *Striga hermonthica* seeds in experiment 2. Results are means of water potentials of 0, -0.25, -0.75 and -2.25 MPa and urea concentrations of 0 and 0.083 mM

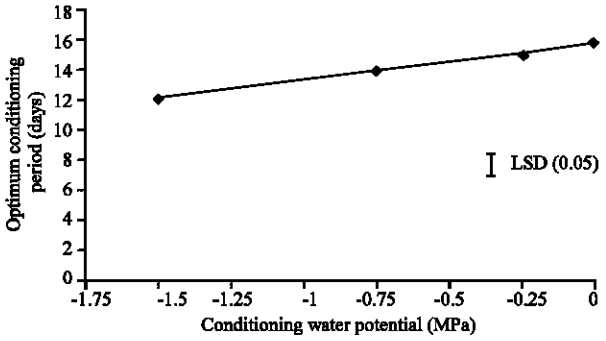

Fig. 8: Relationship between water potential and optimum conditioning period required for *Striga hermonthica* seeds in experiment 1. Results are means of optimum conditioning periods at temperatures of 17.5, 20, 25, 30, 35 and 37.5°C and at urea concentrations of 0.0.316 and 3.16 mM

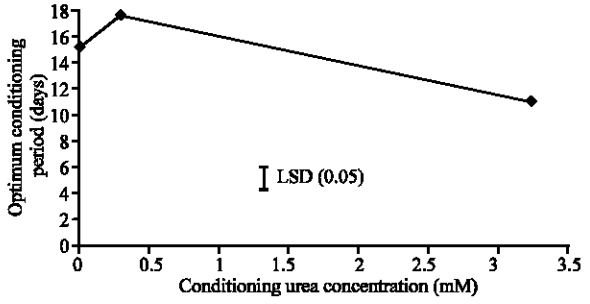

Fig. 9: Relationship between urea and optimum conditioning period required for *Striga hermonthica* seeds in experiment 1. Results are means of optimum conditioning periods at temperatures of 17.5, 20, 25, 30, 35 and 37.5°C at water potential potentials of 0, -0.25, -0.75 and-1.5 MPa at concentrations of 0 to 3.16 mM

concentration depressed the parameter compared with time to germination at 0 MPa (Fig. 9). At the concentration of 3.16 mM, urea enhanced conditioning time of the *Striga* seeds with 10 days required to optimize germination compared to 15 days in the water control (Fig. 9). There was a significant delay of 2 days in the period to attain maximum percentage germination when seeds were conditioned in 0.316 mM urea.

DISCUSSION

The experimental results in this paper are related to the effects of temperature, water potential and urea nitrogen concentration during conditioning on subsequent germination percentage of *S. hermonthica*. Maximum germination in *S. hermonthica* seeds was observed at conditioning temperatures of 20 to 25°C within the range investigated of 17.5 to 37.5°C. The findings support the literature on the best conditioning temperatures for *S. hermonthica* (Vallancce, 1950; Reid and Parker, 1979; Pieterse, 1991). Vallancce (1950) reported that *S. hermonthica* seeds conditioned at 22°C, gave higher germination than at 12, 27 or 32°C. His report further revealed that conditioning of *S. hermonthica* seeds at 22°C under optimum water potential gave a maximum germination of 82%. However, by increasing the conditioning temperature to 32°C, the maximum percentage germination was reduced to 10%. Similarly Reid and Parker (1979) found that conditioning *S. hermonthica* seeds from Ghana, Nigeria and Sudan was better at 23°C than at 33°C.

The results also support the report that *S. hermonthica* seeds could germinate after conditioning at water potentials of -1.5 MPa (Dawoud and Sauerborn, 1994). However, optimum water availability during conditioning was necessary to enhance maximum germination of *S. hermonthica* seeds (Fig. 4).

The results on the effect of urea nitrogen confirm earlier reports on the harmful nature of high urea concentrations (Fig. 3). However, the inhibitory action of urea depended on the conditioning temperature, such that at certain temperatures, in this case 25 to 35°C, the reduction in maximum germination was maximal (Fig. 3). The inconsistent action of nitrogenous fertilizers on *Striga* infestation in the field was attributed to variation in the environmental conditions (Pieterse, 1996) an explanation which is supported by the present *in vitro* results. The lower concentration of urea in the second experiment did not show any consistent effect on maximum germination, probably being too low to have a significant effect.

The conditioning temperature ranges at which maximum germination percentages occur vary with water stress and also urea concentration. This result might

explain why Dawoud and Sauerborn (1994) did not find any effect of water stress of up to -1.5 MPa on maximum germination of *S. hermonthica* since they conditioned their seeds at a constant temperature of 23°C. In the presence of a high concentration of urea (3.16 mM), temperatures required for maximum germination narrowed to between 17.5 to 20°C. Sonko (1998) observed that urea applied at 3.16 to 10 mM during seed conditioning inhibited the subsequent germination of *S. hermonthica* seeds at a constant temperature.

The decrease in optimum period of conditioning (from 25 day at 17.5°C to 11 day at 25°C) with increase in temperature (Fig. 6) is consistent with the literature. Dawaoud and Sauerborn (1994) reported 10 days 23°C and Bebawi *et al.* (1991) observed 8 days at 33°C. Similar trends in optimum conditioning time were reported in a recent review of the conditioning requirements of *S. hermonthica* (Baskin and Baskin, 1998).

Conditioning *Striga* seeds at lower water stress of -1.5 Mpa reduced the optimum conditioning period by 4 days. Dawaoud and Sauerborn (1994) found that reducing the available water from -0.9 to -1.5 MPa during conditioning reduced the time necessary to attain maximum germination by 5 days although these authors only tested seeds at one temperature (23°C).

The optimum period to maximum germination in *S. hermonthica* dependent on urea such that in the absence of urea it took 15 days to reach maximum germination whilst 17 and 10 days were, respectively necessary at 0.316 and 3.16 mm of urea (Fig. 9).

The interaction of water potential and urea in reducing maximum germination (Fig. 4) has never been investigated.

CONCLUSIONS

The impact of environmental factors during conditioning has been studied on the germination biology of *Striga hermonthica* seeds. It has been shown that maximum percentage germination strongly depended on the conditioning temperature, water potential and urea nitrogen concentration with significant first order interactions. Temperatures of 20 to 25°C were optimum for maximum germination. Increasing water stress in the range of 0 to -2.25 MPa strongly suppressed maximum germination of *S. hermonthica* seeds. Similarly, conditioning in 3.16 mM urea suppressed maximum germination.

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