Chapter 7

TEMPERATURE, WATER STRESS AND PLANTING DEPTH EFFECTS ON COTTON SEED GERMINATION PROPERTIES

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INTRODUCTION

Seed germination and seedling growth are exceptionally sensitive to environmental variability. Subsequently, these stages in plant development are critical to successful establishment, survival and crop performance. The increased frequencies of environmental stresses due to climate change have made significant impacts on the world's agricultural production. Anthropogenic and natural factors influence global surface air temperature, which increased by 0.2°C per decade between 1950 and 1993 and is projected to increase by 2 to 4.5°C by 2100 (Meehl et al., 2007). The changes in temperature associated with climate change are associated with changes in the precipitation patterns (Giorgi and Lionello, 2008) as drought affected areas are expanding at an accelerating rate (Delmer, 2005). Changes in the environment modify growth, physiological and biochemical processes in cotton at different stages of development (Gibson and Mullen, 1996; Oosterhuis, 1999; Singh et al., 2008).

Seed germination is a complex biological process commencing with the uptake of water by the quiescent dry seed and concluding with elongation of the embryonic axis (Bewley, 1997). The mechanism of seed germination involves timing of water absorption, membrane reorganization, metabolic restructuring and cell expansion (Hake et al., 1990; Toole et al., 1956). In the first phase of germination, uptake of water and enzyme activation in the endosperm leads to cell elongation and subsequent radical lengthening (Bewley, 1997; Obroucheva, 1999). The splitting of the seed coat allows oxygen to penetrate the seed during the second phase. At this stage, stored endospermic reserves are metabolized and synthesized enzymes stimulate the loosening of cell walls, which leads to further cell elongation and increase in volume. During the third phase, the seedling emerges by rupturing the seed coat. This process is followed by rapid cell elongation and cell division. After radicle emergence, the embryo can access water and nutrients from the environment which leads to a continuous increase in seedling dry weight (Bewley and Black, 1985).

Several growth and developmental processes are affected by ambient growing temperature. In the seed germination process, temperature plays an important role in the removal of dormancy and determination of the germination capacity (Christiansen, 1967; Roundy and Biedenbender, 1996). Temperature response varies across and within species (Farooq et al., 2004; Larsen and

Andreasen, 2004; Ungar, 1978). During seed germination, the increase in thermal activity of chemically reacting molecules is mainly due to an increase in thermal response between minimum and optimum temperatures (Probert, 1992; Roberts, 1988). At high temperature above optimal conditions, there is molecular dysfunction caused by alteration in protein and physiological effects of temperature on membrane components (Hill and Luck, 1991; Hsu et al., 1985; Moot et al., 2000). Exceptionally high or low soil temperature conditions relative to optimum during planting period therefore influences the germinative capacity of the seed.

Water availability is the most critical factor, since water drives germination and emergence (Hegarty, 1978; Vertucci et al., 1989). Several studies have successfully simulated the effects of osmotic stress on seed germination properties using polyethylene glycol (PEG) as an osmoticum (Murillo-Amador et al., 2002; Okcu et al., 2005). Germination rates generally decrease with decreasing water potential (Emmerich and Hardegree, 1990). Seeds generally experience periods of alternating dry and wet conditions (Baskin and Baskin, 1982; Berrie and Drennan, 1971) due to periodic nature of precipitation (Groisman et al., 2005).

Modeling is a powerful approach to understanding complexity of biological systems (Meng et al., 2004). Crop models are developed for various purposes of predicting plant growth, development, yield testing and decision support through synthesis of plant genetics, physiology, and environmental interactions (Boote et al., 1998). Biological systems modeling is based on quantifying the environmental effect on various plant physiological and phenological processes from sowing to maturity (Reddy et al., 1997). The extent, uniformity, and speed of germination are important attributes of all seeds, and these parameters can be modified by existing environmental conditions. The germination rate and germination percentage are two important parameters seeds and affected by temperature and moisture. Studies conducted by Gracia-Huidobro et al in (1982) and Schimpf et al. (1977) reported positive correlation of germination rate and percentage with temperature up to an optimum. After this point, the rate of germination decreases at maximum temperature to zero (Ellis et al., 1986). The effect of a specific environmental factor on germination is commonly characterized by a sigmoidal curve, relating the germination percentage to time and quantified by standard normal distribution (Janssen, 1973). The purpose of these studies were to test alternative modelling schemes for estimating cotton seed germination capacity and rate response to temperature, water stress and planting depth.

TEMPERATURE EFFECTS ON COTTON SEED GERMINATION

Seed germination is a complex process involving many individual reactions and phases, each of which is affected by temperature. The temperature effect on germination can be expressed in terms of 3 cardinal temperatures: minimum, optimum, and maximum temperatures at which germination can occur. The minimum temperature is sometimes difficult to define since germination may actually be proceeding but at such a slow rate that determination of germination is often made before actual germination is completed. The optimum temperature may be defined as the temperature resulting in the greatest percentage of germination in the shortest period of time. The optimum temperature for most seeds is between 15 and 30°C. The maximum temperature is governed by the temperature at which essential proteins for germination are denatured. The maximum temperature for most species is between 30 and 40°C. This drastic over-simplification of; therefore, the temperature response may change throughout the germination period because of the complexity of the germination process.

The response to temperature depends on a number of factors, including the species, variety, growing region, quality of the seed, and duration of time from harvest. As a general rule, temperate-regions seeds require lower temperatures than do tropical- region seeds, and wild species have lower temperature requirements than do domesticated plants. High-quality seeds are able to germinate under wider temperature ranges than low-quality seeds. The severity of the effects that cool temperatures have on the cotton plant varies according to the age of the plant and the duration of exposure to low temperatures.

The successful emergence and initial growth of cotton seedlings is important for the establishment of healthy and improved productivity. Wanjura and Buxton, (1972 a, b) showed that when the minimum soil temperature at planting depth dropped from approximately 20°C to 12°C, the hours required for initial seedling emergence increased from 100 to approximately 425 hours. In many cotton-growing areas the soil temperature can be significantly lower than the optimum when seeds are planted thus impacting the final yield.

Protocol and Curve Fitting Techniques to Quantify Seed Germination Related Parameters

Availability of heat tolerant cotton cultivars, in particular to seed germination, can overcome high temperature related germination problems. Similarly, the identification of cold tolerant cultivars becomes important for cold weather conditions. The rate of both germination and emergence significantly decreases at low temperatures. Thermal time (degree-day or hour), the heat unit for plant development is a well established developmental principle for plants. The thermal time model has been successfully used to predict seed germination under non-water limiting conditions. According to the model, based on many crops, the existing soil temperature determines both the maximum seed germination (MSG) and the rate of germination (SGR). Using this model, cardinal temperatures (Topt, Tmax, and Tmin) for both MSG and SGR, and maximum SGR and MSG can be identified. Such thermal responses from each cultivar are used to identify temperature tolerance.

Time-series seed germination data at various temperature treatments was carried out as a simple experiment to determine above parameters related to seed germination of given cotton cultivars. Seeds in replicates of 4 containing 100 seeds each were placed in a 9-cm sterilized plastic tray layered with two sheets of moistened, vaslin clothes and then placed in incubator (Fisher Scientific, Suwanee, GA) in the dark under a range of temperatures from 5 to 55°C at 5 °C intervals. The trays were covered to minimize moisture loss and the vaslin clothes containing seeds were moistened with distilled water daily, as needed. Germinated seeds were counted, recorded, and discarded every six hours. A seed is considered germinated when the radical length is equal or longer than the diameter of the seed. Temperature and cumulative seed germination time-course data were fitted with a 3-parameter sigmoidal function given below (Equation 01; Figure 1) using Sigma Plot 1.

$$Y = \mathrm{SGmax}/\{1 + \exp[-(x - x50)/\mathrm{Grate}]\} \qquad [1]$$

This function estimates a, the maximum cumulative germination percentage (germination capacity); b, the shape and steepness of the curve; and x_0, time to reach germination half maximal (time to 50% of maximum germination).

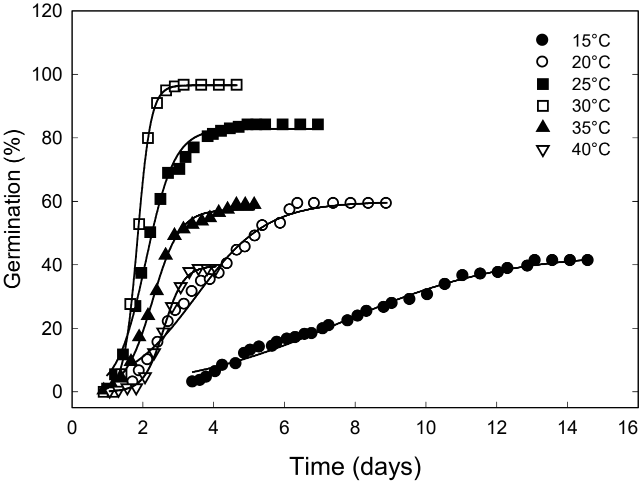

Figure 1. Observed (symbols) and predicted (lines) germination time course of cotton germinated at a range of temperatures (15 to 40°C). The symbols indicate the observed cumulative germination and the lines indicate the germination time courses fitted using a three-parameter sigmoidal function. Data are means and ± SE of four replications.

The rate of development was derived by the reciprocal of time to 50% of maximum seed germination, T50). The maximum percentage germination and the reciprocal over time to 50% germination (GR) were used for further analysis to determine cardinal temperatures explained below.

Both linear and nonlinear models can be used to analyze maximum seed germination (MSG) and germination rate (GR) responses to temperature. The best models are determined based on the overall highest coefficient of determination (R^2) and the least root mean square error (RMSE) values using non-linear regression procedure. Based on these criteria, the model which best described the MSG responses and seed GR responses to temperature can be estimated by linear or non-linear regression procedures using a statistical software (PROC NLIN in SAS) by a modified Newton Gauss iterative method (Garcia-Huidobro et al., 1982). The modified bilinear model was best fit for MSG. Optimum temperature (Topt) in modified bilinear model was generated using [Eq. 2], by PROC GLM in SAS, while Tmin and Tmax were estimated by the following equations [3, 4 and Figure 2].

$$SGR = a + b_1 (T - T_{opt}) + b_2 \times ABS (T_{opt} - T) \quad [2]$$
$$T_{min} = [a + (b_2 - b_1) \times T_{opt}] / b_1 - b_2 \quad [3]$$
$$T_{max} = [a - (b_2 + b_1) \times T_{opt}] / b_1 + b_2 \quad [4]$$

Where T is the treatment temperature and a, b1, and b2 are cultivar specific constants generated (PROC NLIN in SAS). A mean curve is fitted to MSG to determine the parameter estimates. The above proposed protocol based on sigmoidal curves and subsequent model fitting provide a valuable approach to determine temperature related cotton seed germination parameters.

The quadratic model was the best fit model for SGR. For the quadratic function model [Eq.

5], the three cardinal temperatures (Tmin, Topt, and Tmax) can be estimated using the following equations [6, 7, and 8 and Figure 2].

$$\mathrm{MSG} = a + bT - cT^2 \qquad [5]$$
$$T_{opt} = -b / (2c) \qquad [6]$$
$$T_{min} = -b + (\sqrt{b2 - 4ac}) / 2c \qquad [7]$$
$$T_{max} = -b - (\sqrt{b2 - 4ac}) / 2c \qquad [8]$$

Where T is the treatment temperature at which MSG were determined for each cultivar and a, b, and c are cultivar specific constants generated by statistical software (PROC GLM by SAS).

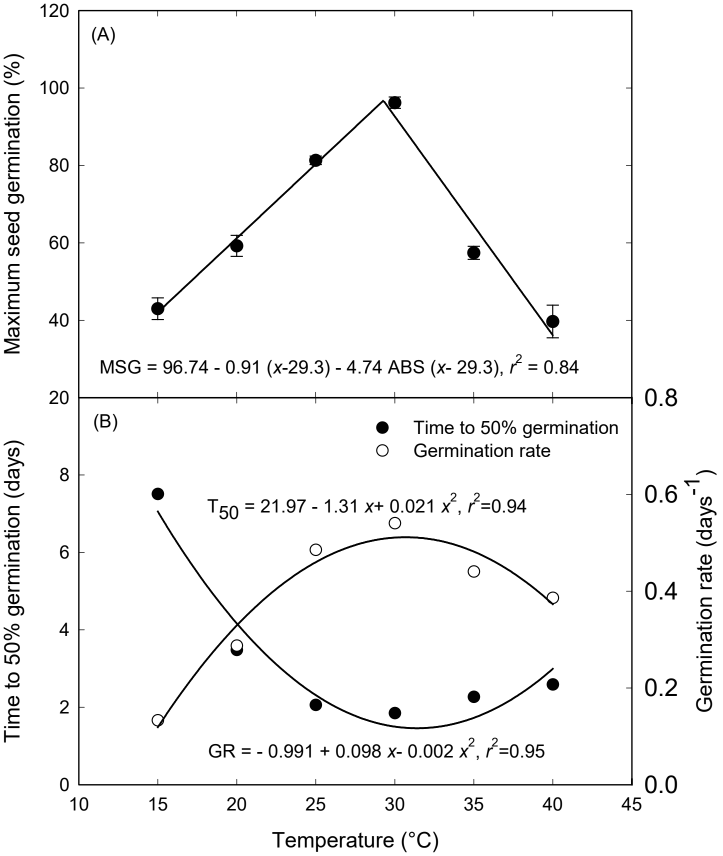

Figure 2. Temperature effects on (A) maximum seed germination for cotton and (B) time to 50% of maximum seed germination and germination rate for cotton along with the fitted linear and quadratic equations. In (A), the symbols are recorded maximum seed germination and the lines are fitted using modified bilinear equations. In (B), the symbols are derived time to 50% of maximum seed germination and germination rates and the lines are fitted using quadratic equations. Data are means and ± SE of six replications.

Germination of cotton seed is favored by high soil oxygen concentration, adequate soil moisture, and soil temperature above 17.5°C. Temperature affects the seed germination process (percentage and rate) through at least three separate physiological processes namely (1) seed continuously deteriorate and rate of deterioration depends on both moisture content and temperature, (2) seeds are initially dormant and relatively dry seeds continuously lose dormancy at a rate which is temperature dependent. The rate of losing viability however remains constant over a wide range of temperatures, and (3) once seeds have lost dormancy; their seed germination rate shows a positive linear relation between the base temperature and the optimum temperature and negative linear relationship between the optimum temperature and the ceiling temperature.

Temperature effects on cotton seed germination was extensively studied under laboratory conditions. According to Toole and Drummond (1924), cotton seed showed fast germination at 25°C as well as 15–36°C alternating temperatures. The optimum temperature for both germination rate and percentage lies at alternating temperatures of 15 and 36°C. According to the modified bilinear function which describes the response of MSG to temperature, T_{opt} for MSG lies around 29.3°C and T_{opt} for SGR lies around 31.1°C. A recent study by Krzyzanowski and Delouche (2011) reported that the optimum temperature for cotton seed germination lies between 28 to 30°C.

Even though cotton can withstand many stresses, planting at optimum temperature conditions producers can get the maximum emergence and survival. During the critical germination period, soil temperatures below 10°C can cause chilling injury to germinating cotton seed resulting in malformed seedlings, loss of the tap roots resulting reduced vigor and stand establishment, and the increased seedling diseases. The factors affecting cotton seed germination including temperature is well documented, any interaction between temperature and other factors and their influence on seed germination require more investigations.

Temperature and Root Growth

The temperature of the soil can have a significant influence on the growth of cotton root systems. Most research has shown that in general, the growth of cotton roots increases with increasing soil temperature until an optimal temperature is reached beyond which growth declines. Early work suggested that the optimal soil temperature for the growth of cotton roots was approximately 35°C (Bloodworth, 1960; Lety et al., 1961; Pearson et al., 1970; Taylor et al., 1972). Kaspar and Bland (1992) indicted that changes in soil temperature can affect growth of a number of root system components. For example, low temperatures generally reduced cotton root branching (Brower and Hoagland, 1964), while higher temperatures approaching the optimum tend to increase branching (Nielsen, 1974). When the root temperature was low (20°C), root growth was reduced regardless of the temperature of the air (shoot) (McMichael and Burke, 1994). The cotton taproot may be more adapted to adverse soil temperatures than subsequent branch roots at least until the taproot had developed to approximately 10 cm in length (Arndt, 1945; McMichael and Burke, unpublished data). Genetic diversity has been shown to exist in cotton for root development between genotypes (Bourland et al., 1985; Quisenberry and McMichael, 1996).

Effect of Low Temperature on The Root System

Cotton is often planted into cool, wet soils in the US eastern and midsouth regions, leading to problems in germination, emergence, root growth and subsequent seedling development. Christiansen (1967) found that the cotton seedling is hypersensitive to chilling at certain growth stages. One of these stages is when the seed is imbibing water, and the other is 18 to 30 hours after germination when the radicle and the hypocotyl elongate. In these chilled conditions root membranes lose permeability, and this lack of control in the membranes reduces water uptake by plants (Kramer, 1942; Yoshida and Eguchi, 1990). Chilling effects are expressed as reduced vigor, abnormal growth, and death of the seedling (Kaspar et al., 1981). Chilling injury might result in plant stunting later in the life of the plant because, during early germination and hydration, activation of RNA synthesis and active protein synthesis occur (Christiansen, 1967). Lateral root growth is reduced in cool temperatures as cotyledon storage is depleted (McMichael and Burke, 1998), which could retard the growth of the seedling. Also, low temperatures result in a reduced leaf expansion of the plant by slowing metabolism and reducing the size of the plant at harvest (Christiansen and Thomas, 1969). Leaf area of the cotyledons and true leaves of cotton are negatively affected by root exposure to cool temperatures, while the stem is least affected, since it recovers turgidity more rapidly than other components (Nelson, 1967). Another effect of cool temperature on roots is chilling injury, where the taproot is swollen and aborted and described as “nub rooted” (Cole and Christiansen, 1975). The swollen root structure is caused by a buildup of starch and sugars at low temperatures due to slow metabolism (Schrier et al., 2000; Hesketh and Wiginton, 1980). In nub root, when the taproot is aborted, the lateral roots emerge from the swollen hypocotyl to bring nutrients and water to the plant. Aborted root meristem damage is not as serious as injury to the cortex, because the lateral root growth supplements the taproot functions (Christiansen, 1963). Low temperatures can cause a reduction in water uptake by decreased permeability in seedling root systems (Kramer, 1940) and a reduction in cell expansion in cotton (Quisenberry et al., 1994; Nelson, 1967). Guinn and Hunter (1968) also reported that low root temperatures caused rapid increases in sugar contents of all plant parts (leaves, epicotyls, hypocotyls and roots). Hypocotyls contained the most sucrose whereas epicotyls contained the most glucose, fructose and total sugars. Roots contained the lowest concentrations of glucose and fructose. In addition, low root temperatures increased the starch contents of leaves, epicotyls and hypocotyls, except that a root temperature of 10C caused wilting and a very low starch content of the leaves. The authors attributed the increase in carbohydrate concentration to altered respiration rates due to lower than optimum temperatures. Once the roots have been established and the seedling emerged, 35ºC is the optimal temperature for 10 days after planting (McMichael and Burke, 1994). The metabolism of the roots and ability to take up water and nutrients are hindered if the seedling is grown in less than optimal temperatures (Nelson, 1967, 1974). Roots are also highly vulnerable to pathogens during this time of slow metabolism and stress (McMichael and Burke, 1998). Genetic diversity has been shown to exist in cotton for root development between genotypes (Bourland et al., 1985; Quisenberry and McMichael, 1996). Mills et al. (2012) also reported significant variation in response to low temperatures of a number of root parameters such as lateral root number, length and branching after studying four genetically and geographically diverse cotton cultivars. Therefore, improvement of cold tolerant cotton should be possible. If the root system is better adapted to a cool environment, the uptake of nutrients and water will improve, and therefore, the metabolism and maturity level of the plant would increase (McMichael et al., 2010). An earlier planting time and an increased metabolism should mean a greater profit for cotton producers as well as increased economic revenues for the U.S. economy.

WATER STRESS EFFECTS ON COTTON SEED GERMINATION

Drought tolerance is a complex quantitative multigenic trait with considerable intraspecific variation existing for cotton morphology and physiological processes (Cushman and Bohnert, 2000). Seed germination is a triphasic process initiating with imbibition (phase I) resulting from the water potential gradient between the seed and imbibition solution, followed by a plateau phase with minimal changes in water content (phase II) and culminating in an increase in water content coinciding with radicle emergence (Bradford, 1990; Wanjura and Buxton, 1972a). Water stress influences the rate of each phase thereby reducing the rate of water uptake, germination rate, and germination percentage (Heikal and Shaddad, 1982). In addition, water availability influences cotton emergence, seedling vigor, stand establishment and ultimately crop performance. Water stress induced by the long chain polymer, inert, non-ionic and highly water soluble polyethylene glycol (PEG) has been successfully used to study physiological processes in cotton (Nepomuceno et al., 1998).

Using seed germination parameters such as maximum seed germination and germination vigor, Meneses et al. (2011) classified genotypes based on their sensitivity to water stress. Water stress was simulated with PEG 8000 using Michel's (1983) equations to produce solutions with the desired osmotic potential. Cotton seeds were placed in covered trays with PEG saturated germination paper which was replaced twice weekly to prevent the accumulation of PEG. Cumulative seed germination time series data were fitted similarly to the temperature study previously described. Cotton germination did not occur at -1.2 or- 1.4 MPa and was completed by day 12 (Figure 3).

Lower osmotic potential inhibited seed germination by reducing the movement and imbibition of water by the germinating seed. Previous studies have also reported complete inhibition of germination at -0.1MPa osmotic potential (Heikal and Shaddad, 1982; Meneses et al., 2011; Murungu et al., 2005). As osmotic potential decreased, the maximum seed germination decreased while the time required for the onset of germination increased with decreasing osmotic potential (Figure 3). The elongation of the hypocotyls is more sensitive to low soil moisture than the radicle elongation. At -0.3 MPa, hypocotyl length increased to 2.5 cm compared to no elongation at -1.0 MPa after 120 hours of imbibition (Wanjura and Buxton, 1972b). The radicle length at -0.03 MPa is 118.3 cm, as soil moisture stress increased to -0.3 MPa, radicle length increased to 29.7 cm and decreased to 22.5 cm at -1.0 MPa. The hypocotyl:radicle ratio decreases with increased moisture stress from 0.43, 0.21 and 0.15 at -0.03, -0.3 and -1.0 MPa, respectively indicating that in inadequate soil moisture conditions, the development of the radicle supersedes the hypocotyl development (Meneses et al., 2011; Wanjura and Buxton, 1972b). The decrease in the rate of hypocotyl elongation is attributed to the disparity between the flux of germination factors to the embryo and the reaction rates which are producing growth (Wanjura and Buxton, 1972b).

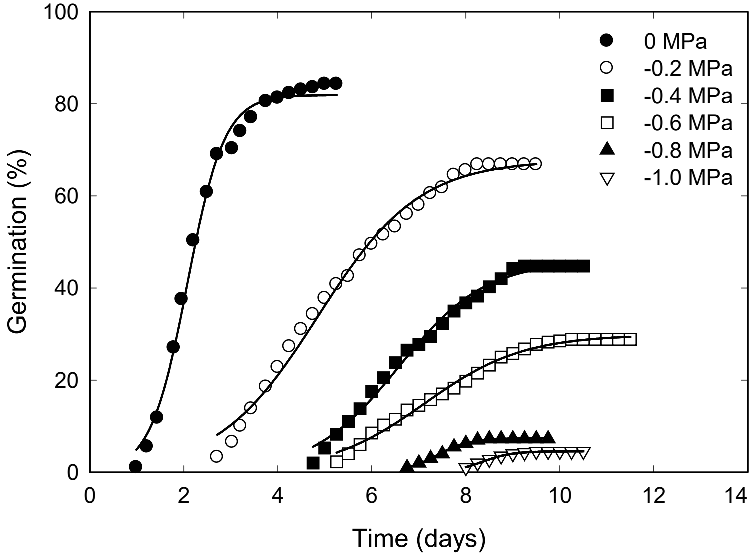

Figure 3. Observed (symbols) and predicted (lines) germination time course of cotton germinated at a range of osmotic potentials (0 to -1.4 MPa). Cotton did not germinate at -1.2 or -1.4 MPa. The symbols indicate the observed cumulative germination and the lines indicate the germination time courses fitted using a three-parameter sigmoidal function. Data are means and ± SE of six replications.

This is related to the rate of water absorption which decreases with increased osmotic stress (Heikal and Shaddad, 1982; Wanjura and Buxton, 1972a). For example, at -0.03, -0.1, -0.3 and -1.0 MPa soil moisture, the seed-moisture percentage at 3 mm radicle emergence was 79.3, 76.1, 77.0 and 73.4% at 32.2°C, respectively. This relationship between imbibition and soil moisture was influenced by temperature (Wanjura and Buxton, 1972a). Normal seedling development also decreases with osmotic potential (Meneses et al., 2011).

Maximum seed germination was estimated from each sigmoidal curve fitted to the time series response to osmotic potential. MSG declined linearly with osmotic potential with each incremental decrease in osmotic potential decreasing the maximum seed germination by 40%, similar to Heikal and Shaddad (1982) and Murungu et al. (2005). The time to achieve 50% germination increased quadratically with osmotic potential (Figure 4). For example, at -0.4 MPa, cotton required 6.2 days to achieve 50% germination, as the osmotic potential increase to -0.6 MPa, the time to 50% germination increased to 7.3 days. Median germination at the extreme osmotic potential (-1.0 MPa) was 8 days. At optimum temperatures, germination occurred at 54, 118 and 209 hours at -0.03, -0.3 and -1.0 MPa, respectively.

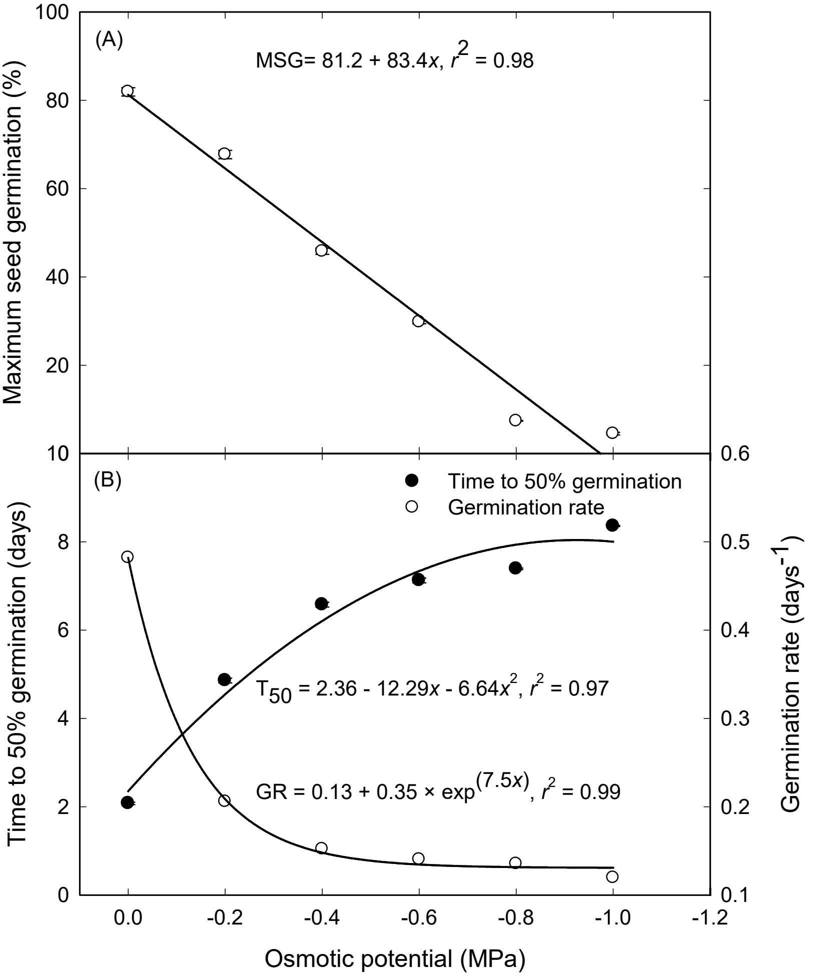

Figure 4. Osmotic potential effects on cotton (A) maximum seed germination for cotton and (B) time to 50% of maximum seed germination and germination rate. In (A), the symbols are recorded maximum seed germination and the lines are fitted using linear equation. In (B), the symbols are derived time to 50% of maximum seed germination and germination rates and the lines are fitted using quadratic and exponential equations. Data are means and ± SE of six replications.

Germination rate is the inverse of the median germination (GR $=1/T_{50}$) and represents the daily rate of germination. An exponential decay function best described the relationship between germination rate and osmotic potential. The germination rate at 0 MPa was 0.5 declining sharply to 0.2 at -0.2 MPa and remained relatively constant at osmotic potential beyond -0.6 MPa (Figure 4), similar to Murungu et al. (2005) results.

Under conditions of water stress, germination is delayed and this can have implications for the rate of germination and uniformity of emergence and establishment. The maximum seed germination and the germination rate decreased with decreasing osmotic potential while the time to 50% germination increased with increasing osmotic stress. The functions developed can be used in modeling cotton germination potential under variable soil moisture conditions.

PLANTING DEPTH EFFECTS ON COTTON SEED GERMINATION

In addition to temperature and water stress, the planting depth also affects the germination and emergence of cotton. Usually, cotton is seeded from 1.3 to 2.5 cm depending on the soil moisture levels and temperature. Planting deeper in crusted seed beds or early in the season with frequent rains reduces germination rates and may require replanting. Increasing seeding depth increases the heat requirement for seedling emergence (De Jong and Best, 1979), emergence time (Nasr and Selles, 1995), and the time for 50% emergence (Loeppky et al., 1989), in addition to decreasing the emergence rate (Hucl and Baker, 1990).

Cotton seeds were germinated at different planting depths from 1.3 to 6.4 cm and seedling emergence was monitored every 6 h. Using the cumulative seed emergence, sigmoidal curves and maximum emergence and time to 50% emergence were extracted similarly as described previously. The time required for the onset of seedling emergence increased with increasing planting depth (Figure 5). As seeding depth increased, the maximum seedling emergence decreased from 87% at 0.25 cm to 71% at 6.4 cm. Seedling emergence was similar for the 2.5, 3.8 and 5.1 cm and averaged 83% emergence (Figure 5). The time to 50% emergence increased linearly with planting depth from 4.9 days at 1.3 cm to 7.9 days at 6.4 cm. On the contrary, emergence rate decreased linearly from 0.21 at 1.3 cm to 0.13 at 6.4 cm (Figure 5). These trends are similar to those previously reported (Hucl and Baker, 1990; Loeppky et al., 1989; Nasr and Selles, 1995).

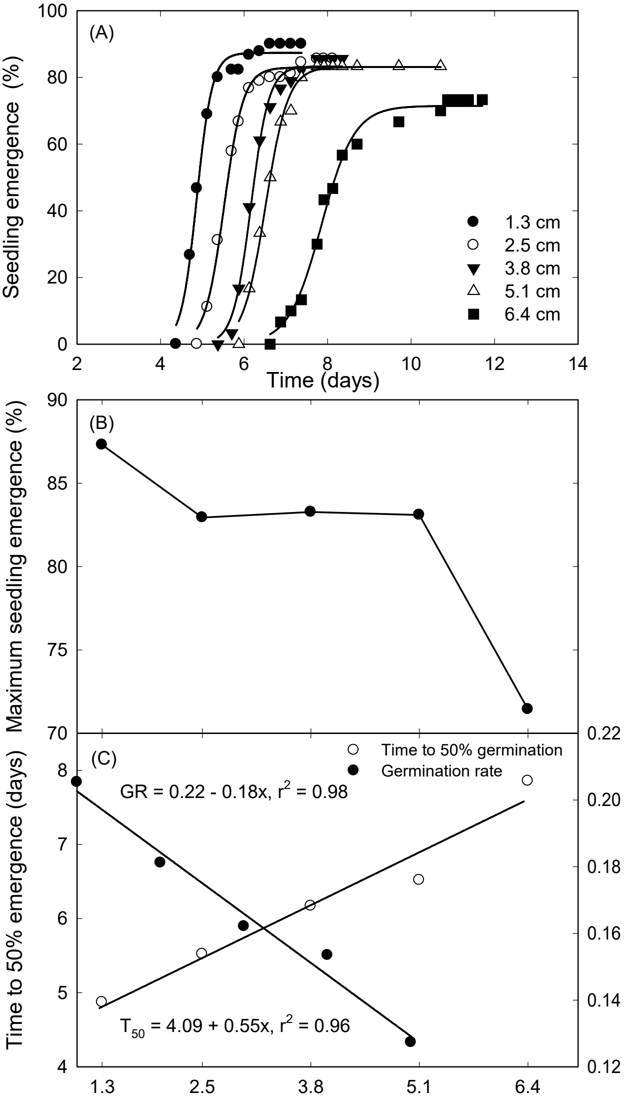

Figure 5. (A) Observed (symbols) and predicted (lines) emergence time course of cotton emerged at a range of planting depth (1.3 to 6.4 cm. The symbols indicate the observed cumulative emergence and the lines indicate the emergence time courses fitted using a three-parameter sigmoidal function. (B) Maximum seedling emergence for cotton. The symbols are recorded maximum seedling emergence. (C) Time to 50% of maximum seedling emergence and emergence rate. The lines are fitted using linear equations while the symbols are derived time to 50% of maximum seedling emergence and emergence rate. Data are means and ± SE of six replications.

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