Chapter 6

LOW TEMPERATURE AND MOISTURE STRESS EFFECTS ON COTTON SEED GERMINATION

Bhupinder Singh[1], Daryl R. Chastain[1], Gurpreet Kaur[1],
John L. Snider[2], and K.R. Reddy[3]
[1]Delta Research and Extension Center,
Mississippi State University, Stoneville, MS
[2]Department of Crop and Soil Sciences,
University of Georgia, Tifton, GA
[3]Department of Plant and Soil Sciences,
Mississippi State University, Mississippi State, MS

INTRODUCTION

Seed germination is an orderly process that begins with imbibition of the seed and ends with the emergence of the radicle from the seed coat (Rajjou et al., 2012). Seed germination is considered one of the most vulnerable stages to biotic and abiotic stress (Rajjou et al., 2012). Upland cotton *(Gossypium hirsutum* L.) grown in the U.S. cotton belt is commonly exposed to varying temperatures ranging from 20° to 35°C (Reddy et al., 1991). Little information is, however, available for cold and drought stress during the early growth stages of cotton (Pearson et al., 1970; Reddy et al., 1992a). The reason may be that past studies have identified the reproductive stage as the most sensitive growth stage to these abiotic stresses (Reddy et al., 1992b; Reddy et al., 1992c; Reddy et al., 1995; Reddy et al., 1999). Despite the extensive research, studies which investigated the cold and drought effect on seed germination and seedling growth characteristics in upland cotton were more than two decades old (Arndt, 1945; Ashraf et al., 1994; Pearson et al., 1970). Seed germination in cotton is considered to be very sensitive to sub-optimal temperatures (< 30°C) at planting. Cotton production guides for the southern US recommend for cotton producers to plant early season cotton (Late-April) at about 2.54 cm deep when the five-day forecast of soil temperature is above 18.3°C, provided adequate soil moisture conditions are present (Bradow and Bauer, 2010). Early planting of cotton is always favored in the U.S. cotton belt which lengthens the growing season, minimizes late-season insect pressure, and improves lint yields (Bradow, 1991; Pettigrew, 2002; Wrather et al., 2008). However, early season planting may very often expose early growth to low temperatures (< 30°C) and variable soil moisture conditions that result in poor seed germination and establishment (Barpete et al., 2015). These negative effects of low temperature are aggravated by varying soil moisture conditions, especially during seed imbibition. While soil temperature cannot be altered to facilitate optimal seed germination under field conditions, supplemental irrigation can alter soil moisture at the time of planting. Therefore, information about cotton seed germination in response to sub-optimal temperature and soil moisture is a matter of utmost importance. This chapter provides the review of effects of low temperature and moisture stress on cotton seed germination.

SEED IMBIBITION

Seed imbibition is the first stage of seed germination that involves water uptake, and increases in respiration soon follow (Rajjou et al., 2012). The rate of seed imbibition is considered to be highly controlled by the properties of the seed and water, in particular seed coat permeability, seed moisture content, temperature of water, and rate at which water is taken up by seed (Vertucci et al., 1989). Low temperatures (< 20°C) can substantially change the viscosity of water as well as membrane properties of the seed, influencing water uptake (Murphy and Noland, 1982). During imbibition, low temperatures inhibit the reorganization of the seed membrane upon rehydration into one with semipermeable properties but make it completely permeable to heavy metals, like lead (Wierzbicka and Obidzińska, 1998). Additionally, excessive permeability can cause leakage of cellular components such as lipids, enzymes and phenolic compounds from the embryo to the outside medium, which makes the embryo more susceptible to microbial attack (Woodstock, 1988). Membrane leakage due to chilling (5°C) during imbibition can substantially be prevented with the addition of calcium to the system (Christiansen et al., 1970). Cotton seeds also showed more rapid uptake of water at high temperatures (>30°C) than low temperatures (<30°C) (Wanjura and Buxton, 1972a). Christiansen (1964) observed the symptoms of radicle injury after seeds were imbibed at 10°C, and these symptoms were more apparent and severe when imbibed at 5°C. Soil water potential also impacts the rate of water uptake but has a lesser influence than low temperatures during imbibition (Wanjura and Buxton, 1972a). However, low moisture in combination with low temperature can reduce water uptake to a greater extent when compared to low temperature alone (Bradow and Bauer, 2010). Genotypic differences in the rate of water uptake do exist among different species or cultivars under low temperatures. Phillips (1968) observed that water diffusivity of soybean seeds was 18 times greater than cotton seeds and four times greater than corn seeds when germinated at 28 ± 1°C. The time to seed imbibition has also influenced the sensitivity of cotton seeds to chilling environments. Chilling during imbibition is the most damaging. So, if the seeds are kept warm during water uptake, they can withstand chilling temperatures later. Both upland and Pima cotton showed reduced germination under chilling temperature (5°C) effects, but the sensitivity to chilling temperatures declined in both species after cotton seeds were preconditioned to warm temperatures for a few hours (Buxton et al., 1976; Christiansen, 1968). BÖLEK et al. (2013) observed decreasing germination percentage with increasing period of seed priming at 5°C among all cotton cultivars. However, the studies have reported significant genotype x chilling time interactions for percent seed germination. Two species, *G. barbadense,* and *G. hirsutum*, had significantly different responses to the duration of chilling time (Cole and Christiansen, 1975). Cole and Christiansen (1975) observed reduced percent germination of Pima S-4' *(G. barbadense* L.) than genetic selection M-8 *(Gossypium hirsutum* L.) over same temperature range (5°C in water) after seeds were subjected to different durations of chilling time (0, 1, 2, 4, 8, 16, and 32 days). The author further reported higher germination and emergence rate in pre-conditioned seeds than chilled seeds, where the rate of water uptake by Pima S-4 was greater than M-8. Therefore, the selection of genotypes for cold tolerance varies depending upon the duration of chilling and imbibition. Buxton et al. (1976) observed similar responses of commercial Pima type cultivars on exposure to chilling at 5°C, but the cultivars differed significantly at 7°C and 10°C. Thus, the authors concluded that higher temperatures (>5°C) are more desirable for selection of cold tolerant genotypes in cotton. Likewise, Christiansen (1968) observed that genotypes of *G. hirsutum* L., M-8, and Deltapine 14, showed a similar response to exposure to chilling temperatures (5°C) during the initial hours of imbibition. The author further reported that after the cotton seeds hydrated for 4 hours at 31°C, subsequent seedling growth occurred normally under chilling temperatures (5°C) for 48 hours. In nutshell the above evidences reveals imbibition as the most chilling-sensitive stage of seed germination.

SEED RESERVE MOBILIZATION AND CONVERSION EFFICIENCY

Seed imbibition is followed by activation and formation of enzymes to metabolize storage compounds and synthesize new proteins (Rajjou et al., 2012). The activity of certain enzymes such as α-amylase and protease is regulated through phytohormones including gibberellins, cytokine, ethylene, and abscisic acids and is controlled by genotype and environmental factors like temperature (Srivastava, 2002), salinity (Ashraf, 2002) and drought (Ashraf et al., 1995). The metabolic activity and respiration rate increase as germination progresses and eventually drop at radicle emergence (Srivastava, 2002). High temperatures (>30°C) can accelerate seed aging which can have a marked influence on the heterotrophic growth of the seedling. The ability of a seedling to sustain itself during the heterotrophic phase of growth can be determined from seed reserve mobilization (SRM) also sometimes called seed reserve utilization and conversion efficiency of seed reserve utilized (SUE) (Nik et al., 2011; Sikder et al., 2009). Seed reserve mobilization depends upon two components: a) initial seed weight and b) seed depletion ratio (SDR), which describes a fraction of seed reserve that is mobilized. By comparison, conversion efficiency of seed reserve utilized (SUE) describes the efficiency with which mobilized or utilized seed reserve is converted to seedling tissue. Therefore, heterotrophic growth based on seed reserve can be determined as follow:

$$\text{SRM (mg seed}^{-1}\text{)} = \text{initial seed dry weight - unutilized seed dry weight}$$

$$\text{Seed reserve depletion ratio (SDR)} = \text{SRM / initial seed dry weight}$$

$$\text{SDR (\%)} = \text{(SRM / initial seed dry weight)} * 100$$

$$\text{SUE (\%)} = \text{(Seedling dry weight / SRM)} * 100$$

The decline in either of the components of SRM as a result of biochemical deterioration in the seed can reduce seedling growth (Nik et al., 2011). Being an oil-seed crop, cotton contains a substantial amount of seed storage reserve, especially lipids and proteins (Bradow and Bauer, 2010). The embryo serves as a sink for the energy derived from photosynthesis and other metabolic activities during seed development and accumulates storage reserves primarily in the cotyledons. These reserves are mobilized post-germination to fuel early seedling growth until the seedling becomes photosynthetically active. (Ichie et al., 2001). Thus, SRM declines with the change from heterotrophic growth to autotrophic growth. Seed size determines the amount of storage reserve available to the developing seedling and contributes to improved seedling vigor (Soltani et al. 2002; Snider et al., 2014). However, seed size may not positively relate to improved seedling vigor under stress conditions (Soltani et al. 2002) or necessarily to improved lint yields in cotton (Liu et al., 2015; Snider et al., 2016).

Past studies have recognized that SRM is more sensitive to various abiotic stresses than SUE (Soltani et al., 2002; Soltani et al., 2006; Nik et al., 2011). The growing conditions, particularly high temperatures during the reproductive stage of the parent plant, can adversely affect SRM at post-harvest seed germination (Rao and Sinha, 1993) which is very specific to the genotypes or species depending upon their tolerance levels (Hasan et al., 2013). Genetic variation for SRM under heat stress has been observed in corn (*Zea mays*) (Sikder et al., 2009), sorghum (*Sorghum bicolor*) (Gophane et al., 2005; Rao and Sinha, 1993), wheat (*Triticum aestivum*) (Khatun et al., 2015), and moringa (*Moringa oleifera*) (Tesfay et al., 2016). In addition, various other factors, including drought (Ansari et al., 2012; Soltani et al., 2002; Soltani et al., 2006), salinity (Soltani et al., 2002), nutrients (Seyyedi et al., 2015), seed aging (Mohammadi et al., 2012; Nik et al., 2011; Sung, 1996), and seed coat (Gorim and Asch, 2012) can significantly affect SRM. Higher SRM and SUE are desirable to prevent uneven and delayed emergence, especially under drought stress in the field (Sikder et al., 2009). Soltani et al. (2006) observed decline in seed reserve mobilization with increasing drought stress, while no effect was observed on SUE in Chickpea (*Cicer arietinum*) Further, osmo-or-hydro priming the seeds can significantly lower the reduction in SRM under drought stress compared to unprimed seeds (Maasoumeh and Mohammad, 2014; Ansari et al., 2012). Quantitative trait loci (QTL) approaches have also been exploited that successfully investigate the genetic characteristics of seed reserve utilization during seed germination stages (Cheng et al., 2013). N-acetylphosphatidylethanolamine, a phospholipid, has been found to be responsible for maintaining membrane integrity of cotton seed and promote SRM (Bewley, 1997). There is limited information available on cultivar-specific SRM across a wide range of temperatures and drought conditions for cotton in the peer-reviewed literature. This indicates the need for further research on SRM along with other seed germination parameters to a better understanding of seed and seedling vigor responses to multiple stress conditions.

RADICLE EMERGENCE AND GROWTH

Seed emergence is characterized by protrusion of the radicle and marks the completion of the seed germination process (Weitbrecht et al., 2011; Rajjou et al., 2012). The rapid increase in water and nutrient uptake determines radicle emergence which involves cell division and elongation. As a result, the hypocotyl elongates and pulls the cotyledons and epicotyl above the soil surface. This is followed by a subsequent drop in respiration level as seedling cotyledons begin to photosynthesize. Studies have generally considered seed as germinated after the radicle had protruded beyond the seed coat and attained a certain length (Christiansen and Rowland, 1986; Oosterhuis and Jernstedt, 1999; Bradow and Bauer, 2010; Turley and Chapman, 2010; Snider et al., 2014; Singh et al., 2017a). Extensive research has been conducted in the past to determine the environment x genotype interaction on radicle growth and development (BÖLEK et al., 2013; Barpete et al., 2015). Several abiotic factors, including temperature (McQuigg and Calvert, 1966; Wanjura and Buxton, 1972a; Ashraf et al., 1994;), seeding depth (Wanjura et al., 1969), salinity (Fuxin and Fuquan, 2000; Ashraf, 2002; Wang et al., 2007), and drought (Naim and Ahmed, 2015; Singh et al., 2017a, b; Singh et al. 2018) were found to influence germination and early seedling growth. Cotton seeds exposed to chilling temperatures (<10°C) during initial water uptake exhibit radicle abortion followed by profuse lateral roots and a swollen hypocotyl (Bradow and Bauer, 2010). The radicle abortion is primarily determined by the degree of damage to cortex cells under low temperatures (Christiansen, 1968). Christiansen et al. (1970) found increased solute (amino acids and sugars) loss from the radicle with increasing length of chilling (5°C) time. Longer periods of chilling treatments can significantly induce chilling injury. Christiansen (1968) observed reduced germination and induced root abnormalities after cotton seeds were exposed to chilling temperatures for 30 minutes. Further, the author noted that longer periods of chilling for 12 hours at the time of imbibition caused permanent damage to the seeds and hence, failure of the radicle to emerge. The rate of radicle emergence and subsequent growth in responses to low temperatures have also been studied to identify cold avoidance or tolerance mechanisms in cotton (BÖLEK et al., 2013; Barpete et al., 2015). Barpete et al. (2015) studied changing germination and seedling growth behavior at different temperatures to identify cold tolerance among cotton cultivars. They found cultivar SG-125 showed maximum germination and radicle length at 30°C among the five cotton cultivars including SG-125, ST-468, Ozbek-100, Ozaltin-404, and Ayhan-107. The values for maximum germination and radicle length declined significantly at 20°C and no germination was observed at 4°C for all cultivars. Also, radicle emergence was more sensitive to low temperatures than drought stress in cotton (Wanjura et al., 1971; Singh et al., 2018). Singh et al. (2018) observed a significant increase in time to reach 50 % emergence (TTE) under low temperatures (22°C) for seedlings of nine elite cotton lines representing nine different breeding programs when compared to optimum temperatures (30°C). Further, the study observed significant variability among the lines for emergence rate, where Ark 0504-4 took longest, and PD05064 took the shortest time to emerge, and no effect of drought stress (50 % of the optimum moisture) on seedling emergence of the cotton lines was observed.

Several methods have been developed to induce germination and emergence rate at low temperature (BÖLEK et al., 2013). BÖLEK et al. (2013) observed hydropriming at 25°C could induce germination and seedling emergence in cotton. However, primed cotton seeds at 5°C showed significantly lower germination percentage and emergence rate than 25°C, especially under longer priming duration (> 2 hours) (BÖLEK et al., 2013). The authors further identified cultivar Stoneville-468 had the highest germination and emergence rate among the three cotton cultivars, including Stoneville-468, Maraş-92, and Sayar-314, when primed in distilled water at 5°C and 25°C for 2, 4, 6, 8, or 10 hours. Secondly, they observed increased germination and emergence rate at low temperature after the cotton seeds were subjected to high temperature for 10 seconds which was applied using hot water (96 ± 1°C) bath. Cole and Wheeler (1974) observed that preconditioning Pima S-4' cottonseed with hot water at 70°C for 5 min significantly reduced sensitivity of seeds to gibberellic acid, thereby reducing percent emergence relative to seeds preconditioned with water at 30°C. The author further reported that preconditioning cotton seeds with water or exogenous gibberellic acid or adenosine-3':5'-cyclic monophosphate can substantially reduce the chilling effect on germination and emergence at the time of planting. Soil physical properties such as soil aggregates (Murungu et al., 2003), soil crusting (Bilbro and Wanjura, 1982; Awadhwal and Thierstein, 1985), and cultural practices that include cover crops and conservation tillage can also alter cotton germination and seedling growth (Nyakatawa and Reddy, 2000). Sowing-time during a day can also alter the rate of seedling emergence and subsequent development under cold soil conditions (Steiner and Jacobsen, 1992). Steiner and Jacobsen (1992) observed cotton seeds planted at 0800 hours in early spring under cool temperatures showed reduced seedling emergence (SE) compared to those planted at 1600 h, while the rate of seedling development (SD) remained unaffected by planting time. However, genotypic differences were observed at 0800 h and 1600 h planting times for both SE and SD in response to cool soil conditions. Seedling emergence and SD were significantly reduced in cultivar GC-510 relative to SJ-2 for the first 100 h and 30 h from planting, respectively, for both sowing times. Hence, the interaction between year, time of planting and genotype could determine the whole-plant rate of development and lint yield in cotton (Bauer and Bradow, 1996).

Variation in seed moisture has been considered an important physiological trait during radicle emergence (Wanjura and Buxton, 1972a). Both temperature and drought stress can cause considerable variability in seed moisture leading to variability in the rate of germination, and variable subsequent growth and development (Wanjura and Buxton, 1972a). Although, the responses to temperature and drought stress can be variable during this stage of physiological development, the combination of two stresses causes a synergistic effect (Wanjura et al., 1971; Wanjura and Buxton, 1972a, b; Singh et al., 2018). A significant increase in the radicle emergence time and rate of hypocotyl elongation with decreasing temperatures (< 30°C) and increasing soil moisture tension (> 0 bar) was observed (Wanjura et al., 1971). However, no germination occurred under the very low temperature (15°C) and very high moisture tension (10 bars) treatment combination (Wanjura et al., 1971). Further, the ratio of hypocotyl to radicle length significantly declines under drought stress due to an increased rate of radicle elongation (Wanjura and Buxton, 1972b; Wanjura, 1986). While, studies have also reported that under a certain range of temperature (38 to 15°C) and soil moisture stress (-0.3 to -10 bars), decreasing temperature can cause a similar change in radicle length as soil moisture stress increased (Wanjura and Buxton, 1972a).

SEED GERMINATION MODELS

Seed germination studies have developed various seed germination models using polyethylene glycol (Singh et al., 2017a), thermotolerance assays (Gajanayake et al., 2011), and hydropriming assays (BÖLEK et al., 2013) to quantify the response of seed germination to abiotic stresses. Such models estimate seed germination parameters and correlate them with relative seedling vigor, growth, and development. Seed germination models aim to observe seed germination time course data that provide maximum seed germination percentage (MSG) and seed germination rate (SGR) (Gajanayake et al., 2011; Singh et al., 2017a). Some seed testing laboratories use cool germination test to determine cottonseed quality and seedling vigor

(Drummond and Savoy, 1996). Under the cool germination test, seeds are incubated at 18 ± 0.5°C (AOSA 1983) for 7 days, and percent germination is recorded after that. This criterion has been used to predict the performance (vigor) of cotton cultivars in the field for early season planting in the United States (Smith and Varvil, 1984). Using cool germination test protocols, BÖLEK et al. (2013) considered cotton cultivars showing MSG more than 60% at 18 ± 0.5°C temperature over a 7-day period as tolerant. However, cultivars with similar MSG may vary for SGR (Maguire, 1962) and therefore, SGR is considered a valuable tool in selecting and evaluating the cultivar tolerance to various stress factors (Maguire, 1962; Gajanayake et al., 2011; Singh et al., 2017a). The thermotolerance models are unique because they estimate MSG and SGR under a wide temperature range among different cultivars (Gajanayake et al., 2011). This determines cultivar-specific optimum temperatures for seed germination and emergence. The response function developed from MSG and SGR can also be useful to estimate cultivar-specific cardinal temperatures which may be useful to classify cultivars for cold and heat tolerance. The information can also be applied to determine cultivar-specific optimum planting times for a specific region.

Seed parameters such as seed weight, seed size, seed storage reserves, seed mobilization efficiency, seed coating, radicle length and dry weights, also contribute to the difference in seedling vigor among cotton cultivars (Snider et al., 2014; Liu et al., 2015; Snider et al., 2016). However, certain seed quality parameters that are not necessarily linked to genotype may lower the validity of cultivar-specific seed germination models. The best way to nullify such effects is to collect the seeds from parent populations grown at the same time under a uniform seed production and seed storage environment for use in future experiments. Post-harvesting treatments and seed storage conditions can also influence seed germination, irrespective of cultivars or species. The time of seed storage can affect the seed quality and subsequent germination processes. Storing cotton seeds for a longer period than recommended could cause deterioration, membrane leakage, and decreased germinability. Goel and Sheoran (2003) identified differences in germinability of two cotton cultivars, HS6, and H1098 based on electrolyte leakage and correlated them with seed aging. They concluded that seed aging could be determined from membrane lipid peroxidation due to lower activity of antioxidant enzymes. Further, the ambient conditions, especially high temperature and humidity, during seed aging can accelerate the seed deterioration processes. Goel et al. (2003) observed increased lipid peroxidation and reduced activity of peroxide scavenging enzymes in cotton seeds that were stored at 40 ±1°C and 100% relative humidity for four days. The author also found that the aging treatment of 96 hours had a greater decrease in enzyme activity for cv. HS6 than H1098. The differences between cultivars in response to aging treatment in the studies above necessitate further work aimed at identifying cultivar-specific optimum conditions for seed storage.

Seed dormancy prevents the germination of seeds under otherwise favorable conditions and therefore, is an important consideration in conducting seed germination tests. It can be described as the inability of viable seeds to germinate under favorable conditions (Bewley, 1997). Embryo dormancy is a type of primary dormancy caused by internal factors. For instance, a higher concentration of abscisic acid is likely to induce transient dormancy (Halloin, 1986). In contrast, secondary seed dormancy is caused by unfavorable external/environmental factors (Vincent et al., 2010). Temperature, water, light, and oxygen are the major environmental factors that control this type of dormancy. Many plants such as oak (*Quercus spp.*) and apple (*Malus spp.*) require a certain number of chilling degree days or cold temperature treatment of about 5°C to 7°C to break primary dormancy and induce germination (Srivastava, 2002). While species that are sensitive to chilling temperatures like cotton on exposure to very high or low temperatures would induce secondary dormancy and fail to germinate even if favorable conditions are provided (Vincent et al., 2010). While cottonseed hydrated to 12-13% can significantly lower the chilling injury effect, seeds with moisture less than 10% develop a hard seed coat (Bradow and Bauer, 2010), making the seed membrane impermeable for water uptake. One way to eliminate the dormancy on freshly harvested cotton seeds is to dry and store them for a short period (Simpson, 1935).

SUMMARY

Cotton planted in early spring in the US does not necessarily exhibit uniform stand establishment across the field. The major reason is that environmental conditions, especially temperature and soil moisture, that vary across the field and during different phases of seed germination. Initially, exposure of cotton seeds to sub-optimal temperatures causes decreased membrane integrity during seed imbibition, making the embryo more susceptible to seedling disease. Further, variable soil moistures developed across field under minimum tillage practices can reduced rate of water uptake. The lowered seed moisture, as a result, reduces the rate of respiration causing a reduction in enzymatic metabolism of the seed reserves. As a consequence, heterotrophic phase of growth based on seed reserve slows down leading to reduced rate of hypocotyl elongation. Both hypocotyl and radicle elongation decreases with decreasing temperature and soil moisture from optimum, but show differential sensitivity to given stress. Thus, the ratio of hypocotyl/radicle is another important to study extensively under drought and cold stress during this stage of development. However, significant genotypic variability has been identified among cotton germplasm under low temperature and moisture environment for germination and physical characteristics of seed. Appropriate seed germination models are being developed studying these characteristics under controlled conditions to correlate with the post-harvesting treatments and early planting practices under field conditions. Future studies are however needed to focus on studying the mode of resistance identified in the cotton gene pool to improve region-specific cotton cultivars. The development of resistant cultivars could provide long-term benefits to cotton producers along with simultaneous advantage from early season cotton planting.

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