Chapter 5

GERMINATION AND SEEDLING DEVELOPMENT

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1. INTRODUCTION

The responses of cotton (*Gossypium* spp.) seeds to the germination environment depend upon (1) the point in the germination-through-emergence sequence at which conditions cease to promote germination and seedling development, (2) the magnitude and duration of the deviations from conditions promotive of germination, and (3) seedling development 'success' potentials determined by the genetic and seed vigor of a particular cotton seed lot and genotype. Suboptimal environmental factors, both abiotic and biotic, modulate, delay, or terminate cotton seed germination and seedling development during any of the four universal phases of seed germination: (1) imbibition, (2) mobilization of seed reserves (cotyledonary lipids and proteins in cotton), (3) radicle protrusion and elongation through resumption of cell division, and (4) hypocotyls and cotyledon emergence above the soil with the shift from metabolic dependence on seed storage compounds to photosynthetic autotrophy. In cotton and other oilseeds, cotyledonary lipid mobilization depends upon subcellular organelle-cooperativity and membrane-transport phenomena elucidated as the gluconeogenic glyoxylate cycle of oilseed species.

Among the environmental factors that affect cotton seed germination and seedling establishment are temperature, water availability, soil conditions such as compaction, rhizosphere gases, seed and seedling pathogens, and interactions among theses and other biotic and abiotic factors that are present in the seed bed and post-emergence micro-environments. This chapter refers to earlier reviews of cotton seed germination and seedling establishment and provides a guide to recent investigations of the two essential physiological processes, seed germination and seedling establishment, that ultimately determine both the yield and the quality of a crop.

2. PHYSIOLOGY OF GERMINATING COTTON SEEDS

Under promotive environmental condtions, the four sequential phases of cotton seed germination and seedling emergence occur during a relatively brief period (*ca.* four to six days) in the physiological progression from fertilized ovule to the mature plant that produces the next crop of seeds and fiber. When a quiescent, but viable, seed is planted (Baskin *et al.,* 1986; Delouche, 1986; Association of Official Seed Analysts, 1988; McCarty and Baskin, 1997), the return of the embryo and the sustaining seed storage tissues to active metabolism is initiated by water imbibition, the first step in seed germination (Ching, 1972; Bewley and Black, 1978; Pradet, 1982; Simon, 1984; Christiansen and Rowland, 1986). However, in 'hard" seeds of some cotton species and varieties, this chalazal pore is plugged with water-insoluble parenchymatous material (Tran and Cavanaugh, 1984). The presence and persistence of the plug can produce 'hardseed' or 'seed-coat' dormancy, a form of dormancy in which there is no or minimal water uptake (Christiansen and Moore, 1959; Benedict, 1984; Christiansen and Rowland, 1986, Delouche *et al.,* 1995). Seed coat impermeability can also be induced in cotton when seed water content is reduced to ≤10% before planting or germination testing (Delouche, 1986; Delouche *et al.,* 1995).

2.1 Early Imbibition

In the presence of adequate water and oxygen, viable, non-dormant cotton seeds, depending on the ambient temperature, require four to six hours for full hydra-

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tion (Benedict, 1984; Christiansen and Rowland, 1986). Initially, seed rehydration is a consequence of the matric potential (Ψ_m) of the cell walls and cell contents of the seed (Bewley and Black, 1978). Thus, the earliest phase of imbibitional water can occur in both in dead and viable seeds.

Exposure of imbibing Upland cotton seeds to temperatures below 5°C during the initial phase of imbibition results in seedling death (Christiansen, 1967; Christiansen, 1968). Depending on the duration of chilling exposure, imbibitional temperatures below 10°C cause radicle abortions or, in cotton seedlings that survive chilling injury, necrosis of the tap root tip and abnormal lateral root proliferation (Christiansen, 1963). Germination of Pima cotton seeds is inhibited by exposure to temperatures of 5 to 10°C at the beginning of the imbibition period (Buxton *et al.,* 1976). Pima seeds have been reported to be resistant to chilling damage after four hours of warm imbibition.

Significant chilling injury is induced by exposure of cotton seeds to cold water during the initial hours of imbibition. Chilling during earliest seed imbibition has also been associated with increased leakage of solutes from seeds (Simon, 1979, 1984). Both chilling injury and solute leakage reduce seedling vigor and increase seed and seedling susceptibility to pathogens. Both processes are manifestations of events during the first few hours of imbibition, and the severity of both chilling injury and solute leakage may be reduced if the seeds are preconditioned under warm, germination-promotive conditions (Christiansen, 1968; Simon, 1979).

2.2 Post-Imbibitional Periods of Sensitivity to Chilling Temperatures

In viable seeds only, the initial phase of imbibition is followed by an apparent 'lag phase' characterized by reduction in the rate of water uptake, rapid increases in metabolic activity, *e.g.,* protein and mRNA synthesis, and reactivation of preexisting organelles and macromolecules (Ching, 1972; Bewley and Black, 1978; Pradet, 1982; Simon, 1984). Significant water uptake resumes when protrusion of the radicle through the seed coast signals 'true' germination with the concomitant resumption of cell division in embryonic axis coupled with rapid mobilization of seed storage reserves (Ching, 1972; Simon, 1984).

During the germination process, seed respiration rates follow a triphasic curve similar to the cubic rate of imbibition (Ching, 1972; Simon, 1984). The initial period of high respiration overlaps the rapid initial stage of imbibition and the second germination phase characterized by the reactivation of preexisting macromolecules and organelles. The post-imbibitional phase in seed germination represents a 'steady state' for both water uptake and respiration during which preexisting metabolic systems synthesize the substrates needed for biogenesis of new proteins, mRNA, membranes, and organelles. Upland cotton seeds showed increased sensitivity to chilling between 18 and 30 hours after exposure to initial germination temperatures of 31°C (Christiansen, 1967). A similar period of increased sensitivity to chilling was observed at 28 to 32 hours when Pima seeds were germinated at 35°C and 40 to 56 hours when germination was at 25°C (Buxton *et al.,* 1976). Respiration and water uptake both increase rapidly after radicle protrusion and the resumption of cell division in embryo tissues. These processes occur in Upland cotton seeds after a rehydration/germination period of approximately 48 hours at 30 to 31°C, the temperature considered optimal for cotton seed germination (McCarty and Baskin, 1997). One field study also identified a third, later period of chilling sensitivity at *ca.* 140 to 170 h after planting (Steiner and Jacobsen, 1992). Under the conditions of that study, the third period of sensitivity corresponded to the 'early crook' stage of development for the chilling-stressed seedlings when the hypocotyls were near the soil surface and ready to emerge.

2.3 Glyoxylate Cycle and Storage Lipid Metabolism

In the lipid-storage tissue of cotton cotyledons, mitochondrial respiration is intergrated with glyoxysomal gluconeogensis (Trelease, 1984; Trelease and Doman, 1984). Thus, lipid mobilization during cotton seed germination involves four subcellular compartments, *i.e.,* lipid bodies, glyosomes, mitochondria, and cytosol. As germination and seedling development progress, lipases associated with the lipid bodies liberate fatty acids stored in the cotyledons as triaclyglycerides during seed development. The free fatty acids are transported across the membranes of the lipid body and glyoxysome into the glyoxysomal matrix. Within the single unit membrane of the glyoxysome are the enzymes necessary for the β-oxidation of the fatty acids to acetyl-CoA and the specialized glyoxylate cycle by which the acetyl-CoA is metabolized with the result of net synthesis of succinate within the glyosome (Goodwin and Mercer, 1983; Trelease and Doman, 1984).

Enzymes needed for further metabolism of succinate synthesized during the glyoxylate cycle are not located in the glyoxysomes, and succinate must be transported across the glyoxysomal and mitochondrial membranes for conversion the oxaloacetate in the tricarboxylic acid cycle of mitochondrial respiration (Goodwin and Mercer, 1983; Benedict, 1984; Trelease, 1984; Trelease and Doman, 1984). Additional information on the biochemistry of embryogenesis and the development of glyoxylate cycle organelles and enzymes during seed maturation are discussed in Chapter 25 of this book.

Nearly all lipid reserves in oil-rich seeds like cotton are mobilized *after* radicle protrusion (Trelease and Doman, 1984). Once lipid mobilization is initiated during the imbibition period, lipid utilization is rapidly completed over a relatively brief period during the first week of cotton seedling development (Smith *et al.,* 1974, Trelease and Doman, 1984). The activity of isocitrate lyase (ICL, EC 4.1.3.1), a marker enzyme unique to glyoxysomes and the glyoxylate

cycle, peaked after two-days germination in the dark, and ICL activity slowly declined to undetectable levels after eight days (Smith *et al.,* 1974). Exposure to light accelerated the decline in ICL activity, which was no longer detectable in illuminated cotton cotyledons after four days.

Radicle protrusion through the seed coat marks the completion of seed *germination.* Thus, lipid mobilization and the associated membrane transport and organelle cooperativity of the glyoxylate cycle are more precisely treated as seedling *emergence* phenomena. Glyoxylate cycle activity peaks when seedling survival and development are dependent on cotyledonary reserves and photosynthesis is beginning in the greening cotyledons and hypocotyl. When true leaves appear seven to ten days after emergence, cotyledonary lipid reserves have been metabolized and the transiently essential glyoxysome-mitochondria complex has disappeared. However, during the period between radicle protrusion (*ca.* 48 h post-planting) and full photosynthetic autotrophy, cotton seedling growth and emergence depend on the organellar enzymatic complex composed of the mitochondria and glyoxysomes. Studies of temperature and other factors that affect seed germination must, therefore, include consideration of the mechanisms by which environmental factors modulate both the primarily physical phenomena of imbibition and the biochemical and physiological phenomena of metabolic reserve mobilization and seedling development.

3. TEMPERATURE

Of the many abiotic factors that influence seed germination, seedling emergence, and stand establishment, temperature, which the cotton producer can monitor but not modulate, is the most important (Waddle, 1984; Stichler, 1996; Spears, 1997). Insufficient rainfall before or after planting can be augmented by irrigation, but the producer can neither schedule nor accelerate the rise in spring air temperatures to 16°C (60°F), the temperature below which cotton ceases to grow (Tharp, 1960; Munro, 1987; Edminsten, 1997a). This significant relationship between cotton production practices and temperature is usually quantified by the Degree-Day-60°F (DD-60) or Degree-Day-16°C (DD-16) heat unit frequently cited in cotton production guides and research reports (Bradow and Bauer, 1997; Edminsten, 1997a; 1997b).

3.1 Planting Date Criteria

Each spring, cotton producers in areas where cotton is grown as an annual must select the 'most favorable planting date' based on current and historic mean temperatures from analyses of long-term weather patterns (Waddle, 1985; Norfleet *et al.,* 1997). Several temperature criteria are included in this selection process. During the first five to ten days after planting, soil temperatures <10°C cause significant chilling injury (Gipson, 1986; Edmisten, 1997c). Therefore, production consultants in the short-season areas of the U.S. Cotton Belt east of the Mississippi River advise growers to delay planting until (1) the *soil* temperature at a depth of 7.6 cm (3 inches)has reached 18°C at 1000 hours standard time, and (2) more than 25 DD-60 heat units are predicted with the temperature to be >10°C for the first two nights after planting (Ferguson, 1991; Edmisten, 1997c). In Califorina, Kerby and coauthors (1989) concluded that cotton should not be planted when fewer than 10 DD-60 heat units per day were expected for the five days after planting. Similar 'rule of thumb' recommendations have been developed for the Texas High Plains and Mid-South regions of the U.S. Cotton Belt (Gipson, 1986). The relationship between yield and the number of degree days below 16°C after planting is seen in Figure 5-1 on which yield date were regressed on the number of days after planting for which the minimum temperature was <60°F (<15.6°C). The regression line plotted in Figure 5-1 was derived from yield data of PD-3 from 1991 through 1994 in South Carolina (Camp *et al.,* 1997).

Planting date selection and risk management techniques based on historical weather records and current meteorological predictions are often inadequate for cotton, a highly temperature-sensitive plant for which both early and late planting reduces yield (Kittock *et al.,* 1987; Bauer and Bradow, 1996; Edminsten, 1997c). Further, producers prefer to plant cotton as early as possible to maximize growing season length and yield, reduce post-emergence insect infestations, and avoid fall storms that lower fiber quality and interfere with crop defoliation and harvest (Edminsten, 1997c, Steiner and Jacobsen, 1992; Bird, 1997). When early planting exposes cotton seeds to cool, wet conditions, germination is delayed or fails to occur and seedlings are damaged or killed (Bird, 1986; Christiansen and Rowland, 1986; Wanjura, 1986; McCarty and Baskin, 1997; Spears,

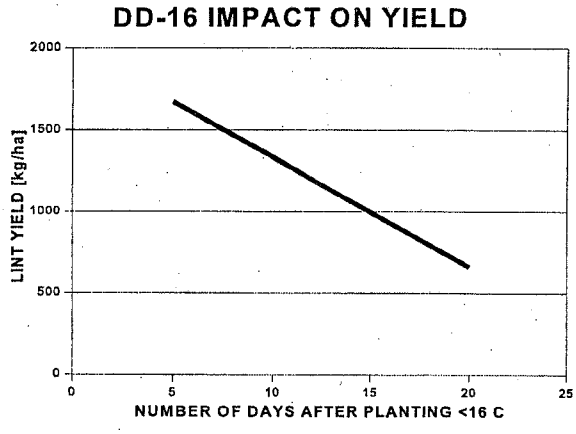

Figure 5-1. Impact of number of days after planting on which minimum temperatures were <60°F (15.6°C) on lint yield of trickle-irrigated 'PD-3' cotton in Florence, S.C. Regression line based on 1991, 1992, 1993, and 1994 treatment means (Camp *et al.,* 1997).

1997). Stand establishment in cool wet soil is often so poor that replanting, which entails significant costs for additional seeds and pesticides, becomes necessary (Edmisten, 1997a). There are no universal guidelines for cotton replanting decisions (Jones and Wells, 1997). The advantages of a more uniform stand must be balanced by the reduced maturity of late-planted cotton, and no guarantees for the uniform emergence of a second planting.

3.2 Seed Germination and Seed Vigor Testing

Growers regularly attempt to compensate for uncertain and suboptimal planting conditions by sowing extra seeds and/or using high quality, *i.e*, high vigor, seed lots (Kerby *et al.,* 1989; Bird, 1997). High vigor seeds emerge faster (Quinsenberry and Gipson, 1974) and from lower soil depths (Wanjura *et al.,* 1967). The potential of a seed to germinate or a seedling to survive in a chilling environment depends on the vigor of the seed (Bird, 1986; 1997; Spears, 1997). Thus, the well-characterized sensitivity of cotton seeds to chilling stress has become the basis for the 'cool germination test' (CGT) of cotton seed vigor (Smith and Varvil, 1984; McCarty and Baskin, 1997; Spears, 1997; Tolliver *et al.,* 1997).

The CGT is conducted in addition to the standard germination test (SGT), which is performed under temperature and moisture conditions that are highly favorable for germination and seedling development (McCarty and Baskin, 1997; Spears, 1997; Tolliver *et al.,* 1997). In both the SGT and CGT, cotton seeds are planted on special moistened towels scrolled to hold the seeds in place and to reduce drying (McCarty and Baskin, 1997). In the SGT, the scrolls are placed in a germinator operated at constant 30°C or in a 20/30°C cycle (16 h at 20°C and 8 h at 30°C). The SGT consists of four replicates of 50 or 100 seeds each.

The first SGT evaluation is made four days after planting. The scrolls are unscrolled, the normal seedlings are counted and removed from the towels, and the count data are recorded. The towels containing the ungerminated seeds are rescrolled and returned to the germinator. The second SGT evaluation is made eight days after planting. If no additional *normal* seedlings have developed, the SGT is terminated. If the SGT is not terminated at eight days, the towels are rescrolled and returned to the germinator until the final SGT evaluations are combined, and the 'standard' germination percentage is calculated and printed on the tag attached to the bag of seeds (seed lot) from which the SGT subsamples were drawn.

Cotton seeds tested under the SGT protocol are tested under laboratory conditions that are much more promotive of seed germination than normal field conditions are. In the CGT, seed scrolls and four replicates of 50 seeds each are also used; but the CGT germinator is held at a constant 18°C (Smith and Varvil, 1984; McCarty and Baskin, 1997). The contents of chilled CGT scrolls are evaluated once at seven days after planting. Only strong, vigorous seedlings that reach a combined root-hypocotyl length of 4.0 cm (1.5 in.) are counted. The percentage of high-vigor seedlings is calculated and reported as 'percentage cool test germination.'

There remains considerable variability among laboratories performing the CGT, and CGT results are not printed on the official seed-lot tag (Tolliver *et al.,* 1997). Further, the CGT ratings do not predict the success of either field germination or stand establishment (Spears, 1997). However, producers should obtain CGT information from seed dealers since there is a significant difference between the vigor levels of cotton seed lots with 85 percent and 60 percent CGT ratings. A seed lot with a high CGT percentage is more likely to perform well under chilling conditions, *i.e.*, at 18±1°C, the temperature of the CGT protocol (Smith and Varvil, 1984; Bird, 1997). Indeed, the *minimum* recommended soil temperature for planting cotton is the temperature used in the CGT (McCarty and Baskin, 1997). When field temperature are similar to those used in the SGT, lower vigor seed lots will usually perform as well as high vigor seed lots.

3.3 Seed Vigor and Emergence Prediction

Incubation periods in the SGT and CGT protocols approximate the lengths of time required for completion of the imbibition-to-emergence sequence of seed germination and seedling establishment. Thus, SGT and CGT data should be useful for predicting cotton seedling emergence (Buxton *et al.,* 1977; Smith and Varvil, 1984; Kerby *et al.,* 1989). However, seed vigor, quantified as the ratio of seedling axis weight to total seedling weight (percent transfer), was a poor predictor of field emergence (Buxton *et al.,* 1977). Further, combining percent transfer with percent germination into a 'germination index' (Buxton *et al.,* 1997) did not consistently improve emergence prediction, compared to predictions based on percent germination alone.

Combining SGT and CGT percentages improved the prediction of cotton seedling emergence under fluctuating soil temperature conditions. Kerby and coauthors (1989) used multiple regression analyses of (SGT% + CGT%) and DD-60 heat unit accumulations at ten days after planting to explain >64% of the variation in cotton seedling emergence. When interaction terms from the multiple regressions were included in the predictive equations, the combination of (SGT% + CGT%) DD-60 heat units at five days after planting, and the interaction term explained >68% of the variation of seed vigor and potential yield capacity (Wanjura *et al.,* 1969).

More recently, Steiner and Jacobsen (1992) examined the effects of planting time of day and cool-temperature stress from naturally varying soil temperatures by following seedling emergence and seedling rate of development. Final seedling emergence percentages were not affected by planting-day heat units, although seeds planted in the

morning (0800 hours) were more sensitive to soil temperature than were seeds planted in the afternoon (1600 hours). There was no defined relationship between emergence and seedling rate of development. However, genotype-related differences in cotton response to cool soil conditions at planting were reported. The authors suggested that high levels of cotton emergence under cool soil conditions could be achieved if chilling-tolerant genotypes were selected and planting was done in the afternoon to take advantage of diurnal warming of the seed-zone environment.

An examination of the relationships between seed quality (vigor) and preconditioning at 50°C and 100% relative humidity indicated that warm, moist preconditioning decreased cotton seed resistance to chilling (Bird, 1997). Pre-conditioning for ≤2.5 d increased germination percentages at 18°C, but field emergence was reduced by seed preconditioning. The reduced stands obtained from preconditioned seeds were associated with infection by pathogenic (damping-off) fungi.

3.4 Temperature and Post-Emergent Cotton Seedling Physiology

Most studies of responses of cotton seeds and emerging seedlings to chilling temperatures have concentrated on germination *per se* (Christiansen, 1963; 1967; 1968; Guinn, 1971; Cole and Wheeler, 1974; Buxton *et al.,* 1976) or low temperature effects upon seedling emergence (Pearson *et al.,* 1970; Wanjura and Buxton, 1972a, 1972b; Fowler, 1979; Wanjura and Minton, 1981). Relatively little is know about the effects of suboptimal temperatures on photosynthetic seedlings that have successfully emerged from the soil (Bradow, 1990a). Even less is know about seedling physiology during recovery from exposure to suboptimal temperatures (Clowes and Stewart, 1967; Bagnall *et al.,* 1983; Bradow, 1990a; 1990b). A few cotton genotypes have been screened for chilling resistance (Anderson, 1971; Krieg and Carroll, 1978; Bradow, 1991; Bauer and Bradow, 1996; Schulze *et al.,* 1997), but most such studies have concentrated on germination and heterotrophic seedling growth.

Without a simple assay for suboptimal-temperature sensitivity in photosynthetic seedlings, growers have relied on personal experience and anecdotal information when selecting cotton genotypes that might survive the effects of cold weather fronts which arrive after seedlings have emerged from the soil. This problem was addressed by adapting the SGT protocol to provide uniform seedling populations 48 hours after planting (Bradow, 1990a, 1991). Using a modified CGT protocol, morphologically homogeneous populations of photosynthetic seedlings of three cotton genotypes were exposed to light (14-h day) and growth temperatures of 10, 15, 20, 30, or 35°C for seven days (ten days total from imbibition to seedling harvest and evaluation) (Bradow, 1991). The effects of suboptimal temperatures on seedling root and shoot growth were evaluated by separate measurements of root and shoot lengths, fresh weight, dry weights, and relative water contents (Weatherley, 1950; Bradow, 1991). Significant genotype differences in seed vigor, inhibition of root and shoot elongations, fresh weight, and relative water contents were reported (Bradow, 1991).

The most marked differences between genotypes were in the capacities to resume growth, and to reestablish normal root and shoot water relations, after a five-day exposure to suboptimal temperatures (≤20° for roots and ≤25°C for shoots) (Bradow, 1991). The capacities of cotton seedling roots and shoots for recovering rapidly and fully from exposure to moderate suboptimal temperatures (>15°C) can be a strong determinant of stand establishment and subsequent yields in years in which post-emergent chilling occurs (Kittock *et al.,* 1987, Bauer and Bradow, 1996). Genotype recovery capacity in seedlings exposed for five days to temperature below 30°C could be gauged by changes in root relative water contents after a 48-h 'recover' period at 30°C (Fig. 5-2).

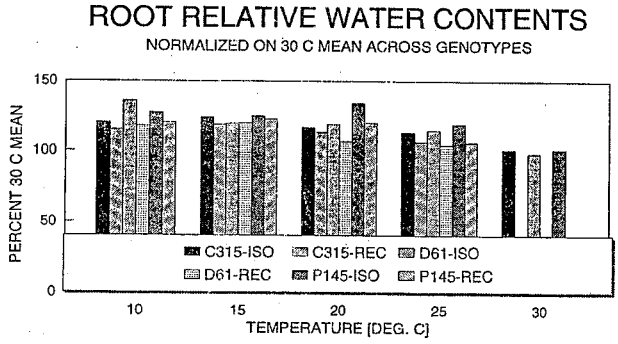

Figure 5-2. Root relative water contents of 10-day seedling roots of 'Coker 315' (C315), 'DPL 61' (D61), and 'Paymaster 145' (P145) exposed to 10, 15, 20, 25, or 30°D for seven days before evaluation (ISO treatment) or to 10, 15, 20, 25, or 30°C for five days, followed by two-day recovery at 30°C (REC treatment). Treatment relative water content percentages were normalized on the isothermal 30°C mean across all genotypes (adapted from Bradow, 1991).

Moderate chilling stress alters the water relations of both roots of shoots of photosynthesizing cotton seedlings by decreasing the shoot water content and increasing root water content in a cultivar-specfic manner (Bradow, 1991). However, the changes in root and shoot steady-state water relationships after a chilling-stress period differ from the shoot dehydration [wilting] observed under cold-shock (≤10°C) conditions (Bradow, 1990a). Recovery from chilling is related to the capacity of a seedling to resume normal water translocation from the roots and the capacity of shoot tissue to rehydrate upon restoration to growth-promoting temperatures (Fig. 5-3). At temperatures < 30°C, the root relative water contents of the three genotypes in Figure 5-2 increased after 48 h at 30°C, seedling root relative water contents of the three genotypes were lower (Fig. 5-2) and the shoot relative water contents of chilled 'Coker 315" seedlings were higher (Fig. 5-3). An increase in shoot

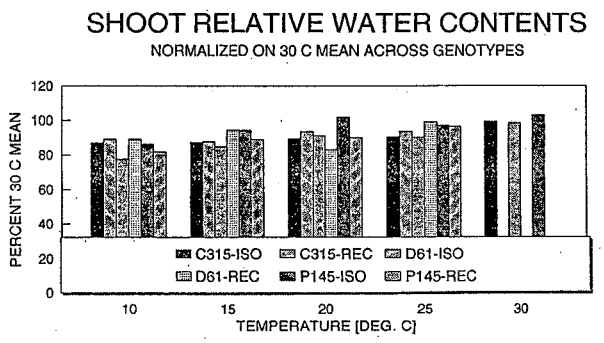

Figure 5-3. Shoot relative water contents of 'Coker 3115' (C315), 'DPL 61' (D61), and 'Paymaster 145' (P145) 10-day seedlings exposed to 10, 15, 20, 25, or 30°C for seven days before evaluation (ISO treatment) or to 10, 15, 20, 25, or 30°C for five days, followed by two days at 30°C (REC treatment). The treatment relative water content percentages were normalized on the isothermal 30°C mean across all genotypes (adapted from Bradow, 1991).

relative water content after a 48-h recovery period was also observed in 'DPL 61' seedlings that had previously been chilled at 10, 15, and 25°C. No post-chilling shoot rehydration was observed in 'PM 145' seedlings. Instead, 'PM 145' shoot relative water contents decreased during the 48-h recovery period (Bradow, 1991).

Seedling root elongation studies of 'DPL 20', 'PL 50', 'PL 5690', and 'DPL Acala 90' revealed genotype differences in response to temperatures <30°C in a controlled environment (Bauer and Bradow, 1996). 'DPL 20' root elongation was most inhibited by moderate chilling, and in the year in which planting was followed by cold weather, 'DPL 20' lint yields were lower than the yields of the three genotypes that were less sensitive to chilling stress.

3.5 Early-Season Heat Unit Accumulations, Yield, and Fiber Quality

Temperatures and heat unit accumulations during the first 50 days after planting (DAP) affect both fiber yield (Camp *et al.*, 1997) and fiber maturity (Bradow and Bauer, 1997). The impact of the number of heat units during the first 50 DAP is seen in the regression of lint yield for four years on the cumulative heat units at 50 DAP in those years (Fig. 5-4).

The effects of temperature, treated as heat unit accumulation, are equally clear in the relationship of fiber maturity to DD-16 accumulations (Bradow and Bauer, 1997). In Figure 5-5 is described the dependence of Immature Fiber Fraction (IFF) (Bradow *et al.*, 1996a) on DD-16 heat unit accumulations during the first 50 DAP in a two-year planting-date study of 'DPL 20', 'DPL 50', 'DPL 5690', and 'DPL Acala 90' grown in Florence, South Carolina. Overall, 1991 was the shorter, hotter, drier crop year, but

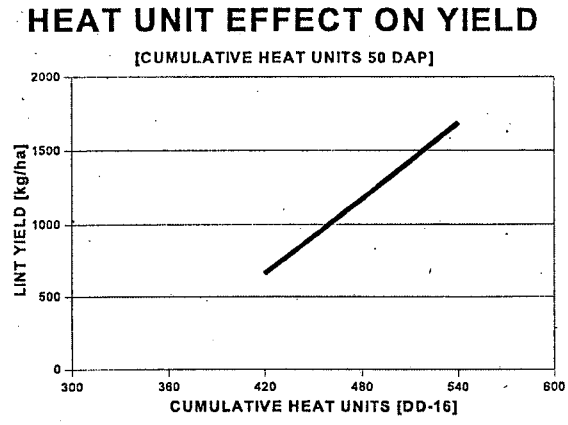

Figure 5-4. Impact of the number of heat units during the first 50 days after planting on lint yield in trickle irrigated cotton at Florence, S.C. The genotype was PD-3, and heat units were calculated as $\sum$ ((daily high temperature + daily low temperature)·0.5) - 15.6°C.

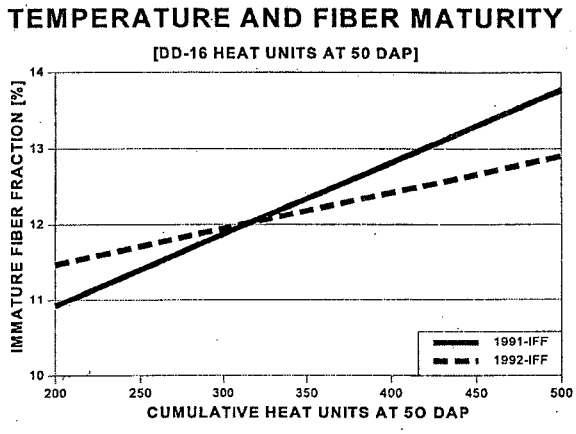

Figure 5-5. Impact of temperature during first 50 days fter planting on fiber maturity. Fiber maturity was quantified as Immature Fiber Fraction (Bradow *et al.*, 1996), and data were pooled across four genotypes within years (1991 and 1992).

the differences in the 1991 and 1992 thermal environments derived mainly from the higher spring temperatures during the first 50 DAP in 1991. When data were pooled across genotypes and IFF data were regressed on DD-16, the 1991 maturation rate (rate of decreasing IFF) was 1.6 times higher than the maturation rate in 1992, the cooler year. The same 1991:1992 maturation rate ration (1991 rate= 1.6 x 1992 rate) was found when fiber maturity was quantified as micronaire (Bradow and Bauer, 1997).

Temperature modulated and controls cotton seed germination, stand establishment, and post-emergence seedling growth and development. The effects of suboptimal temperatures extend beyond mere decrease in seed germination and stand percentages to significant reductions in the yield from cotton plants that survive exposure to chilling temperatures and consequential decrease in fiber quality,

particularly fiber maturity. Indeed, just as soil and air temperatures before planting can be used to estimate the probabilities of germination success, temperatures (as DD-60 or DD-16 heat unit accumulations) during the first 50 days after planting are valid indicators of yield, fiber quality and, therefore, the value of the cotton crop to both producers and processors.

4. WATER, LIGHT AND COTTON SEEDLING PHYSIOLOGY

4.1 Soil Moisture and Planting Date

Selection of the optimum planting date can depend as much upon the quantity and timing of the water supply as upon soil and air temperatures (Munro, 1987). In cotton-growing regions where the rainfall pattern is unimodal (a single wet period lasting up to six months and followed by a significantly drier period during the rest of the growing season), the best yields are obtained from cotton sown as early as possible in the wet period. In temperate cotton-growing areas, planting date selection must be governed by both water supply and temperature to minimize exposure of seeds and seedlings to cool, wet soil. When soil moisture content was at field capacity (-0.033 MPa), Upland and Pima genotypes attained 50% emergence 36 h earlier when soil temperatures were 31 to 36°C than when soil temperature ranges were 26 to 29°C or 32 to 45°C (Gonzales *et al.*, 1979). Low soil moisture and elevated temperatures (32 to 45°C) either prevented seedling emergence or increased the time required for 50% emergence by more than 100 hours.

Generally, *ca.* 50 mm of soil-penetrating rainfall should be recorded before cotton is planted (Munro, 1987). High initial water contents in clay and sandy soils accelerated cotton emergence and counteracted the negative effects of soil compaction or high soil impedance (Gemtos and Lellis, 1997). High soil physical impedance (1.12 to 3.36 kg cm^{-1}) reduced both hypocotyl and radicle elongation in cotton seedlings grown at 32°C and -0.03 MPa (Wanjura and Buxton, 1972a). Decreased hypocotyl elongation was consistently noted with lower soil moisture contents, but decreasing soil moisture increased root elongation as roots sought water at lower depths.

4.2 Light and Cotton Seeds and Seedlings

Seeds of commercial cotton genotypes do not require light for germination and the far-red/red (FR/R) light response is not a factor in cottonseed germination. Thus, depending on soil type and condition, a sowing depth of 2 to 4 cm is recommended (Munro, 1987). Shallow sowing decreases the amount of moisture available to the germinating seeds. Deeper sowing increases soil impedance and reduces seedling emergence. In a good stand of cotton seedlings the cotyledons are 4 to 7 cm above the soil surface.

Unlike the germinating seed, cotton seedlings are morphologically responsive to FR/R light ratios from the time of emergence (Kasperbauer and Hunt, 1992; Kasperbauer, 1994). Cotton seedlings were highly sensitive to FR/R ratios at the end of the day, and the responses were photoreversible so that the plants responded to the color received last (Kasperbauer and Hunt, 1992). Seedlings that received a high FR/R ratio last on each day developed lower specific weights, longer and heavier stems, less massive roots, and higher shoot/root biomass ratios. When the responses of cotton seedlings to FR/R ratios reflected from the soil surface were characterized by growing the plants over red, green, or white soil covers (mulches) in the field, stems of the five-week-old seedlings grown in sunlight over green or red surfaces were 130% longer than the stems of similar seedlings grown over white surfaces (Kasperbauer, 1994).

5 IMPACTS OF TILLAGE AND OTHER SOIL FACTORS ON COTTON SEEDLING EMERGENCE

5.1 Soil Impedance, Crusting, and Compaction

Soil physical impedance inhibits the elongation of both radicles and hypocotyls (Wanjura and Buxton, 1972a, Wanjura, 1973). Soil compaction and crusting are also important factors in cotton seedling emergence (Bennett *et al.*, 1964; Wanjura and Buxton, 1972a, Wanjura, 1973; Munro, 1987; Tupper, 1995). Emerging cotton hypocotyls are particularly sensitive to soil-surface crusting (Bennett *et al.*, 1964; Wanjura, 1973; Stichler, 1996). In addition to soil 'caps' formed when the surface dries, soil crusting due to the impact of rain or aerial irrigation water droplets mechanically impedes the emergence of seedlings (Arndt, 1965; Munro, 1987). When the soil crust forms a seal or cap above the germinating seed, the U-bend of the emerging hypocotyl may fracture before the emerging cotyledons are pulled free of the soil (Munro, 1987). If the soil type or prevailing weather conditions at planting increase the probability of surface crusting, producers are advised to sow seeds more thickly since the combined emergence pressure of three or four closely-spaced cotton seedlings may break through a soil cap that a single seedling could not penetrate. Soil sealing and crusting also increase runoff and erosion; and cover-crop residue management practices or soil-surface treatments have been developed to reduce soil-crust formation and the related inhibitions of seedling emergence (Bradford *et al.*, 1988; Pikul and Zuzel, 1994; Zhang and Miller, 1996).

5.2 Impacts of Tillage Methods and Equipment Traffic on Soil Aeration and Seedling Growth

Inhibition of seedling radicle elongation by soil impedance and the related slowing of emergence and early-season growth (Wanjura and Buxton, 1972a; Burmester *et al.,* 1995) have been related to tillage methods (Burmester *et al.,* 1995; Busscher and Bauer, 1995), equipment traffic patterns (Khalilian *et al.,* 1995; Gemtos and Lellis, 1997), and soil strength differences among soil horizons (Box and Langdale, 1984; Busscher and Bauer, 1995). The growth of seedling radicles is also restricted by soil compaction or 'sealing' that results when knife openers are used on overly moist soils (Stichler, 1996). When cotton seedlings in conservation-tillage plots were dug up two weeks after emergence, many plants had developed lateral taproots that ran along the top of a compacted zone 5 to 10 cm below the soil surface (Burmester *et al.,* 1995). Cotton growth and yield depend on efficient root penetration to reach nutrients and water in the subsoil horizons. Therefore, equipment traffic patterns must be controlled to limit soil compaction in the root zone and to reduce the formation of the high-impedance subsoil zones associated with some equipment and cultural methods. Use of some seed planters and tillage methods may lead to hypoxia (<3.5 mmol O_2•mol^{-1}) or increases in soil CO_2 levels (>20 mmol CO_2•mol^{-1}) that result in inhibition of cotton root elongation (Leonard and Pinckard, 1946; Minaei and Coble, 1989; 1990).

Cotton seed germination is also affected by the O_2:CO_2 ratios. Germination was suppressed at concentrations <5 mmol O_2•mol^{-1}, regardless of CO_2 concentration (Minaei and Coble, 1990). Higher concentrations (20 to 30 mmol CO_2•mol^{-1}) promoted germination but inhibited root elongation. Higher oxygen levels, combined with CO_2 concentrations of 1.5 to 2 mmol CO_2•mol^{-1}, promoted radicle elongation.

The low tolerance of cotton roots for poor soil aeration is also a factor in reduced seedling emergence and root elongation associated with flooding and water-logging of the soil (Jackson *et al.,* 1982; Hodgson and Chan, 1982; Lehle *et al.,* 1991). Ethanolic fermentation was induced immediately after introduction of imbibed cottonseeds to N_2 or CO_2 atmospheres at 28°C (Lehle *et al.,* 1991). During a 2-h hypoxic stress period, cotton radicle elongation was briefly halted before growth resumed at a reduced rate. Upon restoration of aerobic conditions, radicle growth recovered fully; and ethanol produced by hypoxic fermentation was assimilated rapidly once hypoxic stress was relieved.

5.3 Conservation Tillage and Cotton Seedling Growth

Conservation tillage systems represent one of most common methods for reduction of soil erosion on cotton acreage (Valco and McClelland, 1995). However, slower early-season growth has been reported for cotton planted into no-till cotton or no-till wheat residues (Burmester *et al.,* 1995). In comparison to conventional tillage, use of conservation tillage also reduced cotton stand populations at four weeks after planting (Colyer and Vernon, 1993). Other researchers have also reported reduced plant populations under reduced tillage (Brown *et al.,* 1985; Rickerl *et al.,* 1984; 1986; Chambers, 1990).

Conservation-tillage and the sometimes negative effects of cover crop residues on cotton stand establishment have been attributed to increased seedling disease (Rickerl *et al.,* 1988; Chambers, 1995b); ammonia toxicity (Megie *et al.,* 1967), seedling growth inhibition by volatile organic compounds released by cover crop residues decomposing in the root zone (Bradow and Connick, 1988; Bradow and Bauer, 1992; Bradow, 1993; Bauer and Bradow, 1993), and seedbed moisture depletion by the cover crop (Bauer and Bradow, 1993). When 'Coker 315' seedlings were grown for two weeks in soil collected immediately after zero (Day 0) or seven days (Day 7) after cover crop (fallow weeds or crimson clover) residue incorporation, cotton seedling root elongation was inhibited 50%, compared to root growth in a sterile control soil of similar impedance (Bradow and Bauer, 1992; Bauer and Bradow, 1993). The Day 0 soil samples containing decomposing residues also inhibited shoot elongation (>25%) and cotyledon expansion (>20%). The inhibitory activity of decomposing plant residues was increased by soil crusting but disappeared with time (*ca.* 14 days after residue incorporation). Seedling growth inhibition by cover crop volatile emissions was minimized when cotton planting was delayed two weeks after residue incorporation or until no recognizable plant residues remained in the soil.

6. SEEDLING DISEASE COMPLEX AND OTHER BIOTIC STRESS FACTORS THAT AFFECT COTTON SEEDLING EMERGENCE

6.1 Seedling Disease and Seedbed Environment

Conservation tillage, specifically no-till, increases the severity of seedling disease, particularly in early plantings (Chambers, 1995b). Even when warm, dry soil conditions are present at planting, stand counts and plant vigor were lower in no-till than in conventional tillage. Seedling disease complex, which causes an estimated 2.8 to 5% annual loss, is the most important disease problem of cotton in the United States (Rothrock, 1996; Bailey and Koenning, 1997). For example, in controlled-environment studies of

cotton black root rot caused by *Thielaviopsis basicola,* the weights of infected seedlings were reduced 22 to 31% at 20°C and 13 to 19% at 24°C. The effects of seedling infection persisted as reductions in yield. Crop rotation or summer flooding reduced *T. basicola* frequency in areas where *T. basicola* was found in 100% of fields planted to continuous cotton (Holtz *et al.,* 1994). However, rotation with peanut did not reduce the severity of seedling disease caused by *Rhizoctonia solani* (Sumner, 1995).

Seedling diseases are caused by several soil-borne fungi that thrive under cool, wet conditions and seem more prevalent in sandy, low-organic matter soils (Ferguson, 1991; Bailey and Koenning, 1997). Other factors that increase seedling disease frequencies are planting too deep, poor seedbed conditions, compacted soil, nematode infestation, and misuse of soil-applied herbicides such as the dinitroanilines. The primary agents of seedling disease are the fungi *Rhizoctonia solani, Pythium* spp., and *Fusarium* spp. The same fungi may cause seed decay, seedling root rot, or both. *Pythium* and *Fusarium* spp. usually attack the seed and below-ground parts of the young seedlings. *Rhizoctonia* spp. infections appear as reddish brown, sunken lesions at or below ground level ('sore-shin') and may occur at anytime from emergence until the seedlings are six inches tall.

The control of seed and seedling diseases is preventive, rather than remedial (Garber, 1994; Bailey and Koenning, 1997). Fungicides (as seed treatments, in-furrow applications and hopper-box treatments) are the primary control program components. In most years, seed treatment fungicides are sufficient unless the seed is of low quality or the weather is unfavorable for germination. In some years, protection from the seed-applied treatment may not persist until the cotton seedlings have grown to a stage of lower disease susceptibility; and in-furrow fungicide application is recommended for early plantings or when cool, wet weather is expected after planting (McLean *et al.,* 1994; Bailey and Koenning, 1997). The hopper-box method is less expensive and less effective than the in-furrow application.

Cultural practices that reduce the severity of seedling diseases are use of high-quality seed that grows more rapidly and produces more vigorous seedlings, delay of planting until the soil has reached 18°C at a three-inch depth; crop rotation; proper fertilization and liming to promote seedling growth, avoidance of excess rates and deep incorporation of herbicides, early cutting and shredding of stalks to reduce the level of inoculum carried over from one year to the next, use of raised beds for early plantings and control of nematodes through crop rotation, planting resistant genotypes, and use of nematicides (Bailey and Koenning, 1997). Recently, several biological fungicides have been developed for use with cotton (EI-Zik *et al.,* 1993; Bauske *et al.,* 1994; Brannen and Backman, 1994a; Howell, 1994; Kenney and Arthur, 1994; Howell and Stipanovic, 1995). The effectiveness of biocontrol fungicides, however, can be unpredictable and sometimes significantly lower than the commercial seed-treatment fungicides (Davis *et al.,* 1994).

Although the weather cannot be controlled, cotton producers can and should choose those cultural practices that create the most favorable conditions for seedling germination and emergence (Garber, 1994). Choice of planting dates, seed bed depths, and cultural practices that create an environment favorable for 'friendly' microorganisms antagonistic to seedling pathogens allow the producer to modulate the temperature-related factors so that a good stand of vigorous cotton seedlings is obtained under suboptimal and inhibitory conditions.

7. SUMMARY

Cottonseed germination and seedling development are highly sensitive to the environment at planting and for several weeks after that. The environmental impacts on germinating cotton seeds and emerging cotton seedlings depend on the point during the germination-through-emergence sequence at which conditions cease to promote germination and seedling development and the magnitude and duration of the deviations from conditions promotive of germination. Further, the stand establishment 'success' potential of a particular cotton seed lot and genotype is determined by genetic factors and seed vigor of that seed lot or genotype. Suboptimal environmental factors, both abiotic and biotic, modulate, delay, or may terminate cotton seed germination and seedling development at any point from seed imbibition to photosynthetic autotrophy. Among the environmental factors that affect cotton seed germination and seedling establishment are temperature, water availability, soil conditions such as compaction, rhizosphere gases, seed and seedling pathogens, and interactions among these and other biotic and abiotic factors that are present in the seed bed and post-emergence micro-environments. This chapter provides a guide the impacts of the seedbed environment on two essential physiological processes, seed germination and seedling establishment, that ultimately determine both the yield and the quality of a cotton crop.