

## Chapter 5

# WATER STRESS AND REPRODUCTIVE DEVELOPMENT IN COTTON

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## INTRODUCTION

Water is the most limiting factor for plant growth and crop productivity (Kramer, 1983), and water-deficit stress adversely affects crop growth and yield throughout the world (Boyer, 1982). Crop yields are being reduced by drought and the increasing scarcity of water for irrigation, and changing world climatic trends may increase the severity of the problem (Le Houerou, 1996). Water availability and quality affect the growth and physiological processes of all plants, since water is the primary component of actively growing plants, ranging from 70-90% of plant fresh mass (Gardner *et al.*, 1984).

Due to its predominant role in plant nutrient transport, chemical and enzymatic reactions, cell expansion, and transpiration, water-deficit stress alters how plants grow, their morphology, and the biochemical processes that occur in them (Hsiao, 1973; Kramer, 1980). In general, plant water-deficit stress is defined as the condition where a plant's water potential and turgor are decreased sufficiently to inhibit normal plant function (Hsiao 1973). The effects of water stress depend on the severity and duration of the stress, the growth stage at which stress is imposed, and the genotype of the plant (Kramer, 1983). The effect of water-deficit stress on the growth, physiology and yield of cotton was recently reviewed by Loka *et al.* (2011). This review discusses the effects of water-deficit stress on reproductive development of cotton (*Gossypium hirsutum* L.).

## Sensitivity of Cotton to Water-deficit Stress

Crop sensitivity to water deficit varies by growth stage and is crop-dependent (Doorenbos and Pruitt, 1977; Saini and Westgate, 2000). In many crops, reproductive development is the most sensitive period to drought stress following seed germination and seedling establishment (Saini, 1997), and cotton appears to follow this pattern, as well (Loka, 2012). Cotton is sensitive to water deficit during both flowering and boll development (Constable and Hearn, 1981; Cull *et al.*, 1981a,b; Turner *et al.*, 1986). Recent research has shown that the developing pollen (Burke *et al.*, 2002) and pollen tube growth (Snider *et al.*, 2011) are highly sensitive to environmental stress.

The perennial nature and indeterminate growth pattern of cotton results in the simultaneous occurrence of several stages of flowering and fruiting. This ambiguity has contributed to conflicting reports on which stage of crop reproductive development is most sensitive to water deficit (Loka *et al.*, 2011). According to Reddell *et al.* (1987), the early flowering period in cot-

ton is the most sensitive to water stress, whereas Orgaz *et al.* (1992) concluded that water stress during peak flowering had the most detrimental effects on cotton yield.

On the other hand, a number of reports (Radin *et al.*, 1992; Plaut *et al.*, 1992; de Cock *et al.*, 1993) state that boll development, particularly well after the end of effective flowering, is the most water-deficit-sensitive period for cotton. Additionally, in an earlier experiment, Harris and Hawkins (1942) reported that delaying irrigation at fruiting could increase yield by inhibiting excessive vegetative growth, a result reinforced by Singh (1972), who reported increased number of flowers and bolls per plant as well as increased yield when cotton plants were stressed during the pre-flowering season.

Conversely, Stockton *et al.* (1961) and Lashing *et al.* (1970) observed that increased irrigation resulted in increased flowering. Guinn *et al.* (1981) concluded that a moderate water-deficit stress early in the season could be beneficial to the plants by slowing vegetative growth, but that the risk of negative results meant that these practices should be approached with caution.

The effects of water deficit on different plant physiological processes are complex and inter-related. Cellular water content largely controls stomatal aperture, and stomatal conductance directly affects CO<sub>2</sub> diffusion and photosynthetic carbon fixation, which in turn affects carbohydrates and metabolic functions such as translocation, respiration and available energy. However, for ease of discussing these physiological functions, we have addressed the effects of water deficit pre-flower, during flowering and after flowering on boll development.

## Water-deficit Stress Prior to Flowering

As stated by Grimes *et al.* (1969), cotton yield is positively correlated to the number of bolls produced. Initiation of floral buds, however, occurs 35-40 days before anthesis, while the number of carpels and anthers is determined 30-35 days before anthesis (Stewart, 1986). Because fiber production is based on the number of ovules contained in a boll, and that the number of ovules is determined 15-25 days before anthesis, pre-flowering is a critical period for yield determination. Hence, environmental conditions that occur during this period and cotton's responses are extremely interesting. Nevertheless, little information exists on the effect of water-deficit stress during pre-flowering.

As early as 1932, Beckett and Hubbard conducted field experiments with Upland cultivars and reported that limited water supply before flowering had minimal influence on the number of carpels per flower. Similar results were observed by Leding and Lytton (1933), who found that water stress decreased the number of carpels in the flower, albeit not significantly. Singh (1975) reported increased numbers of flowers and bolls per plant accompanied by yield increase when irrigation was withheld at the preflowering stage, and similar results were reported by El-Zik *et al.* (1977) and Mauney *et al.* (1980). Young squares, however, appeared more prone to abscise when the plant was subjected to lower than optimal moisture (McMichael, 1979), with their most sensitive period being the first week after visibility (Ungar *et al.*, 1989). In view of these observations, Rijks (1965) reported that limited supply of water before flowering increased fruit retention, but reduced nodes, fruiting branches, and fruiting sites. Similar results were reported by Stockton *et al.* (1971), whereas increased flowering rates with increased irrigation were

reported by Bruce and Romkens (1965) and Lashin *et al.* (1971). Krieg (2000) concluded that inhibition of flowering site initiation rather than square shedding was the reason for decreased fruiting sites due to water-deficit stress prior to flowering.

Zhao and Oosterhuis (1997) reported that in growth chamber experiments, dry weight of water-stressed floral buds was significantly lower compared to the control. Tarpley and Sassenrath (2006) monitored carbohydrate concentrations of floral buds starting from 10 days before anthesis until 2 days after anthesis under water-sufficient conditions. They reported that carbohydrate (glucose, fructose, sucrose and starch) concentrations and water content of flower buds were relatively stable until the day of anthesis, when they showed a significant increase in both carbohydrate and water content. Guinn *et al.* (1990) reported that 3 days before anthesis, flower buds contained higher concentrations of indoleacetic acid (IAA) compared to the control, while abscisic acid (ABA) concentrations remained unaffected.

### Water-deficit Stress during Flowering

Cotton white flowers have not been reported to abscise, but to actually sustain expansion under extreme water-deficit conditions, even after leaf emergence and expansion have been arrested. However, significant reductions in yield are observed when water-deficit stress occurs during flowering. Redell *et al.* (1987) reported that conditions of limited water supply during early flowering can result in significantly decreased yields, while Orgaz *et al.* (1992) argued that peak flowering is the most sensitive stage of cotton development to water-deficit stress.

Trolinder *et al.* (1993) reported that in field studies where plants were subjected to mild and severe limited water conditions, water stress resulted in petal water potentials that were significantly higher than leaf water potential. In addition, it was observed that even though petal water potential varied in accordance with plant water status, due to the direct vascular connection between the petals and the plant stem, the water potential gradient the petals required for their expansion did not exist. They speculated that this inverted gradient could be attributed to metabolic reasons, such as rapid solute breakdown. However, further investigation under conditions that restrained metabolic activity resulted in the same inverted gradient (Trolinder *et al.*, 1993). Loka and Oosterhuis (unpublished data) observed significantly higher carbohydrate concentrations in petals than leaves under both well-watered and water-stressed conditions. In addition, Loka and Oosterhuis (2011) reported that water potential of the ovary and the style of white flowers were significantly higher compared to the leaves under both well-watered and water-stressed conditions.

Guinn *et al.* (1990) conducted field experiments where plants were subjected to two cycles of water stress and flowers were collected the day of anthesis in order to investigate the effect of limited water supply on ABA and IAA concentrations. ABA levels of water stressed flowers were increased compared to the control, while after irrigation its levels decreased. Conversely, water-deficit stress had a minimal effect on IAA concentrations, resulting in increased levels of conjugated IAA in water-stressed flowers, whereas free IAA concentrations of water-stressed flowers were similar to those of control. The authors speculated that the lack of an effect of water-deficit stress on the levels of free IAA was due to the small increase in ABA levels of the flowers.

## Water-deficit Stress during Boll Development

Cotton bolls appear to be less sensitive to water-deficit stress than the leaves since they are significantly resistant to water loss and are considered essentially non-transpiring (McMichael and Elmore, 1976; Radin and Sell, 1975; Wullschleger and Oosterhuis, 1990; Trolinder *et al.*, 1993; Van Iersel and Oosterhuis, 1994; 1996). A number of researchers however, have reported that limited supply of water during boll development can result in significantly lower yields (Radin *et al.*, 1992; Plaut *et al.*, 1992; de Cock *et al.*, 1993). In support of these observations, McMichael *et al.* (1973) observed that if water stress occurs during the first fourteen days after anthesis, young bolls generally abscise. However, after that period, bolls are retained.

Wullschleger and Oosterhuis (1990) conducted growth chamber experiments where bract and capsule wall water potential of 5-, 20-, and 30-day old bolls was monitored along with leaf water potential under a moderate and a severe water stress regime. They reported that mild water stress had no effect on bract and capsule wall water potentials while leaf water potentials were significantly decreased. A similar pattern was observed under severe water stress conditions with the exception of the dark respiration rates of the capsule wall that were significantly decreased under water-deficit stress conditions. Trolinder *et al.* (1993) reported that the inverted water potential gradient that was observed for the petals was also present in 20-day after anthesis bolls. Van Iersel and Oosterhuis (1995, 1996) investigated water relations of cotton fruits in field as well as growth chamber experiments. Water and osmotic potential of bracts and subtending to the bolls leaves compared to the bolls. This was attributed to the xylem connections of the fruits being immature and, hence non-functional, until three weeks post anthesis, and it was concluded that since the water potential gradient is directed from the fruits to the leaves, the main entrance of water in cotton bolls is through the phloem.

However the apoplastic isolation of the bolls and their independence from the water status of the plant, cotton boll hormonal balance appears to be significantly affected by water-deficit stress. Guinn (1976) observed that ethylene evolution rates of 3-day old bolls were significantly increased under conditions of limited water supply. Similarly, free and conjugated ABA levels of 3-day old water-stressed bolls as well as their abscission zones were reported to be significantly higher compared to the levels of well watered plants (Guinn and Brummett, 1988). Free and conjugated IAA of 3-day old bolls followed a differential pattern with free IAA decreasing when soil moisture became limiting while conjugated IAA significantly increased in both water-stressed bolls and their abscission zones (Guinn and Brummett, 1988).

Despite the differences in ABA, IAA and ethylene, no effect of water-deficit stress was observed on the carbohydrate content of 3-day old bolls (Guinn and Brummett, 1988). Krieg and Sung (1986) conducted translocation experiments with  $^{14}\text{C}$  and reported that direction of the photosynthate flow was not affected by the water-deficit stress treatment while no differences in dry weights were observed between water-stressed and well watered bolls. Further research by Krieg (2000) concluded that if water-deficit stress occurs after flowering young fruits are more likely to abort due to decreased carbon and nitrogen supply as well as perturbations in hormone metabolism.

## SUMMARY

Water-deficit stress has a significant effect on cotton's growth and development. The effects of water stress depend on the severity and duration of the stress, the growth stage at which stress is imposed, and the genotype of the plant. The cotton crop is sensitive to water shortage at all growth stages, but particularly reproductive development is the most sensitive period to drought stress following seed germination and seedling establishment. In cotton, water sensitivity during flowering and boll development has been well established. Recent research has shown that the developing pollen and pollen tube growth are highly sensitive to environmental stress. However, the exact physiological metabolic processes responsible for this sensitivity remains to be elucidated.

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