

# Simultaneous Stem Diameter Expansions and Apoplastic Electropotential Variations Following Irrigation or Rainfall in Cotton<sup>1</sup>

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## ABSTRACT

Temporary and permanent expansions of the stem diameter result from rainfall and irrigation of cotton under field conditions. This study is concerned with the simultaneous use of physical and invasive electrochemical sensors to monitor the timing of these expansions. The measurements were made over three seasons and have yielded a set of generalizations concerning the timing and magnitude of the expansions. The plant begins expansion during the night and/or next night following irrigation and/or rainfall. At the onset of the expansion there is a large magnitude precipitous drop in electropotential. Both the physical expansion and the electropotential drop are systemic, i.e., they occur simultaneously at widely separated parts of the plant. Several possible mechanisms giving rise to the physical and electropotential variations are discussed.

**Additional index words:** Electrophytogram, Systemic variation, Irrigation response, *Gossypium hirsutum* L.

STEM diameter variations in plants can be divided into two categories: 1) daytime contractions associated with the dehydration and rehydration of the stem and 2) nighttime temporary and permanent expansions.

The daytime contractions have been the subject of a number of previous studies (3, 6, 7, 8, 9). The present paper concerns nighttime expansions observed in the stem diameter following irrigation or rainfall. Simultaneous stem diameter and apoplastic electropotential measurements were taken in order to study the interaction of the physical and electrochemical activity of the plant.

## MATERIALS AND METHODS

The basic approach in the experimental design was to measure simultaneously stem diameter, leaf temperature, and electropotential before, during, and after an irrigation or rainfall disturbance.

The present study extended over three growing seasons, from 1979 to 1981. The siting, plant size and numbers, and conditions associated with the stem diameter measurements have been described previously (3). In 1979, eight temperature measurements were made using type T thermocouples (50.8  $\mu$ m wires) placed in the midrib on the underside of the leaf. Palladium probes were placed in the petioles and/or peduncles of the leaves and bolls on the second or third fruiting branch. In addition, palladium probes were placed in locations diametrically opposite the stem diameter sensors. Twenty-four palladium probes were used in the 32 ha cotton field in the Avra Valley and 57 probes were used at the 0.11 ha Prince Road site. Data was recorded manually, by a 100 km telemetry net and by on-

site automatic acquisition equipment.

Potential was measured by placing a palladium electrode in the plant with a second reference electrode buried in the soil. The resulting two electrode system forms a galvanic cell whose potential is coherent, reproducible, and exhibits definite patterns and responses to environmental conditions. Details of the galvanic circuit and probe design used to obtain the electropotentials (electrophytograms) have been described previously (2). The location of the probe in the apoplast has been verified by both electron and light microscopy studies (4, 11). The probe is immersed in the extracellular fluid.

Measurements were recorded every 15 min on a 24 h basis for periods varying from 40 to 90 days. Electropotential readings were automatically recorded three times each acquisition to avoid erroneous values. In all cases of automatic acquisition, the equipment and electrochemical reference were themselves tested every 15 min for accuracy. In 1980 and 1981, the equipment was solar powered; connection to line driven punches was either by wireless telemetry or fiber optics.

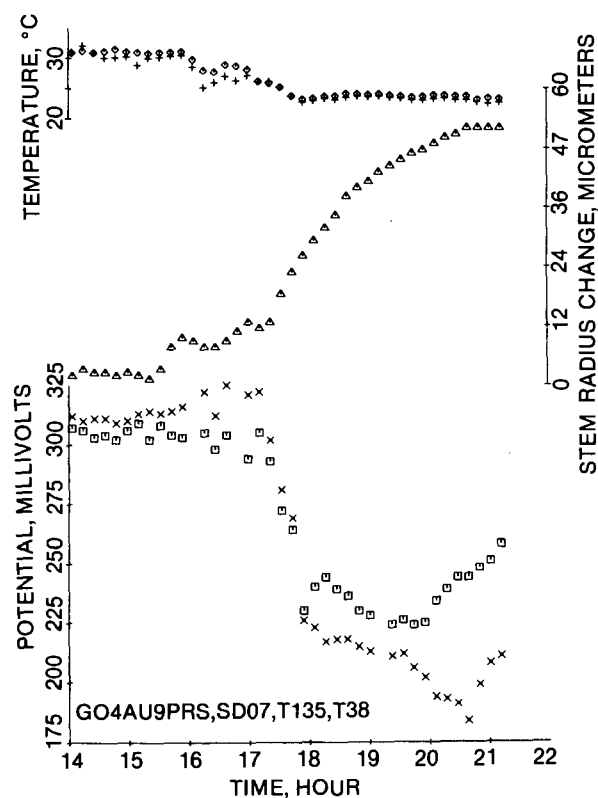


Fig. 1. Typical curves of the leaf and air temperature, stem radius, stem and petiole electropotential on the day after irrigation, 4 Aug. 1979. diamond = leaf temperature; plus sign = air temperature; triangle = stem radius; square = stem electropotential; multiplication sign = petiole electropotential.

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## RESULTS

Furrow irrigation water was applied on 3 Aug. 1979 at 0930 h. At 1100 h the stem diameter responded to the water by ceasing any further contraction. There was no electropotential response at this time. The leaf temperature changed in a manner similar to days when no irrigation occurred. On 4 August, the daytime stem contraction did not occur. Figure 1 shows the set of simultaneous events that began in the late afternoon. The leaf temperature reached a low temperature plateau, the electropotentials precipitously dropped and the stem diameter began an expansion. The response of the plant was systemic, i.e., the drop in electropotential occurred at widely separated locations, from the base of the plant to petioles on fruiting branches. The magnitude of the potential drop in Fig. 1 is very large in the scale of bioelectrochemical events. Drops in excess of 200 mV have been recorded on numerous occasions. The stem diameter expands in a roughly exponential manner as seen in the figure.

A similar simultaneity in stem diameter change and electropotential irrigation responses, measured in 1980, is shown in Fig. 2. Cyclic expansions accompanying rainfall in August 1981, are shown in Fig. 3. An important characteristic of the set of curves in Fig. 3 is the stabilization of the stem diameter before the onset of the expansion. In other words, the expansion is a distinct process following the daytime rehydration. Figure 4 is an expanded plot of the stem diameter change and shift in electropotential on the morning of day 224. Within the resolution of the 15 min data acquisition interval, the drop in potential occurs at the onset of the expansion. Also shown in

Fig. 4 is the progression of events at the end of the nighttime period. The potential rises and remains stable at its previous daytime level. At the same time the stem diameter begins its daily contraction.

In summary, the simultaneous stem diameter expansions and electropotential variations based on three seasons data yield the following generalizations:

1. The onset of expansion occurs at dusk, in the evening on the day of irrigation or on the day following irrigation.
2. At the onset of the expansions, there is a large magnitude, sharp drop in electropotential.
3. The electropotential variation and stem diameter expansions are systemic, i.e., they occur simultaneously at widely separated parts of the plant following irrigation or rainfall.
4. The electropotential rises and the stem diameter decreases at dawn.
5. If the drop in electropotential is very strong on the first night after irrigation, the potential will rise, then fall temporarily midway through this first night period.
6. The stem diameter expansions occur after an equilibration period following a daytime contraction.
7. The magnitude of the nighttime electropotential drop decreases in a proportional manner in the nights following irrigation.

## DISCUSSION

There are many aspects of the above results which require analysis. First of all, the general timing is significant. The expansion occurs basically at night,

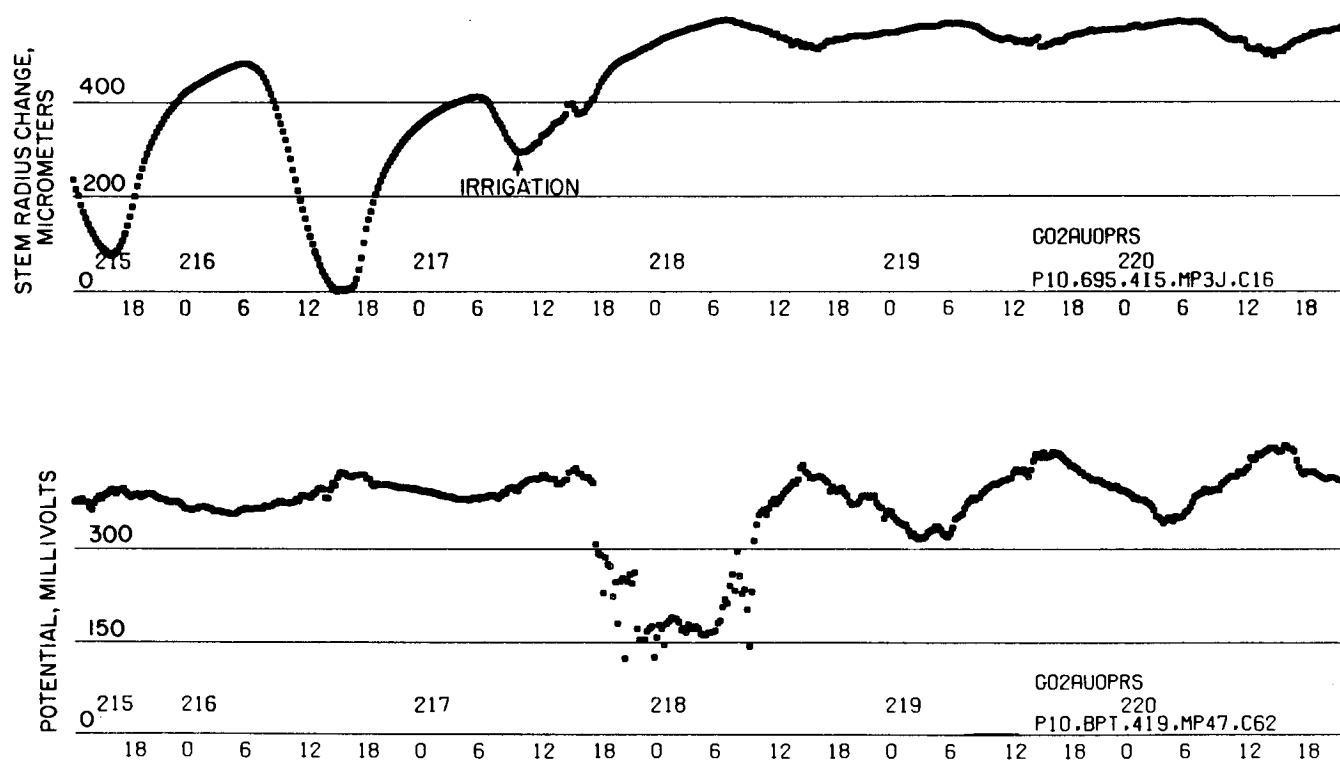


Fig. 2. Petiole electropotential and stem radius before and after irrigation at 1000 h on day 217. (4 Aug. 1980).

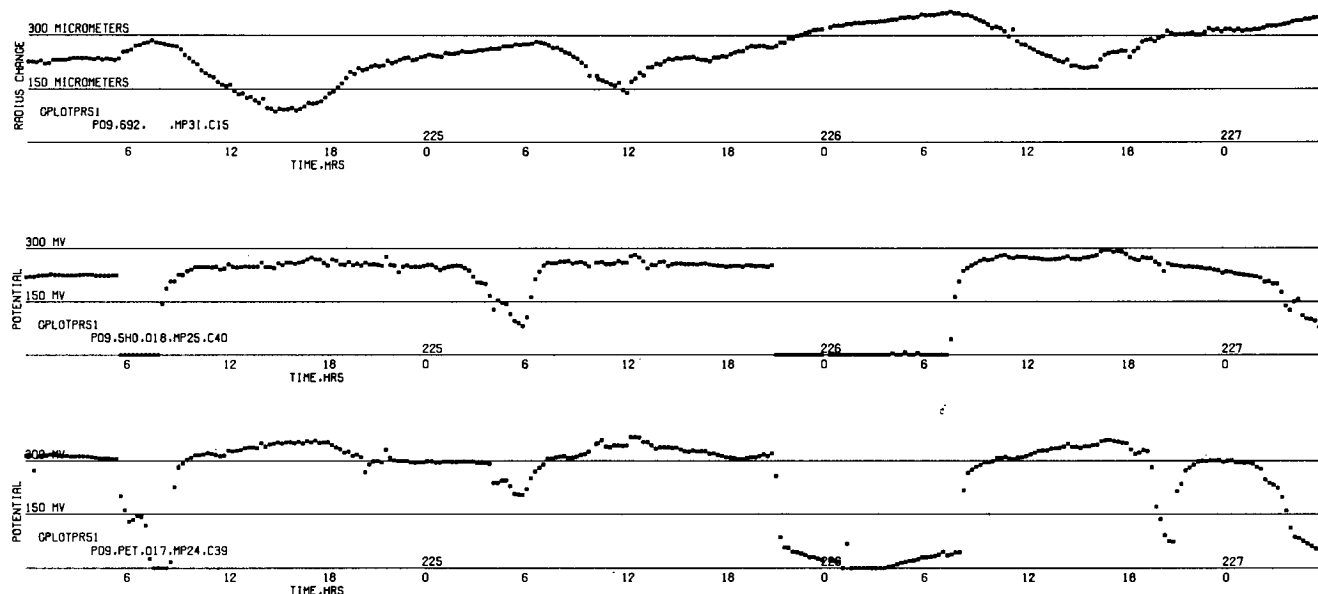


Fig. 3. Variation of the stem radius (top) and electropotential of the stem (middle) and petiole (bottom) for a period of 5 days beginning on day 224 (12 Aug. 1981). Rainfall: 4.8 mm at 0520 h (15 min duration) on day 224; 0.2 mm at 2000 h (120 min duration) on day 225.

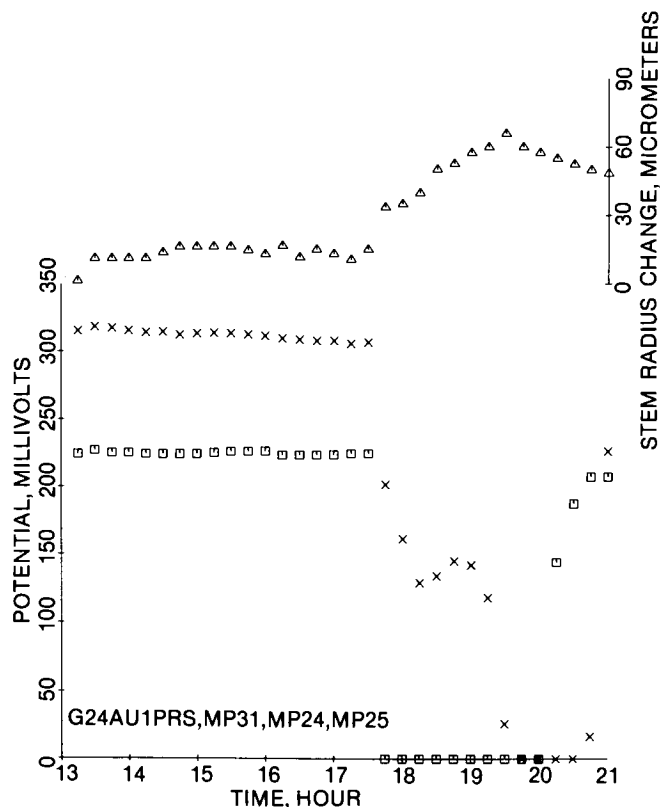


Fig. 4. Expanded plot of stem radius and stem and petiole electropotential response to rainfall on day 224. Triangle = stem radius; square = stem electropotential; multiplication sign = petiole electropotential.

in the absence of a strong radiation loading on the plant. The post-daytime timing of the expansion suggests a precise sequencing of function on the part of the plant. The rapid rise of electropotential at post dawn, in concert with the decrease in stem diameter, signals the end of the process. The 1 day lag in ex-

pansion seen in Fig. 1 is in agreement with the 1 day lag in the growth-temperature correlation in oak obtained by Kozłowski et al. (7).

The precipitous drop in potential indicates some form of triggering is operative. In other words, when a proper set of conditions is present, the electrochemical change is suddenly activated. The set of conditions which actuates the electropotential trigger is present in decreasing magnitude for a number of days following an irrigation or rainfall. The proportional decrease in the magnitude of the electropotential drop during the post irrigation period indicates a proportional trigger process is operative.

The systemic nature of the trigger is very difficult to explain. Events occur simultaneously, that is, within the 15 min resolution of the acquisition equipment, at distances 800 mm apart. Two general interpretations come to mind. The microclimate which the plant is subjected to may be similar enough that an external set of conditions triggers the process at the same time at different regions of the plant. Alternatively, some form of information transmission is present which reaches widely separated parts of the plants at the same time. One possible variable easily capable of doing this is the xylem water potential. This is a systemic variable of very low gradient from one part of the plant to another (1). A change of pressure could be readily felt throughout the plant virtually simultaneously. The origin of such a pressure change could be the gradual recovery of water potential to some relaxed condition not achieved in the presence of water stress. The probe is contiguous to vascular tissue (4, 11). It is possible to sense the apoplast electrolyte in the vascular region.

The precipitous electrochemical change can be analyzed at an individual location. Goldstein and Gensler present three possible origins of apoplastic electropotential shifts: 1) a change in redox status of the apoplast electrolyte contiguous to the probe surface, 2) a change in the physical spacing between the

probe surface and nearly immobile ion impregnated cell walls, and 3) a change in the charge level of the tissue in the vicinity of the probe surface (5). The sudden change in the electropotential and the relatively slow change in the stem diameter would lend support to the first possibility. The extreme sensitivity of the potential to shifts in cell wall location would lend support to the second possibility since physical shifting of tissue is observed.

The above discussion was concerned with the electropotential shift. The mechanism behind the physical expansion must now be considered. Anatomically, the expanding tissue is not the xylem, but the phloem and related tissue of the stem (9). Previous analyses of stem diameter changes have indicated the basic process of stem diameter variation is one of diffusion (8). Quantitatively, Fick's Second Law governing transient diffusion can be employed to describe the change of the water potential of the phloem and related tissue. The physical expansion of the stem is a result of a flow associated with this potential gradient.

With this background it is possible to examine the mechanism of the nocturnal expansion. The change of the water potential can be initiated by a change in the potential boundary conditions at the xylem-phloem interface or within the phloem and related tissue. Once the boundary condition is set up, the potential shift follows in a form describable by Fick's Second Law. An expansion follows. The origin of the expansion in this interpretation is the initiation of new boundary conditions in the xylem or the more radial tissue. A change in the xylem water potential boundary condition could arise from the gradual return to a more relaxed level after daytime insolation. One of the physical observations which does not support this possibility is the period of almost constant stem diameter which separates the daytime contraction regime from the nighttime expansion regime.

A second possibility is a sudden change in the phloem and associated tissue water potential caused by a shift in osmotic pressure. This requires an active cellular interaction on a systemic basis, but the result would produce a condition which would ultimately result in the observed stem expansion.

A third, but more remote, possibility exists to explain the mechanism behind the observed expansion. The speed at which the expansion occurs is a function of the diffusivity in the path of fluid movement. If the diffusivity value was adjusted by some active mechanism the expansion could be initiated in the

presence of slowly varying boundary conditions. In a sense, the diffusivity in this interpretation acts as a type of switchable resistivity element in the manner of a linearized force-flow relation. Molz and Peterson have observed that the resistance to fluid transfer in cotton exists in the vicinity of the vascular cambium (10).

Any causal relation between the physical and electrochemical phenomena is beyond the scope of the present measurements. It is only possible to conjecture that the stem diameter change can be considered a response to some driving function or source. This source has been presumed to be the water potential in the xylem and/or phloem and associated tissue (8, 9). The energy transfer involved in water movement near the probe at potential gradients of the levels commonly measured (in the order of millijoules) is far in excess of the energy level associated with the electropotential (in the order of nanojoules). Any causal relation would have to reconcile, at the outset, this disparity.

#### ACKNOWLEDGMENTS

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