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NYCTITROPIC MOVEMENT AS A FALSE WILT SYMPTOM OF COTTON

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Under field situations cotton leaves frequently exhibit a drooping movement during the late afternoon. This phenomenon is sometimes diagnosed (1) as wilt resulting from insufficient soil moisture or (2) as wilt resulting from an excessively warm day or (3) as wilt resulting from inadequate root activity. Since the same drooping action of leaves also occurs in a controlled environment chamber in a normal, healthy cotton plant, a study was made to determine the cause of this drooping leaf condition in cotton.

Although modern literature does not mention another possible cause of drooping leaves on the cotton plant, Charles Darwin (3) reported about 85 years ago that some cottons exhibit a nyctitropic (or night drooping) movement on their cotyledons and leaves.² If the observed phenomenon is a nyctitropic movement, it will be necessary to determine whether extending exposure of daytime conditions to test plants would be harmful to their normal development.

REVIEW OF THE LITERATURE

Nyctitropic movements in plants are not a recent observation. Bünning (2, Ch. 2) states that Androsthene noticed diurnal leaf movements (nyctitropism) in Papilionaceae while with Alexander the Great about 2,300 years ago. Throughout history many eminent scientists and naturalists were attracted to this phenomenon (2, 3, 6, 7).

Although these light controlled movements, called nyctitropic movements, have long been observed in some plants, most earlier reports failed to mention any important crops, except for some members of the Leguminosae, exhibiting this phenomenon. Darwin (3), however, listed a variety of Nankin cotton, which he

identified as Gossypium arboreum, among 55 seedling plants in which cotyledons exhibited diurnal movement. In this same list, he noted that Gossypium herbaceum, an unknown cotton species from Naples (Italy), a cotton species from Alabama (U.S.), and a sea-island cotton had cotyledons that did not exhibit diurnal movement when grown in the middle of winter. Darwin further stated that leaves of many genera of plant "...must be well illuminated during the day in order that they may at night assume a vertical position." He described these movements in detail and plotted the angle of movement. In 37 genera he noted that leaves or leaflets rose to

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² Underscored numbers in parentheses refer to Literature Cited, p. 11.

a vertical position at night and in 32, that the leaves or leaflets sank to a vertical position. He noted that the leaves of Nankin cotton exhibited 90 degree nyctitropic movement; how-

ever, cottons he describes as Gossypium maritimum and Gossypium brazilense only occasionally showed "sleep symptoms" in a poorly lighted hothouse.

MATERIALS AND METHODS

With control of lighting, temperature, humidity, and gaseous exchange now obtainable within environmental chambers, the causes of nyctitropic movement in plants can be defined more precisely than was formerly possible. Photographic techniques can monitor the movements of an entire plant in response to a particular environment with minimum disturbance. Lights flashing on for 2-second intervals each 45 seconds to photograph the plant did not appear to affect the nyctitropic activity of cotton. Therefore, an isolated cotton plant, growing under controlled situations in an environmental chamber was photographed on movie film using a 45-second delay between each exposed frame. The film was shown on a screen where the position of the leaves was marked and measurements of movement recorded. The dominant test plants utilized in all studies were cotton varieties known as "Auburn 56" and the double haploid (M-8) of "Deltapine 14." Both these cottons are classified as Gossypium hirsutum, although many other local varieties also were observed.

The first studies involved increasing the supply of soil moisture in an attempt to eliminate wilt due to moisture stress from later observations. This was done by first increasing the size of the container about 10 times the volume thought to be adequate and increasing the waterings from once to three times a day. Cotton was also grown in 5-gallon containers of nutrient solution with forced aeration to assure an adequate supply of moisture and oxygen.

The next studies attempted to regulate the ratio of the transpiring sur-

faces to the size of the root system. Young plants, 3 weeks old, with a very small leaf surface area were observed as well as large plants, 3 months old, with large, well-distributed root systems. One older plant, in a very large container (6 feet deep), had 50 percent of its leaves removed to reduce transpiration, after its root system was fully developed.

Another variable related to moisture control is that of the atmospheric relative humidity surrounding the plant. In a third study the relative humidity varied from 80 to more than 95 percent in an attempt to reduce the vapor pressure deficit between the plant and the atmosphere.

Since the drooping leaf movement could not be eliminated by any moisture control, the relative humidity of the chamber for all later observations was maintained over 95 percent and 1-cubic-foot containers with a well-fertilized loam soil were used. The plants were watered twice daily to assure against wilt due to a lack of moisture or low relative humidity.

Next, the effect of temperature on nyctitropic movement was observed. The temperature was held constant during both the light and dark periods at 26.7°, 29.4°, or 32.2° C., and in other observations the temperature was programed to vary similarly with a typical July-August day at Auburn, Ala. Using the programed discs, the night temperature was held at 23.9° for 8 1/2 hours and starting at sunrise raised for 6 1/2 hours to 29.4°, 32.2°, or 35.0°, kept at the peak temperature for 4 hours, then gradually reduced to 23.9° during the next 5-hour period. Although several

additional variations were made, the most severe treatment was a 35.0° temperature for a 6-hour period with an 18-hour "light" period.

In another study the timing of the period was varied with respect to the actual time. The 14-hour daylight period (approximately typical of the local mean July-August day) was adjusted to have a 5:30 a.m. central standard time "sunrise" and a 7:30 p.m. "sunset"; a 9:30 a.m. sunrise and an 11:30 p.m. sunset; a 4:30 p.m. sunrise and a 6:30 a.m. sunset; and a 10:00 p.m. sunrise and a 12 o'clock noon sunset. The length of the day (light period) was also adjusted from 11 to 18 hours. Attempts with a no-light period (except for 2 seconds of light as each frame of the movie was exposed) was unacceptable, because as the rhythm of the previous cycle was dissipating, the plant was unable to produce foods and became physiologically starved. To complete the light study, light intensities of approximately 1,000, 2,000, and 2,700 foot-candles were tested in the con-

trolled environment chamber, and a peak intensity of 8,300 foot-candles was reached in field studies. The field studies were conducted to support and extend some of the studies conducted in controlled environment chambers.

The test plant was allowed 3 to 5 days to become adjusted to the new environment situations before observations started, except those in the studies on container size and moisture-treatment variations which required longer periods of adjustments. In field observations before filming began, all cotton plants for more than a 6-foot radius around the plant to be photographed were removed and a dike was built up about 3 feet from this plant. To insure an adequate supply of water for this plant, about 20 gallons of water was added weekly for 5 weeks to the dike, in addition to the normal rainfall. All test runs were photographed for approximately 2 1/2 days. Although many runs were replicated, not all observations were repeated under completely identical situations.

RESULTS AND DISCUSSIONS

The dominant species background of the cotton grown in Alabama appears to be Gossypium hirsutum, although characteristics of other species may have been introduced into some of the commercial seed now grown throughout the area. In controlled environment studies, Auburn 56, Coker 100A, Coker 413, Deltapine Smooth Leaf, a double haploid (M-8) of Deltapine 14, Dixie King II, Carolina Queen, Stoneville 7A, Stoneville 213, McNair 1032, and okra-leaf variant of Auburn 56 were the varieties used. All of these varieties exhibited nyctitropic movement under the test conditions, as did test plants of a wild hirsutum from Mexico, a wild Gossypium barbadense from Galapagos Island, Gossypium herbaceum (v. indicum) from India, and a diploid, Gos-

sypium arboreum, from Asia. Figure 1, B shows a young cotton plant (Auburn 56) in the drooped leaf condition, and A shows the same plant fully recovered while undergoing nyctitropism.

Regardless of the reduction in transpiration requirements of the environment and the plant, increase in size of root system in soil-moisture content (with aeration), nyctitropic movement still persisted in the test plants. Apparently the drooping leaves in field-grown cotton is a characteristic of the plant and not related to moisture deficiency. On the other hand, early drooping of leaves of cotton, frequently noted in fields, can be caused by moisture stress.

The economic significance of the nyctitropic movement of important



Figure 1.--Nyctitropic movement of cotton, Range of diurnal leaf movement of young cotton: A, Leaf arrangement at 9:30 a.m. when the leaves are fully erect; B, leaf arrangement 12 hours later when "leaf droop" is complete.



Figure 2.--Nyctitropic movement of cotton: A, Typical exposure surface of leaves of a young cotton plant visible to a vertical light source when the leaves are fully erect; B, exposure surface of leaves of the same plant visible to a vertical light source when the leaves are in the complete droop position. (Note that the exposure of ventral side of the leaves accounts for about 30 percent of the total exposure surface in the droop position.)

crops has not been investigated. It is certainly true that the leaves on one side of a plant with 90-degree leaf movement during nyctitropism tend to remain somewhat perpendicular to the rays of a rising sun, and those on the other side of a plant tend to maintain a near perpendicular alinement to the setting sun. In the chamber where overhead lights are stationary,

the "capture" of the sunlight by a plant undergoing nyctitropic movement would not be as efficient. Figure 2 shows the exposed leaf area of a typical young cotton plant, visible to a perpendicular light source: A (fully erect) shows an exposure surface which is usually more than 350 percent greater than B (complete droop) and, if exposure of only the dorsal

sides of leaves is compared, the exposure surface is usually increased to about 500 percent.

Associated with exposure surface of the leaves is the angle of incidence of the light upon the leaves. With permanently mounted overhead lights, the angle of incidence increases from near zero in the erect position to a maximum of 90 degrees as the complete droop position is reached. Leaf canopy inclination may be important, since the intensity of light, as measured in foot-candles by a horizontally placed photoelectric cell, can increase from 10 foot-candles 30 minutes before sunrise to 110 foot-candles at sunrise, to 260 foot-candles 15 minutes later, to 400 foot-candles 45 minutes after sunrise, while the photoelectric cell held perpendicular to the sun's rays can read 2,000 foot-candles 15 minutes after sunrise and 4,800 foot-candles 45 minutes after sunrise.

On a clear summer day at Auburn about 2 hours was required for the intensity to reach 4,000 foot-candles. A peak intensity of about 7,000 foot-candles using horizontal instruments was not obtained until 6 hours after sunrise, while instruments held perpendicular to the sun's rays measured over 7,000 foot-candles for 7 hours throughout the middle of the day. The light intensity reduction during the afternoon hours was somewhat similar to the morning increase on clear days. During cooler days when much less moisture is in the air, perpendicular readings exceeded 12,000 foot-candles most of the day.

Should a plant that undergoes nyctitropic movement and maintains its leaves somewhat perpendicular to the light source have the capability of utilizing the sun's energy more efficiently, it would be important in a plant-breeding program.

During these studies, we noticed that the opening and closing of stomata of the lower leaf surface of cotton coincided with the nyctitropic move-

ment of the leaves very closely. The Agricultural Research Service is studying stomata relations to nyctitropism. If the drooping leaf seriously reduces transpiration, could not this mechanism then reduce the water requirement of the plant?

The mechanism causing the loss of erectness in the leaves undergoing nyctitropism is beyond the scope of the study reported here, but Blackman and Paine (1) apparently believed that there is an outward movement of water from the cells to the intercellular space within the leaves. They recorded an increase in the permeability of the cytoplasmic membranes and a decrease in the osmotically active contents of these cells during nyctitropic movements in Mimosa pudica. Teorell (2) supplemented this observation when he reported that rhythmic changes can occur in membrane potentials, membrane resistance and water flow through artificial membranes under the proper stimuli, as well as in the Nitella algal cell. Many other scientists have detected cyclic fluctuations in functioning capabilities that coincide with nyctitropic movements, and often when nyctitropic movement ceases, these fluctuations cease. Huck, Hageman, and Hanson (3) noted diurnal changes in root respiration occurring in corn and soybeans growing in alternating exposures of light and dark that are missing in plants grown in continuous light. The same situation occurred in excised roots of plants grown under alternating light-dark conditions.

Grossenbacher (4) reported diurnal fluctuations in root pressure of decapitated 5-week old Helianthus. Bünning (2, Ch. 9) states that even enzymes localized in the plastids exhibit endodiurnal fluctuations in their activity and that diurnal changes in photosynthetic capacity have been observed. He further states that the ability to form chlorophyll fluctuates diurnally. The volume of nuclei of guard cells of

Allium cepa has been reported (2, Ch. 9) as varying from a low of $1,500\mu$ about midday to a high of $6,000\mu$ during hours of darkness. Bünning (2, Ch. 9) mentions that many plants and animals have a circadian rhythm of cell division. Regulating the rate of cell division may be an important factor in obtaining the most desirable growth or development of agricultural crops.

The extent of leaf movement during nyctitropism in commercial cottons grown in Alabama can exceed 90 degrees, especially in the younger top leaves that do not have any physical interference from other leaves or branches. Older, lower leaves do not exhibit this degree of movement.

Each leaf on a particular plant does not initiate droop or recovery at the same instant and the cessation of the motion is not uniform. The data presented in table 1 are typical of the extreme range of variations in angle of leaf droop for a 2-month-old cotton plant under an 18-hour-light, 6-hour-dark cycle. The leaves selected did not move through the same arc (arcs vary from 34° to 95°) nor did they reach their peak or minimum values at the same hour; the elapsed time from a peak to a minimum value varied from 6 to 11 hours, and this time is not related to the width of the arc obtained. Most leaves on a particular plant are intermediate of the extremes in table 1.

These findings agree with those of Pfeffer in 1907 according to Bünning (2, Ch. 15) in which Pfeffer observed that single leaves of a plant can oscillate independently of each other if they had been exposed to light-dark cycles with different phases. Certainly, a plant exposed to overhead lighting will have some shaded leaves or parts of some that are shaded. This, then, indicates a possibility that a plant may not have a central "nervous system" that controls the nyctitropic response for the entire plant.

Within a temperature variation of 23.9° to 35.0° C., leaf response of cotton did not vary noticeably under any particular circadian light-dark cycle tested. Sweeney (7) found that when nyctitropic movement measurements made at different temperatures were compared, the value for the length of cyclic treatment did not depend on the ambient temperature; in fact, the movement was almost completely independent of temperature.

Sweeney (7) further reported that circadian rhythms in most plants were also remarkably stable to light intensity and to most chemical factors. The study reported here did not include comparison of chemical factors, although the light intensity variations observed concurred with Sweeney's results. Nyctitropism in cotton appeared similar with illumination intensity up to 8,300 foot-candles.

Sweeney (7) stated that wavelengths of light that are effective in circadian rhythms differ from organism to organism as well as the pigments responsible for active light absorption. In some plants all colors of visible light are said to begin the rhythms. Both incandescent and fluorescent lights were used as the light source for the controlled environment chamber in these studies. No study was made involving the wavelengths of light that are effective in nyctitropic movements of cotton.

Apparently, the effective factor beginning the nyctitropic movement of cotton leaves is the timing of the cyclic periods of light-dark. Since most plants and animals on earth evolved and developed under a circadian light-dark cycle, the cyclic period of 24 hours was maintained in all light-dark applications used in this study. We do not know how far cotton can vary from a 24-hour-cycle period, but such information would have no application to field production as we now know it.

TABLE 1.--Variations in movement of selected leaves of a cotton plant¹

Time	Degrees from horizontal of leaf				
	Leaf A	Leaf B	Leaf C	Leaf D	Leaf E
<u>Dark</u>					
10 p.m.	80°	64°	64°	68°	58°
11 p.m.	86°	70°	70°	66°	58°
Midnight	80°	76°	69°	63°	58°
1 a.m.	78°	76°	65°	60°	58°
2 a.m.	73°	76°	60°	60°	53°
3 a.m.	57°	45°	33°	58°	54°
<u>Light</u>					
4 a.m.	39°	31°	18°	49°	50°
5 a.m.	14°	10°	17°	26°	38°
6 a.m.	8°	9°	15°	14°	34°
7 a.m.	² +5°	3°	15°	14°	34°
8 a.m.	+9°	0°	6°	15°	30°
9 a.m.	+8°	0°	6°	16°	27°
10 a.m.	+5°	0°	0°	18°	25°
11 a.m.	+4°	6°	0°	29°	24°
Noon	+2°	9°	0°	33°	29°
1 p.m.	0°	12°	0°	38°	31°
2 p.m.	6°	19°	0°	41°	34°
3 p.m.	15°	18°	0°	41°	39°
4 p.m.	25°	28°	5°	45°	47°
5 p.m.	45°	42°	12°	57°	48°
6 p.m.	53°	48°	22°	64°	53°
7 p.m.	58°	53°	37°	67°	55°
8 p.m.	63°	55°	43°	69°	56°
9 p.m.	70°	57°	57°	69°	56°
Range	+9° to 86°	0° to 76°	0° to 70°	14° to 69°	24° to 58°

¹ For Auburn 56 and double haploid (M-8) cotton varieties.

² + is movement extended beyond 0°.

Cyclic light-dark periods not only induce nyctitropic leaf movement of some plants but affect such processes as seed germination, growth and metabolic activity, plant shape, leaf coloration, leaf fall, flower production, fertilization, seed production, and dormancy. Sollerger (6) states that in some plants under proper stimuli flower, tendril, and leaf movements, osmosis, water assimilation, turgor, CO₂ metabolism, acidity, phosphatase activity, seedling, root and stem growth, photosensitivity of pigments, and biolumines-

cence have been observed to have circadian rhythms.

In this study only leaf movements were correlated with controlled dark-light cycles. Since normal light periods during the growth season in Alabama approached a 14-hour, sunrise to sunset, period, the basic observations used a 14-hour-light and 10-hour-darkness cycle. All cotton plants observed showed nyctitropic movement regardless of age. The okra-leaf variant was incapable of rising much beyond 45° but the leaves would droop to approximately 90°.

On almost all the other cottons tested, the young, unobstructed top leaves experienced about 90° movements. Whether the 14-hour-light period started before 5:30 a.m. or later than 4:30 p.m. central standard time, the leaves of the plant were obviously in a beginning state of nyctitropic movement prior to 11 hours of light duration. The droop rate increased during the hours of darkness, reached a maximum, then leveled off for a short period before slowly starting to recover. Recovery was not quite complete when the lights came on, but the plant continued to recover until fully erect. The leaves of the plant remained at their most nearly horizontal position (some leaves would rise to 18° over the horizontal position) for about a 6-hour period during each complete cycle.

When the period of illumination more nearly approached that of late fall or early spring, results were similar. For an 11-hour-light, 13-hour-dark cycle, recovery appeared to be complete when the lights were turned on; drooping leaves became obvious just before the lights were turned off. Recovery was not complete until about 1 1/4 hours after sunrise; the plant appeared to be fully erect for about 7 hours before the leaves started their droop. In figure 3 nyctitropism of 2-month-old cotton was photographed under an 11-hour-light, 13-hour-dark cycle.

The extreme light duration cycle was 18-hours light, 6-hours darkness. In this cycle the nyctitropic movement seemed just as extensive as it did in the other circadian light studies. However, this cycle took the

plant more than 4 hours after the lights were turned on to reach full recovery. The plant remained fully erect for about 5 hours, then the leaves began their droop. The maximum droop was reached just before the lights were again turned off, and the plant remained fully "drooped" for about 3 hours before starting to recover.

Figure 4 shows the mean data of leaf movement for all plant age, temperature, moisture, and intensity situations examined at each of the light-dark duration cycles. The mean extent of leaf movement is essentially identical for all the light-dark cycles. The variations in time for the erect and droop positions of the leaves were small and inconsistent for the age, temperature, intensity, and moisture at each light-dark cycle plotted.

Angle of leaf position and timing of various phases of the nyctitropic movement in table 1 are for Auburn 56 and the double haploid (M-8) cotton varieties only. The other cotton varieties observed were not tested thoroughly enough to establish leaf angle or to determine phase timing responses to temperature and illumination intensity variations under various light-dark duration cycles. Should differences in varieties exist and have physiological significance, then an incorporation of the nyctitropic characteristics of cotton in a breeding program may have merit.

With limited replications of cotton grown under the 11, 14, and 18 hours of light, no advantage was seen to having more than an 11-hour-light cycle, nor was there any disadvantage to the 18-hour-light cycle.

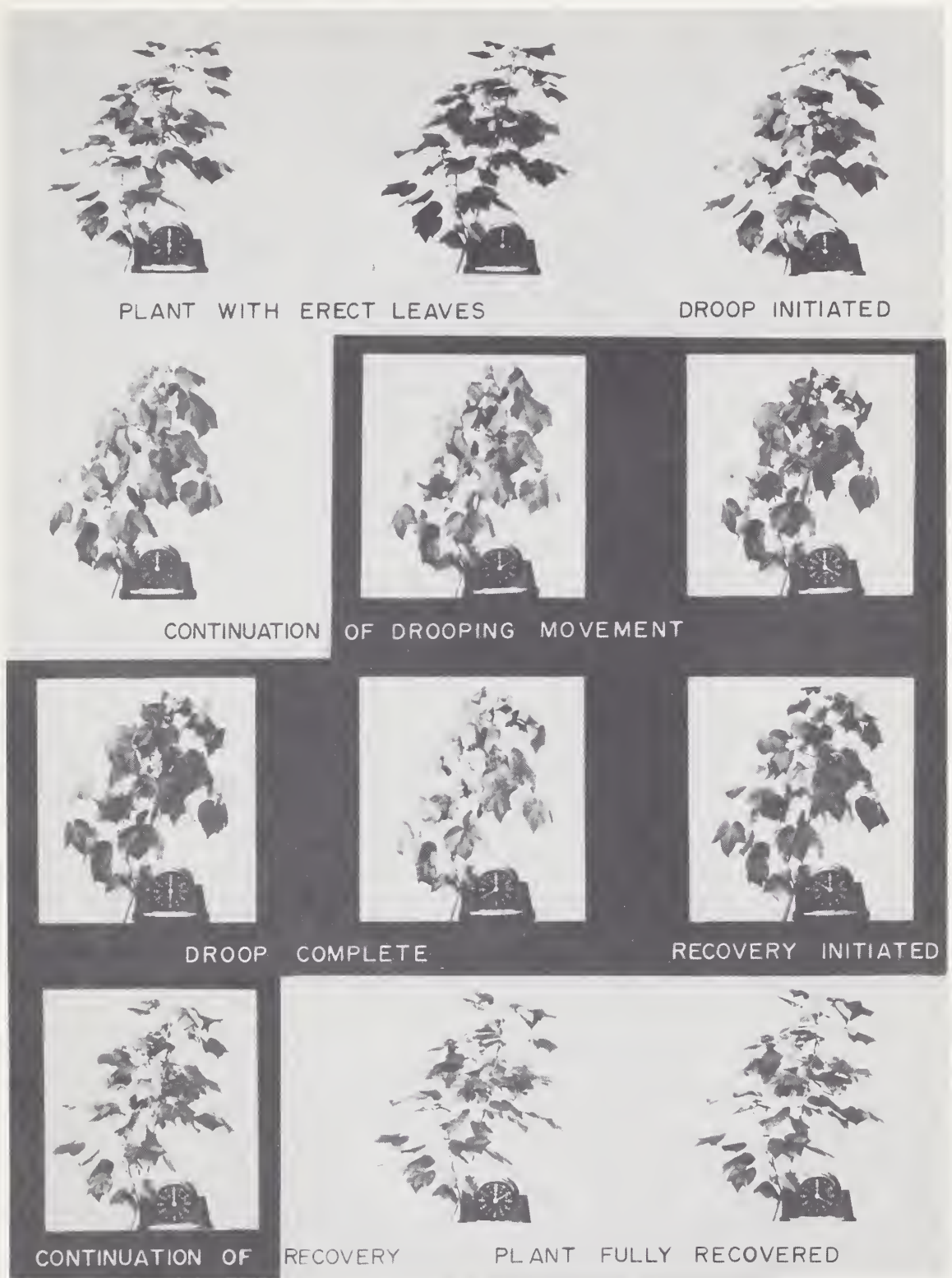


Figure 3.--Two hour sequence of nyctitropic movement of cotton under an 11-hour-light, 13-hour-dark cycle.

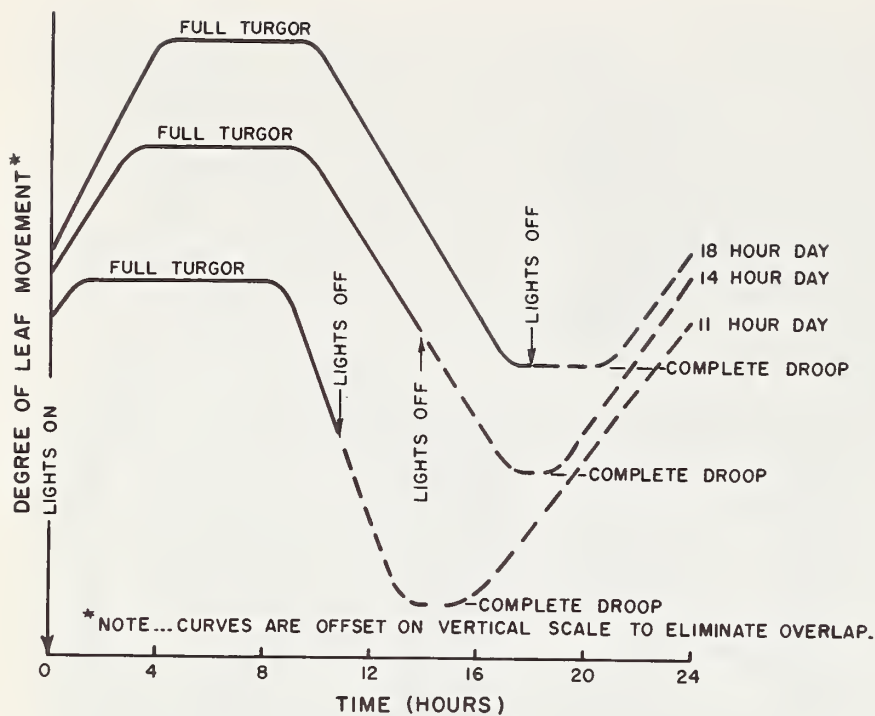


Figure 4.--Mean movement of cotton leaves undergoing nyctitropism during various light-dark cycles.

CONCLUSIONS

Cotton varieties grown in Alabama and some foreign cottons exhibit nyctitropic movement of their leaves. These nyctitropic movements appear to be independent of temperature from 23.9° to 35.0° C. whether the temperature is held constant or allowed to vary in a manner similar to the daily temperature cycle in Auburn, Ala.

The nyctitropic movement appears to be independent of the age of the plant although older leaves do not droop as completely, or recover as fully, as the younger, topmost leaves that are free of any physical obstacles to movement.

Nyctitropism of cotton appears to depend on cyclic diurnal light-dark applications. Definite leaf droop appears to be initiated in all observations prior to 11 hours of light duration, regardless of supplemental variations attempted. The timing of the droop period can be varied somewhat.

Variations in light intensities from 800 to a maximum 8,300 foot-candles

did not appear to affect the movement, nor did variations in wavelength composition as observed by use of actual sunlight, fluorescent lights, or incandescent lights.

Although several days were required for a plant to adjust to a new cycle, once this new pattern was established, the movement responded similarly to all light-dark cycles tested regardless of season or civil time.

Cessation of the drooping movement of leaves of a cotton plant (resembling wilt) could not be effected by additional water, greater expanse of the root system, or decreasing transpirational losses. Apparently a nyctitropic movement is active, and this drooping movement is not wilt.

Extending the light cycle up to 7 hours per day after nyctitropism was apparent had no detrimental effects on the cotton plant. Studies requiring vigorous, healthy cotton plants can be conducted even though the plant exhibits nyctitropic movement.

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