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Identifying Turgor Responses of Water-Stressed Cotton to Rapid Changes in Net Radiation Using Spectral Analysis[1]

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ABSTRACT

The kinetics of stem shrinkage and swelling in response to changes in the radiation loading of field-grown cotton (*Gossypium hirsutum* L.) plants were examined by time series spectral analysis. This technique involves determination in the frequency domain of the relationship between two time series events. The type and degree of relationship are assessed by computing the squared coherency, phase, and gain spectra relating events in the measured net radiation and stem diameter data sets. The squared coherency spectrum shows the statistical strength of the relationship between events in the two time series, while the grain spectrum indicates the amount of response, or the mm of change in stem diameter resulting from a unit change in radiation intensity at each frequency. The phase spectra show the relative positions between maximum points in the two time series.

Plants growing under conditions of water stress respond to changes in radiation much more rapidly than those growing on well-watered, deep soils. Although low frequency (slow) shrinkage response may be caused by factors affecting both evapotranspiration from the leaves and root water uptake, high frequency (rapid) shrinkage or swelling responses are probably controlled exclusively by alterations in the rate of water loss because of the water storage capacity of the plant itself.

Additional index words: Stomata, Transpiration, Roots, Microclimate, Time-series spectral analysis, Kinetics, Water movement, *Gossypium hirsutum* L.

THE expansion and contraction of a plant stem in reaction to changes in water potential have been investigated for many years. The most recent comprehensive review can be found in Kozlowski (1972). Papers by Namken et al. (1969), Klepper et al. (1971), Molz and Klepper (1972, 1973) and Stansell et al. (1973) have taken a more quantitative approach to investigating the events leading to changes in water stress and subsequent changes in cotton stem diameter.

Namken et al. (1969) found a significant relationship between the diurnal changes in stem contractions and in leaf water potential: the contraction and expansion of cotton stems were related to changes in solar radiation, and there were indications that an increased energy load on the leaf resulted in contraction of the stem, while a decrease in energy load resulted in an expansion.

Using net radiation as an indicator of leaf energy load, Klepper et al. (1971) observed that stem diameter decreased during the day as the radiation load increased, while in the evening, as radiation load decreased, the stem diameter increased. Short term shading of the plants by clouds led to an increase in stem diameter with a rapid response time.

Stansell et al. (1973) established a clear relationship between the diurnal trend in net radiation and plant water status but, equally important, they demonstrated that superimposed on the diurnal change were nonperiodic stem diameter fluctuations that occurred in response to short-term changes in net radiation. It should be noted that none of the authors cited above made any attempt to determine the statistical significance of the relationships they observed between radiation load and stem diameter fluctuations.

One of the main objectives of the research on the relationship between stem diameter and leaf water potential was to develop a means of relating stem diameter directly to leaf or xylem water potential (Huck and Klepper, 1977). Molz and Klepper (1972) showed that stem diameter fluctuations were caused almost entirely by water loss from living phloem cells and associated tissue, rather than by changes occurring in dead xylem tissue. They also pointed out that, because of the dominant effect of living tissue in the stem fluctuation process, it is not possible to derive a simple relationship between stem diameter fluctuation and leaf or xylem water potential. In their discussion of the kinetic effects of alternate flow pathways, Molz and Ikenberry (1974) have defined conditions that must be satisfied in any general solution to the flow system.

The objective of this paper was to investigate statistically the stem diameter-net radiation relationships using a time series spectral analysis approach. Through the use of spectral analysis, the variability in the frequency domain of both the stem diameter and net radiation was examined and compared for periods (the inverse of frequency) ranging from 4 min to nearly 10 hours. The response time and gain factor relating stem diameter to changes in net radiation were investigated, and hypotheses are advanced regarding some of the causative factors. We have attempted to look at the spectra in general terms and to discuss patterns in the relationships between net radiation and stem diameter across the spectral bands, using the squared coherency, gain and phase spectra.

MATERIALS AND METHODS

Spectral analysis procedures provide a unique means for studying the relationship between net radiation and stem diameter from a time series standpoint. The technique centers about the decomposition of a stationary time series (or a nonstationary time series which has been transformed into a stationary time series) into an infinite number of frequency bands representing cyclical components in the data. A single time series is stationary when the mean and covariance function do not vary significantly from one portion of the time series to the next. The variance spectrum of the time series data shows how the variance of the time series is distributed over frequency, i.e., the variance spectrum shows the variance contribution of each frequency band. A peak in the variance spectrum at a certain frequency usually indicates that some important generating process within

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the data is operating at that wavelength. Cross-spectral analysis makes it possible to examine in the frequency domain the relationship between two time series (e.g., net radiation and cotton stem diameter). The squared coherency, which is analogous to a squared correlation coefficient, provides a means of determining (again in the frequency domain) the strength of the relationship between the two time series at a given frequency. The squared coherency spectrum may indicate that the two series are correlated at a particular frequency, but one series may lead or lag behind the other series in time. The phase spectrum provides the means to examine this lead or lag. The gain spectrum will allow the user to determine, in the frequency domain, the changes that result in one variable (e.g. stem diameter) from changes in the other variable (e.g., net radiation).

Many time series (e.g., stem diameter) exhibit a long term trend or growth component. Interpretation of the spectrum is easier if the long term trends extending over the time segment under investigation can be removed by expressing the data as a deviation from the long term trend line computed by least squares fitting of the data. If the long term trend were not removed, it would appear as a contribution at the zero frequency point, blurring the spectral function at higher frequencies.

The spectra of primary interest in this study were the squared coherency, phase, and gain spectra. Based on work by Bloomfield (1976), observed values of the squared coherency less than or equal to $\sigma(0.95)^2$ were regarded as not significantly different from zero. The value of $\sigma(0.95)^2$ is given by:

$$\sigma(0.95)^2 = 1 - 20^{-g^2/(1-g^2)}$$
$$g^2 = \frac{2}{\text{degrees of freedom}} \qquad [1]$$

where $\sigma(0.95)^2$ is the 95% point of the distribution of the observed squared coherency when the theoretical squared coherency is equal to zero. Rayner (1971) provides a thorough discussion on calculating spectral estimates.

Table 1. Rhizotron bin treatment.

Rhizotron bin	Water treatment	Soil treatment
Bin 6	Irrigated on 6 and 26 August	Cahaba loamy fine sand (surface to 55 cm) Dothan sandy clay loam, pH 4.6 (55 to 188 cm)
Bin 7	Drying treatment	Cahaba loamy fine sand (surface to 188 cm)
Bin 8	Well-watered treatment	Cahaba loamy fine sand (surface to 188 cm)

Bloomfield also stated that the phase spectra are not well determined at any frequency for which the squared coherency value is less than or equal to $\sigma(0.95)^2$. According to Rayner (1971), phase lag is indeterminate insofar as multiples of the period under investigation may be added; however, in our case, field evidence supports the phase lags stated. The gain and phase spectra values were considered only in those frequency bands that were statistically significant on the basis of the test given by Equation [1].

The spectra used in this paper were calculated using computer programs written by John N. Rayner, Department of Geography, Ohio State University. These programs utilize the Fast Fourier Transform in calculating the spectra. The number of data points (4,410) used in the work is based on the requirement of the Fast Fourier Transform program that no prime number greater than 19 be contained in the number of data points.

Experimental data obtained in a water-relations experiment described by Browning et al. (1975) were analyzed using the variance spectral frequency analysis method described above.

Cotton (*Gossypium hirsutum* L., 'Auburn 623b', hand-pollinated breeding stock from selfed parents supplied by Dr. R. L. Shepherd, USDA, SEA, Auburn, Ala.), a homozygous pure line, was planted in bins 6, 7, and 8 of the USDA rhizotron at Auburn University (Browning et al. 1975). Bin 6 contained 133 cm of Dothan sandy clay loam (pH 4.6) covered with 55 cm of Cahaba loamy fine sand. The soil in bin 6 was irrigated twice during the growing season (6 and 26 August). Bin 7 contained 188 cm of Cahaba loamy fine sand which was allowed to dry during the growing season. Bin 8 also contained 188 cm of Cahaba loamy fine sand which was watered sufficiently to prevent any layer drying to —1 bar soil water potential (Table 1). Plants were thinned to two per bin (one in the north part of the bin and the other in the south part of the bin) 4 weeks after planting. Root development was monitored during the growing season by the line-transect method of Taylor et al. (1970). Soil water content measurements were obtained by neutron probe readings at 2- to 3-day intervals.

Plant-stem diameter was continuously monitored at about 40 cm above ground level by the linear variable displacement transducer (LVDT) system described by Klepper et al. (1971). The input signals were generated by a stabilized 400.00 Hz oscillator, and the transformer output signals were amplified and displayed on a strip-chart recorder for on-line monitoring of the experiment. An automatic data acquisition system monitored the analog output from each LVDT at 2-min intervals and recorded the output voltage onto digital magnetic tape with a precision of 1 part in 10^5. The micrometer holders permitted daily mechanical 0-point readjustment of each LVDT to compensate for long term growth of the plants, and also served as a mechanical check on linearity and stability of the electronic circuitry. Long term accuracy was generally better than 1 part

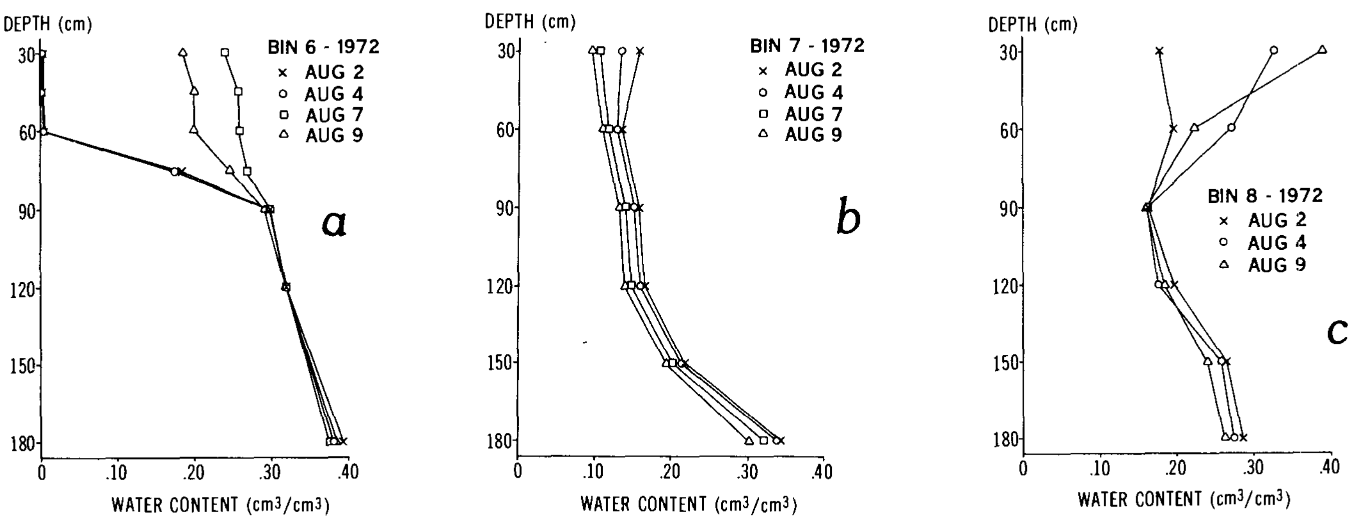

Fig. 1. Water content (cm³ water/cm³ soil) as a function of depth reported by Browning et al. (1975) on dates shown. Fig. 1a = Bin 6, 55 cm topsoil overlying acid subsoil with limited irrigation. Fig. 1b = Bin 7, 188 cm soil allowed to dry with no irrigation during experimental period. Fig. 1c = Bin 8, 188 cm soil irrigated sufficiently to prevent any soil layer from drying below —1 bar soil water potential.

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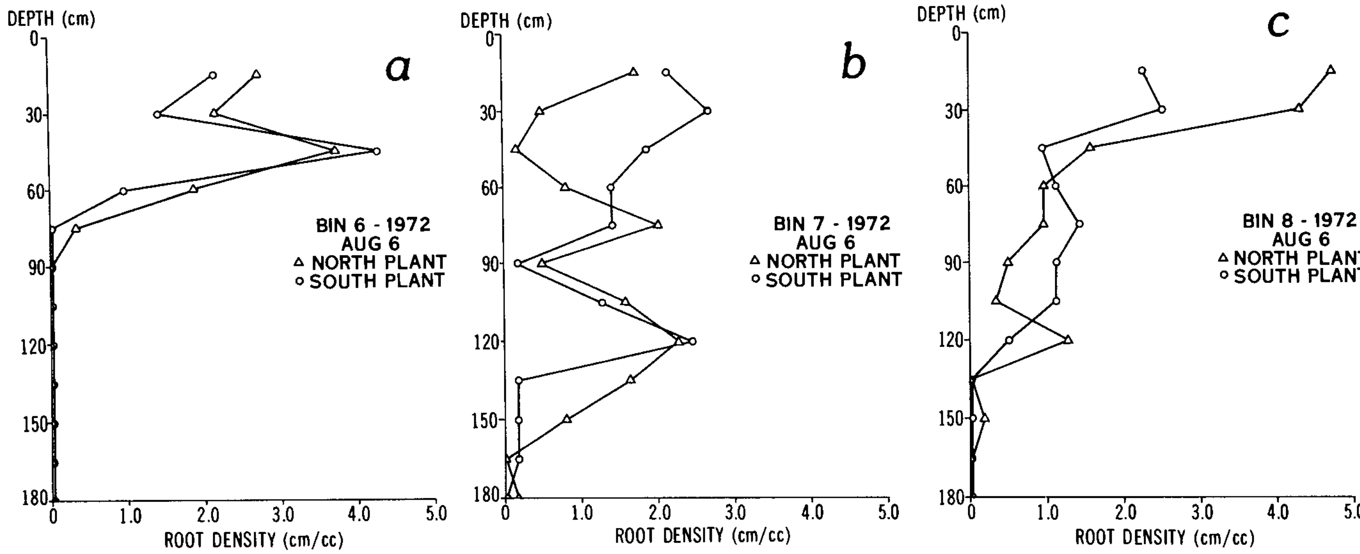

Fig. 2. Root density (cm roots/cm³ soil) measured by Browning et al. (1975) on 6 Aug. 1972. Values attributed to the south plant were obtained by counting roots on the south half of the window in each bin, while those attributed to the north plant are from the north half of each window. Fig. 2a = Bin 6. Fig. 2b = Bin 7. Fig. 2c = Bin 8.

in 10^4, and the response time of the transducers was about 0.1 to 1 sec—principally limited by the mechanical inertia of the system components. Temperature variability due to expansion of the stainless steel holder components was about 0.001 mm/C. From the daily record of micrometer adjustments, it was possible to compute a continuous record of stem diameter changes over a period of several weeks (Browning et al. 1975). The long term growth trend was computed by linear regression analysis, and deviations of measured stem diameter at any instant from the long term regression line were used in subsequent spectral analysis.

A Fritschen (1963) miniature net radiometer was maintained over clipped grass sod at a distance of about 3 m from the rhizotron compartments with the cotton plants. The integrating hemispheres were kept under slight positive pressure by a continuous stream of filtered air blown in by an aquarium pump. The height was fixed at 1 m above the sod (Idso and Cooley, 1971), and the factory calibration value of 3.05 mV/langley was used without further experimental verification. Radiometer response time to a step-change in radiation was nearly 2 min to reach a new equilibrium value, due mainly to the heat capacity of the thermopiles. The initial response to a step-change was observable within a few second. Output from the radiometer was recorded onto digital magnetic tape at 2-min intervals, corresponding to the time of the stem diameter readings discussed above.

After preparation of master-tape files containing records of net radiation and stem diameter at 2-min intervals (Browning et al. 1975), working files were prepared for each individual plant, representing observations from midnight (CDT) 1 Aug. 1972, until 8 August. The final working files consisted of matched data triplets consisting of the time, measured value of net radiation, and deviation of measured stem diameter from the trend line.

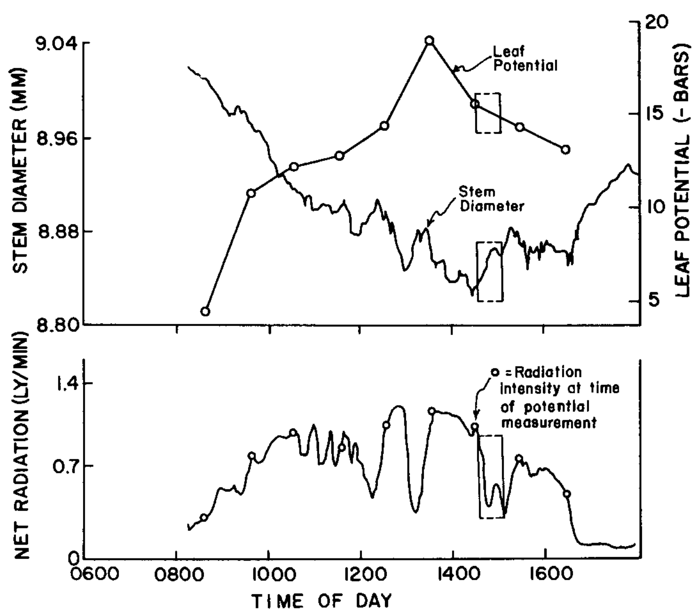

Fig. 3. Net radiation, leaf water potential, and stem diameter during a cloudy period on the afternoon of 19 Aug. 1971 (after Stansell et al. 1973).

RESULTS

During the time period considered in the variance spectral analysis, 2 to 8 August, the well-watered plants in bin 8 had an average morning leaf water potential of —2.3 bars (measured just after sunrise at 0700 hours CDT), whereas the average afternoon water potential reported by Browning et al. (1975) was —11.6 bars. Plants grown in a comparable deep soil, given no additional water (bin 7), had an average morning leaf water potential of —2.4 bars and an average afternoon leaf water potential of —13.4 bars. After 8 August, as the water in bin 7 was depleted, both morning and afternoon water potentials gradually became much more negative than those observed in the well-watered bin. Plants grown in a shallower soil with irrigation (bin 6) had morning leaf water potentials comparable to those in bins 7 and 8; however, during the first few days of the analysis, the average afternoon leaf water potential was about —16 bars. After an irrigation treatment on 6 August, the afternoon potentials were roughly comparable to the deeper rooted plants on bins 7 and 8.

The volumetric water content reported from the neutron probe measurements of Browning et al. (1975) are plotted for the period of analysis in Fig. 1. Be-

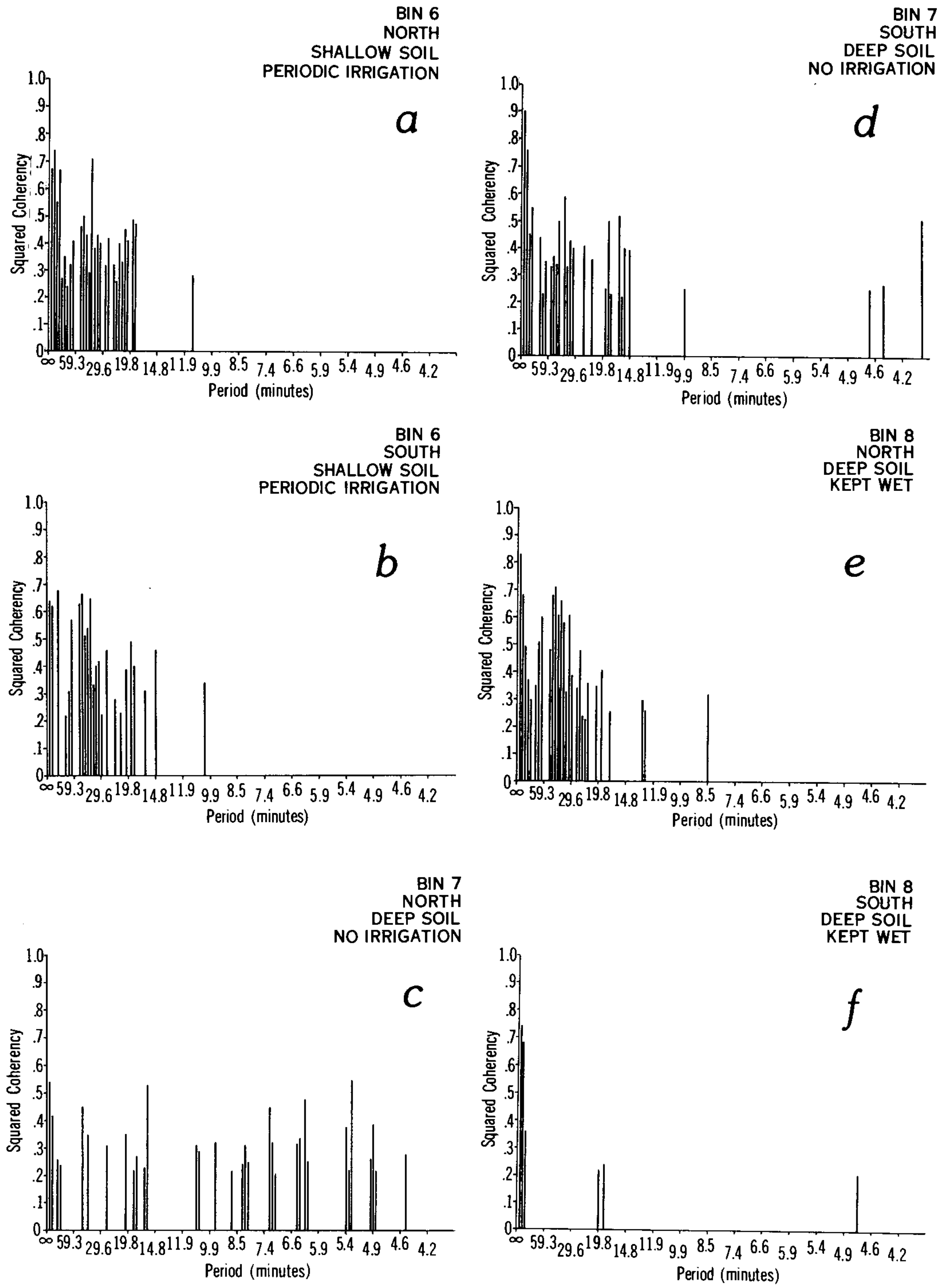

Fig. 4. Coherency spectra indicating the correlation between changes in net radiation and cotton stem diameter of individual plants. Spectra labeled "north" or "south" represent responses from plants growing on north or south sides of the correspondingly labeled bins. Fig. 4a = Bin 6, North. Fig. 4b = Bin 6, South. Fig. 4c = Bin 7, North. Fig. 4d = Bin 7, South. Fig. 4e = Bin 8, North. Fig. 4f = Bin 8, South.

cause of the large volume of soil required for a neutron probe water content measurement, it was not possible to distinguish between individual plants growing in the same rhizotron bin; the values reported are averages for the depth shown. The figures indicate the higher soil water content of bins 6 and 8 compared to bin 7. The measured rooting densities plotted in Fig. 2 were separated into the north and south portions of roots visible at the viewing surface of each bin. In bin 6 there is little difference in rooting densities from the north to the south plant. The main density differences exhibited in bin 7 occur above 75 cm where south plant densities are greater than north plant values. In bin 8, density differences occur main-

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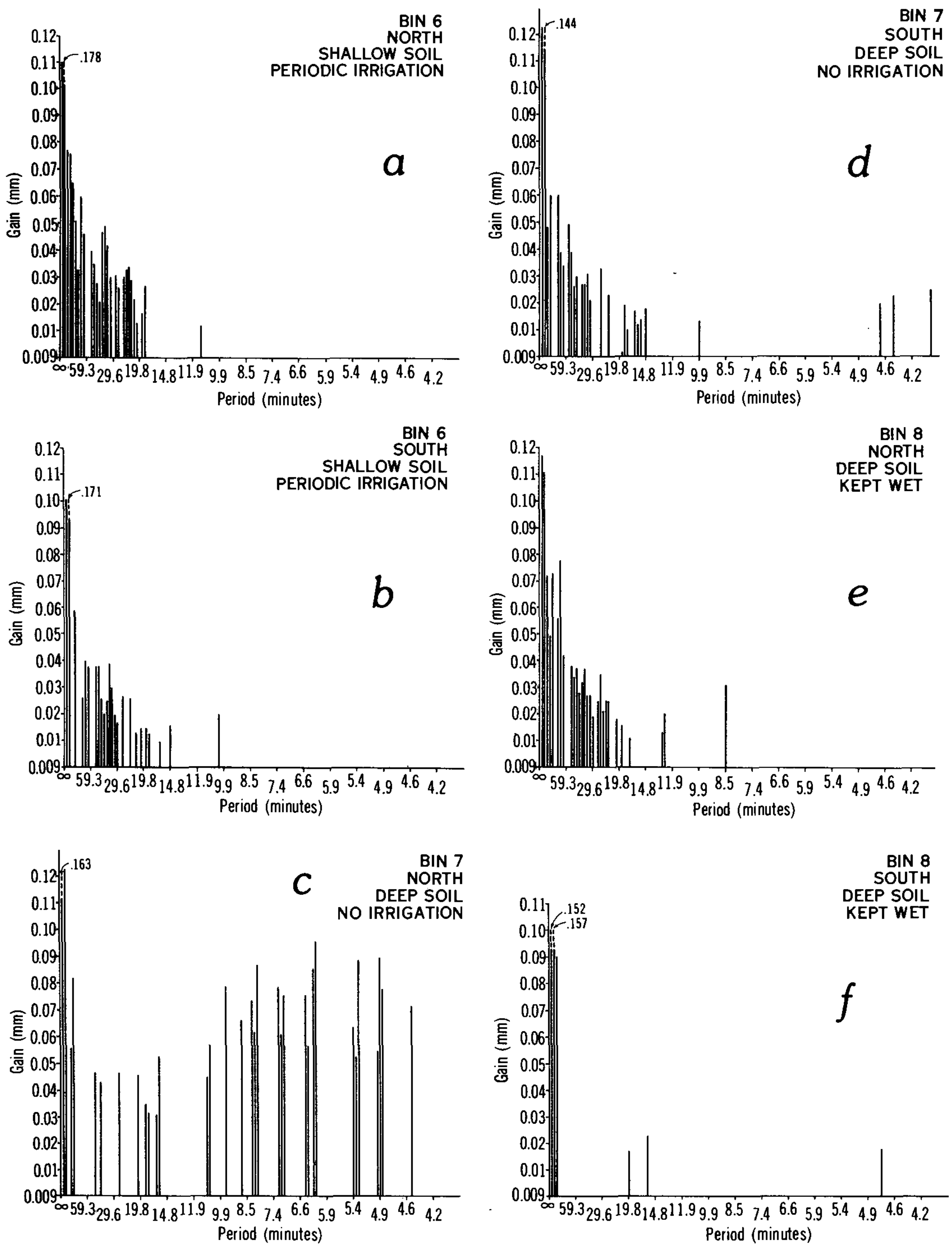

Fig. 5. Gain spectra indicating the amount of change in stem diameter which would be expected from a 1 langley/min change in net radiation received by cotton plants growing in locations indicated by respective labels. Fig. 5a = Bin 6, North. Fig. 5b = Bin 6, South. Fig. 5c = Bin 7, North. Fig. 5d = Bin 7, South. Fig. 5e = Bin 8, North. Fig. 5f = Bin 8, South.

ly above 45 cm, with the greater densities associated with the north plant. Root distribution and effectiveness in extracing water stored in the soil profile is discussed in Taylor and Klepper (1974).

Typical data representing the correspondence between measured net radiation and stem diameter are shown in Fig. 3 (after Stansell et al. 1973). The spectra shown in Fig. 4, 5, and 6 concentrate on the relationship between cycles in stem diameter and net radiation in the time period range from 4 min to nearly 10 hours. Fluctuations with a period greater than 10 hours are not considered here. It should be noted again that period is the inverse of frequency.

The squared coherency spectra (Fig. 4) are plotted only for the frequency bands found to be statistically significant. The extreme lefthand side of each plot

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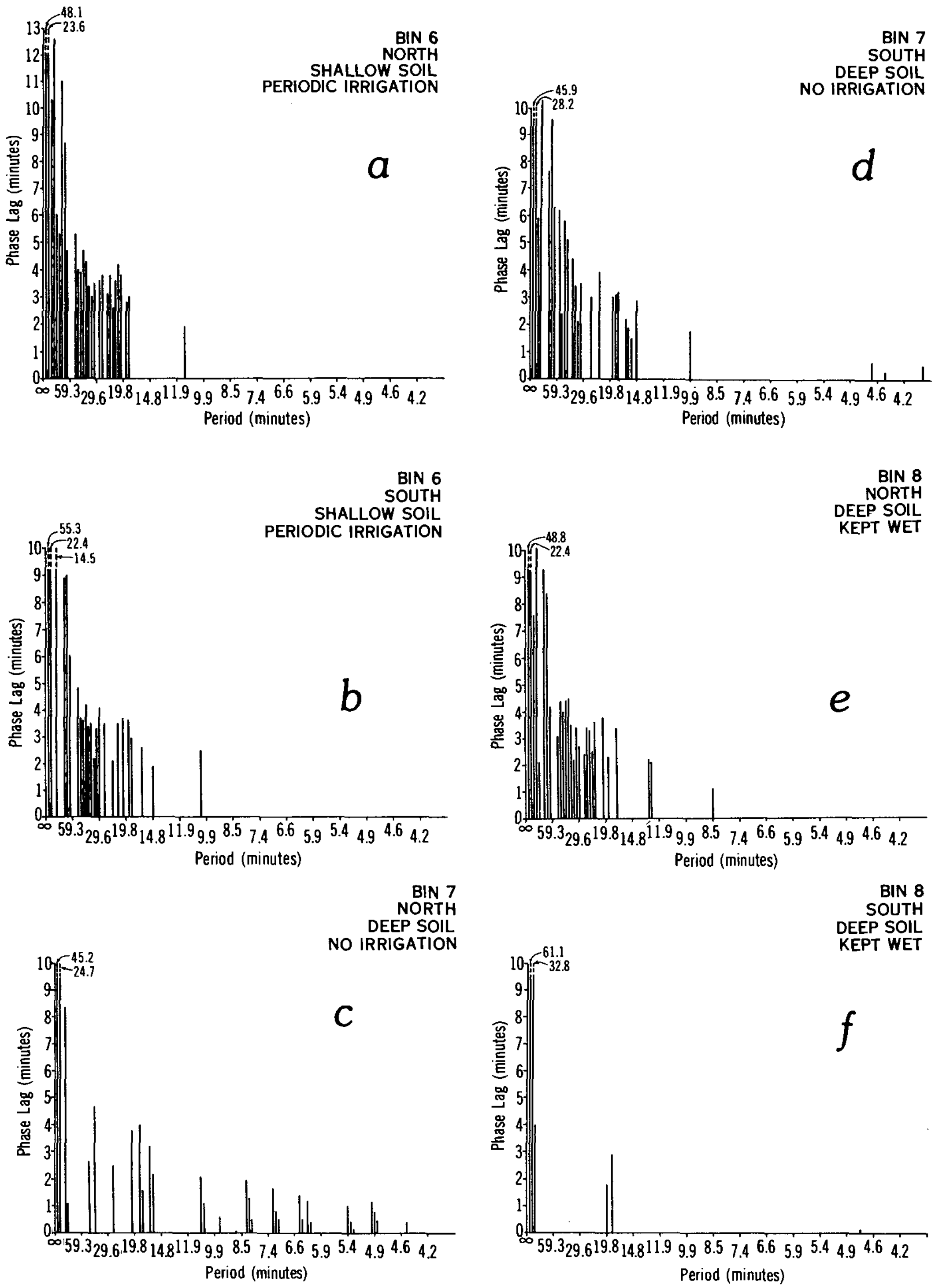

Fig. 6. Phase spectra representing the lag time between a maximum in radiation loading and the corresponding minimum stem diameter at the period indicated. High frequency flutter due to passing clouds produced measurable diameter changes at short periods only in the water-stressed plants of Bin 7, while longer term changes in radiation induced corresponding diameter changes with longer delay times. Rapidity of response may be a function of the amount of readily available water held within the plant. Fig. 6a = Bin 6, North. Fig. 6b = Bin 6, South. Fig. 6c = Bin 7, North. Fig. 6d = Bin 7, South. Fig. 6e = Bin 8, North. Fig. 6f = Bin 8, South.

represents period of infinite length, while the right-hand side represents the minimum period, which can be resolved (Nyquist period, twice the period between consecutive observations, Rayner, 1971). Between these two extremes, variance has been distributed into 147 frequency bands distributed along the axis as indicated. Thus, between the axis point labeled 59.3 min and infinity, there were nine additional frequency bands used in the analysis, centered about periods of 1.1, 1.2, 1.4, 1.6, 2.0, 2.5, 3.3, 4.9, and 9.9 hours.

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Since the squared coherency spectrum is analogous to a squared correlation coefficient for observations in each frequency band of the analysis a squared coherency value of 1.0 means changes in radiation are perfectly correlated with changes in stem diameter at a given frequency, while a squared coherency of 0.0 would mean no relationship at that frequency. Tukey (1967) has noted that a completely incoherent pair of time series will show an average coherence of 2/d.f. (degrees of freedom), if the number of degrees of freedom is small. With 4,410 observations in the data set, a squared coherency of about 0.2 is sufficient to indicate statistical significance at the 0.05 probability level.

While the squared coherency spectrum indicates whether the two time series (radiation and stem diameter) are correlated and the strength of the relationship, the ordinate scale units on the plots of Fig. 5 show the change in stem diameter that would be expected to occur after a 1-langley/min change in net radiation. As expected, there is an increase in the gain factor as longer periods are approached.

The phase lag (shown in minutes on the ordinate axis of Fig. 6) represents the time between a maximum in net radiation and the corresponding minimum in stem diameter (an effect reported by Stansell et al. 1973). The lag time varies from about 1 min for rapid oscillations in radiation load to more than 20 min for changes in radiation for periods of 1 hour or longer.

In both channels of bin 6, the irrigated treatment, most of the significant squared coherency values (Fig. 4) occurred at periods greater than 20 min. The main exception was the peak between 9.9 and 11.9 min. At periods near 20 min, the change in stem diameter for a 1-langley/min increase in radiation load was a decrease of about 0.015 to 0.030 mm in stem diameter (Fig. 5). The gain increased with increasing period and at periods approaching 10 hours, values of 0.17 to 0.18 mm were obtained. The phase lag (Fig. 6) between the time of a maximum in net radiation and a minimum in stem diameter ranged from about 3 min at periods near 20 min to lag times approaching 1 hour at the longer periods.

The two water-stressed plants of bin 7 showed marked differences in response to changes in radiation loading over a wide range of frequencies. The north plant showed significant squared coherency values all across the spectrum, while the south plant had significant coherency squared values principally at periods longer than 15 min. The gain values shown for the north plant were very large. Even at periods between 4.2 and 11.9 min, the gain factors were nearly half as strong as the diurnal stem diameter fluctuations (Fig. 3). Response times for this plant between the periods of 4.2 and 11.9 min were very fast, generally less than 2 min (time from maximum net radiation value to a minimum stem diameter). The spectra for the south plant in bin 7 showed gain increases from about 0.02 mm at a period near 15 min to 0.144 mm at a period of 4.9 hours. Over the same period intervals, lag increased from about 1.5 to 45 min. Clearly, there was a much stronger and more rapid response to change in radiation when the plants were under stress.

In bin 8, strong differences between well-watered plants were noted. Spectra from the south plant showed only six significant squared coherency values from a total of 147 frequency bands. For periods less than 3.3 hours, there seemed to be virtually no relationship between stem diameter fluctuations and net radiation, suggesting a large internal buffering capacity, perhaps due to a higher level of tissue hydration in the succulent tissues of this plant. Results from the north plant of bin 8, both in terms of squared coherency values and the gain and phase spectra, seemed more consistent with those exhibited in bin 6, which was somewhat more water stressed.

DISCUSSION

As radiation increased each morning, the cotton stem diameter temporarily decreased; however, turgor was regained each night as the roots continued to absorb water from the soil to replace that lost from the stem and leaf tissue during the day (Klepper et al. 1973). The rate of change in stem diameter at any given time reflects the algebraic sum of two rates; the rate of water uptake by the root system, and the rate of water loss from the shoot. As discussed earlier, long term growth in stem diameter was removed from data used in the time series analysis by expressing individual measurements as deviations from the least squares regression line. Remaining fluctuations, therefore, represent changes in the instantaneous equilibrium between rates of water loss and water uptake.

Treatment differences in the rate of plant water extraction from the soil must have been largely a function of soil water availability and the spatial distribution of roots with respect to the location of available water. Due to storage capacity of the plant tissue, high frequency changes in radiation intensity probably caused little change in the rate of water uptake by the root system, especially in the irrigated plants of bins 6 and 8. An increase in stem diameter after a short period (high frequency) decrease in net radiation probably results from a reduction in the rate of leaf water loss, rather than from an increase in water uptake rate. Similarly, a reduction in stem diameter after a sharp increase in radiation load represents an increase in transpirational demand rather than a reduction in soil water availability.

However, water held in temporary storage by plant tissue serves as a buffer against extremely rapid changes in the rate of water uptake by the root system. Thus, responses toward the lefthand side of Fig. 4, 5, and 6 (long period, low frequency responses) include the possibility of adjusting potential gradients all along the path from soil to substomatal cavity and, therefore, may reflect changes in both water loss and water uptake rates. Ackerson et al. (1977) reported significant osmotic potential differences between differentially-stressed cotton plants. Compensation of tissue osmotic potential is probably another low-frequency phenomenon which further reduces the amount of diameter response if sufficient water is available.

Because fluctuations in radiation loading were constant over all plants in the experiment, the differential responses shown in Fig. 4, 5, and 6 may be attributed to differences in the accessibility of water to the root

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systems. Bins 6 and 8, with readily available water supplied by irrigation, showed relatively little significant coupling between high frequency changes in radiation loading and corresponding diameter changes. Plants in bin 7, depending entirely upon water stored before the experiment began and available only at lower potential, evidently experienced difficulty in obtaining enough high-potential water to meet transpirational demand and, therefore, were able to store relatively less water in the phloem parenchymal cells. As a result of the smaller reserves, changes in transpirational demand produced immediate and dramatic changes in stem diameter, as was predicted by Molz and Klepper (1972, 1973).

While the spectral analysis suggests that there was a difference between plants growing on the north and south sides of a bin, it is difficult to explain the cause. There were no physical barriers separating the root systems (Fig. 2) of the north- and south-facing plants, so it is possible that some of the roots counted on the north half of the rhizotron windows may have been supplying water to the south-facing plants. Data on relative water availability between one side of a bin to the opposite side of the same bin are not available because of the limited spatial resolution of the neutron probe used for measuring water distribution in the soil profile. Plants in bin 6, with rooting depth restricted to the top 55 cm and a fairly uniform moisture profile maintained by irrigation, showed relatively less difference in shrinkage response to radiation between north- and south-facing plants. Bins 7 and 8 had a greater difference in root distribution and a correspondingly greater difference in correlation between north- and south-facing plants.

CONCLUSIONS

The spectral analysis presented has shown that there are statistically significant relationships between fluctuations in net radiation and cotton stem diameters. The analysis has demonstrated the strength of the relationship as a function of response frequency on the basis of the squared coherency spectra, the magnitude of diameter changes which might be expected for a given change in radiation over a range of frequencies, and the length of time required for a measurable response in stem diameter to be observed after a change in net radiation. Equally significant, the spectral analysis has indicated that the relationship between stem diameter and net radiation varies from plant to plant in response to variation in the availability of stored water to the plant's root system.

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