WATER RESOURCES REPORT NO. 60

RELATIONSHIP OF PLANT MOISTURE STATUS TO IRRIGATION NEED IN CORN AND SOYBEAN CROPS

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ABSTRACT

RELATIONSHIP OF PLANT MOISTURE STATUS TO IRRIGATION NEED IN CORN AND SOYBEAN CROPS

Two of the largest problems in irrigation planning are 1) the measurement of crop moisture status and 2) the interpretation of the measurements in terms of irrigation need. This research program was devoted to both these problems and involved the development of a rapid, simple method for measuring crop moisture status that could be used on the individual farm, and the determination of the physiological response of corn and soybean to low moisture availability. As a result, a small, inexpensive pressure chamber was designed, field-tested, and shown to give reasonably accurate values for the moisture status of corn and soybeans. The response of leaf enlargement, photosynthesis, and dark respiration were measured under laboratory conditions in corn, soybean, and sunflower as moisture availability decreased. These data then were used to simulate these processes during a drought that occurred in the field. The simulation showed that, during vegetative development in corn and soybean, leaf enlargement was much more sensitive than photosynthesis or dark respiration to drought. Consequently, irrigation could be based on the maintenance of leaf enlargement alone. Specifically, if pressures measured with the pressure chamber were 30 psi or less at sundown and 2 hours after sunup in leaves normally exposed to full sun, leaf growth, photosynthesis, and dark respiration would be maximal. This relationship did not hold during reproductive growth, however. Chloroplast photosynthesis was studied and was shown to be limiting photosynthesis in sunflower at low moisture availabilities. Effects on the chloroplasts appeared to be largely in the "light" reactions of photosynthesis, where photosystem II, photosystem I, cyclic photophosphorylation, and noncyclic photophosphorylation were inhibited severely. Irrigation after a period of desiccation often brought about complete recovery of the chloroplasts but only incomplete recovery of the stomata, which had been closed prior to irrigation. Studies of liquid water transport showed that soybean had a higher resistance to water movement than did corn or sunflower and that the high resistance was associated primarily with the roots. The root resistance could be kept reasonably low by infecting the roots with mycorrhizal fungi. This work indicates that the moisture status of crops can be simply measured and interpreted at the practical level, and suggests means for irrigation planning which should maximize the efficiency of water use in corn and soybean growing vegetatively.

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KEYWORDS -- *Irrigation planning/ *crop moisture status/ *photosynthesis/ *leaf enlargement/ chloroplasts/ resistance to water transport/ water use efficiency

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I. INTRODUCTION

1. Project Objectives

Crop production depends on large quantities of water. By far the greatest portion of this water is lost by transpiration and evaporation, which accounts for about 70% of the water falling on the world's land masses.

Considering all of the uses of water by society, irrigated agriculture currently consumes more than all the other forms of consumption combined. Man's requirements for water are growing (14) and with them the necessity for irrigation. However, the economic benefit from water used in agriculture is generally smaller than that from industrial and municipal uses of the same water (15). Therefore, in the face of food supplies which are reasonably adequate for the U.S., increased agricultural use of water is hard to justify.

Within this context, the most effective planning strategy for agriculture is to devise means of irrigating more efficiently. Even a 10 or 20% reduction in water use, because of the immensity of scale, would be a highly significant saving.

Although a part of the problem of improving the efficiency of water use in agriculture is an engineering one, probably the largest problem is a plant one. It is generally agreed that the highest water use efficiency is obtained when crop growth is close to maximum or maximum. However, little is known about quantifying when a crop needs water or how much it needs at a particular time. In the dry regions of the U.S., where rainfall is nil, perhaps some degree of confidence in irrigation practice may be gained by subjective observation of crop development. But in much of the U.S., where rainfall needs to be supplemented by irrigation, the variability of weather and soil make the timing and extent of irrigation extremely hard to quantify on a subjective basis.

Illinois falls into the latter category and, because of its large agricultural economy, the problem is important. In a recent study (19) the need for accurate timing of irrigation was outlined by E.R. Swanson as a major factor in the success of irrigation systems in Illinois. Swanson (19) states:

"Although such yields [large enough to support irrigation] are reported in years with favorable weather, they reflect a high level of management in the form of timely application of carefully selected inputs [of water,]etc. . Such management is a critical factor in determining the success of an irrigation program."

The general objective of the research conducted under this project was to provide a means for quantifying water need by corn and soybean crops that could be used at the level of the individual farm. The method developed was rapid, and, although it required a small pressure chamber, the equipment was inexpensive and simple to use. A large amount of laboratory effort was made to test the instrument and to determine the response of corn, soybean, and sunflower (an increasingly important oil crop for Illinois) to moderate desiccation. The pressure chamber was then field tested and the results were compared with laboratory experience.

On the basis of the field work, it appears possible to evaluate the water status of corn and soybean at specific times during the day so that water availability for vegetative growth and photosynthesis are kept optimum, and so that the degree of inhibition of these processes can be estimated when water availability is not optimum. Generally, measurements need to be made only once every few days so that labor input remains small. Consequently, the pressure chamber is clearly an attractive means of assessing irrigation need. Somewhat unexpectedly, however, the field work also showed that the criteria for irrigation developed with the pressure chamber for vegetative growth do not hold for reproductive growth. Since reproductive growth determines yield in corn and soybean, more study of this phase of crop development is vitally needed to make the economic consequences of irrigation planning more apparent.

2. Summary of Accomplishments

This research program has achieved the following major accomplishments:

(1) A pressure chamber was developed and tested for field use.

Boyer, J.S. Inexpensive pressure chamber for field measurement of leaf water potential in corn and soybean. In preparation.

Describes design and calibration of inexpensive pressure chamber for field use.

Boyer, J.S. and S.R. Ghorashy. 1971. Rapid field measurement of leaf water potential in soybean. Agron. J. 63:344-345.

Shows good agreement between pressure chamber and thermocouple psychrometer measurements of leaf water status in soybean.

(2) The response of leaf growth, photosynthesis and respiration to low leaf water potentials was characterized in the laboratory.

Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at low leaf water potentials. Plant Physiol. 46:233-235.

Shows that leaf enlargement is considerably more sensitive than photosynthesis or dark respiration to low leaf water potentials in corn, soybean, and sunflower.

Boyer, J.S. 1970. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46:236-239.

Points out that the photosynthetic response to desiccation differs in corn and soybean, largely because of differences in stomatal behavior.

Meyer, R.F. and J.S. Boyer. 1972. Sensitivity of cell division and cell elongation to low cell water potentials in soybean hypocotyls. Planta. In press.

Shows that cell enlargement is generally more sensitive than cell division to desiccation, but soybean hypocotyls have an osmotic mechanism which reduces the sensitivity of enlargement.

(3) Leaf enlargement was shown to be more important than photosynthetic activity as an indicator of irrigation need in field-grown soybean and corn.

Boyer, J.S. and R.F. Meyer. Field simulation of photosynthesis and growth in corn and soybean at low leaf water potentials. In preparation.

Indicates that irrigation need can be monitored at sundown and 2 hr after sunup and can be based on the response of leaf enlargement.

(4) Liquid phase water transport to leaves was studied and equations were worked out to describe the process.

Boyer, J.S. 1971. Resistance to water transport in soybean, bean, and sunflower. Crop Sci. 11:403-407.

Demonstrates that soybean has a higher resistance than other species to water transport, largely due to high root resistance.

Safir, G.R., J.S. Boyer, and J.W. Gerdemann. 1971. Mycorrhizal enhancement of water transport in soybean. Science 172:581-583.

Shows root resistance to water transport in soybean is less if roots are associated with mycorrhizal fungi.

Safir, G.R., J.S. Boyer, and J.W. Gerdemann. 1972. Nutrient status and mycorrhizal enhancement of water transport in soybean. Plant Physiol. 49:700-703.

Demonstrates that mycorrhizal effect on soybean roots is due to enhanced nutrient status of plant brought about by fungi.

(5) Studies of chloroplasts showed activity was sensitive to leaf desiccation and provided preliminary indication of the mechanism of inhibition.

Boyer, J.S. and Barbara L. Bowen. 1970. Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials. Plant Physiol. 45:612-615.

Showed that the inhibition of chloroplast activity was quantitatively the same as the inhibition of photochemical activity of intact leaves.

Boyer, J.S. and J.R. Potter. Role of turgor in chloroplast response to low leaf water potentials. Plant Physiol. In press.

Shows that the inhibition of chloroplasts was not due to decreases in leaf turgor during drought.

Potter, J.R. and J.S. Boyer. Role of osmotic potential in chloroplast response to low leaf water potentials. Plant Physiol. In press.

Shows that the inhibition of chloroplasts was not due to a decrease in leaf osmotic potential during drought, but the possibility remained that inhibition might be due to solute-chloroplast interaction.

Keck, R.E. and J.S. Boyer. Inhibition of photosynthetic partial reactions in chloroplasts isolated from sunflower leaves having low water potentials. In preparation.

Shows a number of photosynthetic partial reactions are inhibited during drought.

Boyer, J.S. 1971. Nonstomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. Plant Physiol. 48:532-536.

Demonstrates that the photochemical activity of the leaves apparently inhibits photosynthesis under high light conditions.

Boyer, J.S. 1971. Recovery of photosynthesis following a period of low leaf water potentials. Plant Physiol. 47:816-820.

Shows that leaf photochemical activity can recover completely after exposure of a leaf to desiccation but stomatal behavior does not fully recover. Illustrates that increased resistance to water transport after recovery may result from plant desiccation.

(6) The following three doctoral theses were completed:

Safir, G.R. Mycorrhizal enhancement of water transport in soybean. Parts I and II. Ph.D. thesis, University of Illinois, Urbana, Illinois. 1970. 33 pp.

Morilla, Camila A. Nitrate reductase and polyribosome content of corn having low leaf water potentials. Ph.D. thesis, University of Illinois, Urbana, Illinois. 1972. 51 pp.

Meyer, R.F. Effects of low tissue water potentials on the growth of soybean hypocotyls. Ph.D. thesis, University of Illinois, Urbana, Illinois. 1972. In preparation.

3. Acknowledgments

Several meetings were held with outside consultants including: Dr. C.B. Tanner, Professor of Soil Science, University of Wisconsin, Madison, Wisconsin; Dr. I.R. Cowan, Research Scientist, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia; Dr. K. Mitchell, Director, Plant Physiology Division, Department of Scientific and Industrial Research, Palmerston North, New Zealand; and Dr. P.J. Kramer, Professor of Botany, Duke University, Durham, North Carolina.

Thanks are due Mr. Dale Busboom for the use of his farm in St. Joseph, Illinois for testing a pressure chamber for soybean and corn crops.

II. DEVELOPMENT AND TESTING OF A PRESSURE CHAMBER FOR DETERMINING IRRIGATION NEED IN CORN AND SOYBEAN CROPS

1. Design of Pressure Chamber

Preliminary work (see Termination Report, Allotment Project

A-028-Ill, Water Resources Center, University of Illinois) had shown that the critical water status of corn and soybean needed to maintain maximum photosynthesis could be measured with low pressures in a pressure chamber (2,18). The following work was devoted to the design and testing of a pressure chamber which, because of the low pressures needed, could be made lightweight and inexpensive. The design was planned to permit the system to be used by individual farmers, who could load the system with compressed air at most service stations and carry it easily to the field.

Figure 1 shows the current design of the system. This model was built with state funds. A small pressure chamber is mounted on the end of a standard compressed air tank, which is readily available ($20) at local automotive supply outlets. The pressure chamber required approximately 30 hours to make and, including labor ($7.50 per hour) and materials, cost approximately $250. It is envisioned that a number of simplifying operations could be used in the construction of the instrument which should reduce construction time by half or more on large production runs.

Figure 2 shows the way in which plant tissue is loaded into the pressure chamber. The leaf is placed in an adjustable sealing gland in the top of the instrument so that the cut surface of the leaf may be seen from the outside. The top is then closed and held with the screw on the front of the instrument. Compressed air is permitted to enter the chamber slowly and a wrench is used to tighten the seal around the leaf until no gas can be heard escaping.

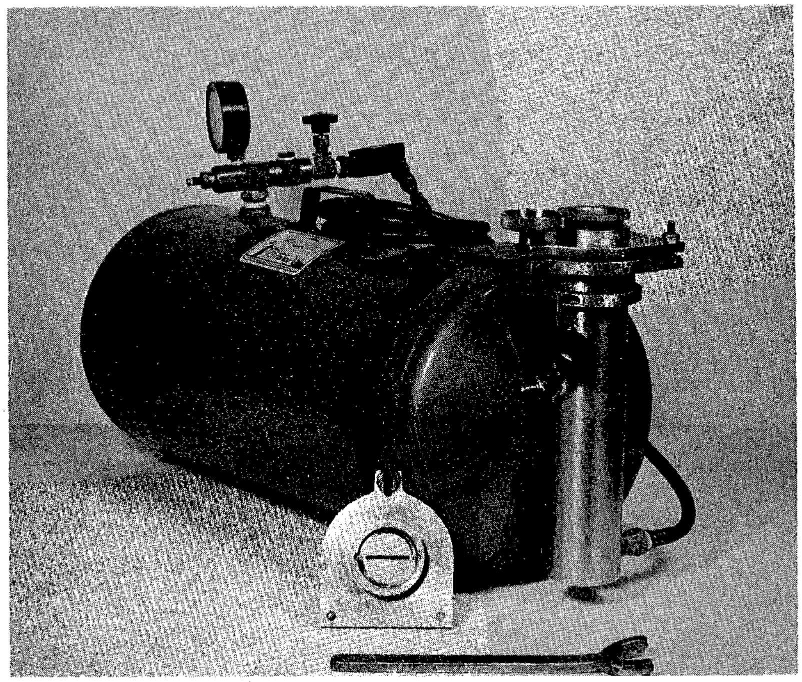

Fig. 1. Pressure chamber and air tank for measuring water potentials of corn and soybean leaves. The tops, one for soybean and one for corn, are interchangeable. The tank is constructed so that compressed air may be obtained from a service station.

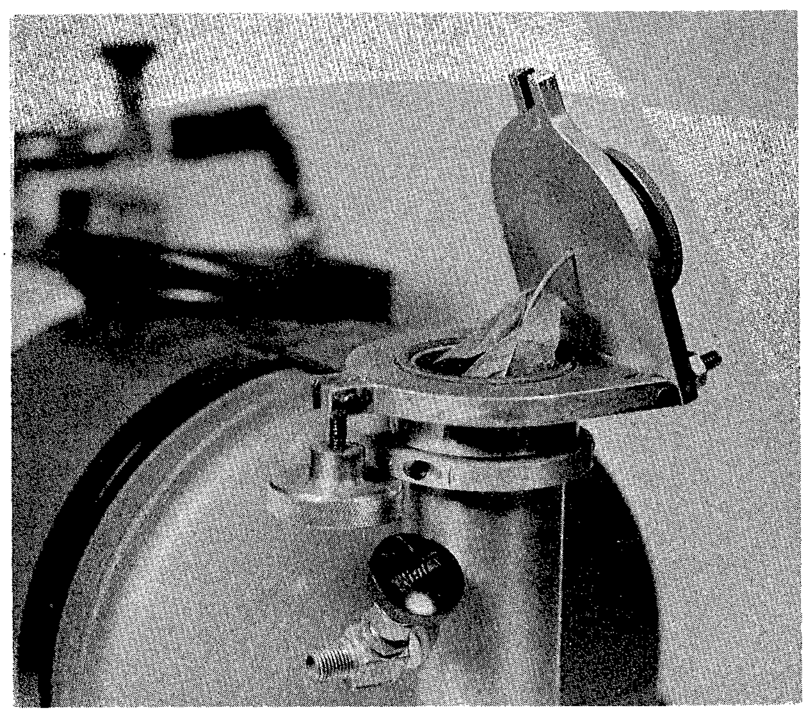

Fig. 2. Arrangement of soybean leaf in pressure chamber. The top of the chamber is partially open to expose the leaf inside. The leaf petiole extends through a seal in the top to the outside of the chamber, where it can be viewed by the operator. During pressurization, the top is closed, and the operator determines the pressure required to make leaf sap just appear at the cut surface of the leaf.

The pressure is slowly increased around the leaf until the sap just appears at the cut surface being viewed by the operator. For field measurements in corn and soybean, this pressure indicates the water status of the leaf, higher pressures indicating a greater need for irrigation.

Use of the instrument deserves several cautionary notes. First, after sap has appeared, the operator should adjust the pressure until the pressure just balances the tendency of the sap to move, and there should be no increase or decrease in the size of the slight film of sap for a minute or two. This assures that the pressure and water throughout the leaf are in equilibrium with each other (2,4,12). Second, in soybean, there is often a preliminary show of sap which appears as a foam at low pressures. In this species, pressure should be increased until a copious flow of sap is observed at the petiole and then the pressure should be decreased until it balances only a small film. This assures that a true balancing pressure is obtained and not a spurious one based on the preliminary show of sap. Finally, the operator should stay clear of the top of the chamber when pressure is applied. Although extremely rare, plant tissue has been known to blow out of the chamber with considerable force and possible danger to the operator. If the instrument is handled as described above, this has never been observed to happen.

Figure 3 shows construction details of the pressure chamber. The entire unit is made of structural aluminum, except for the adjustable nut, and knob, which are

PRESSURE CHAMBER

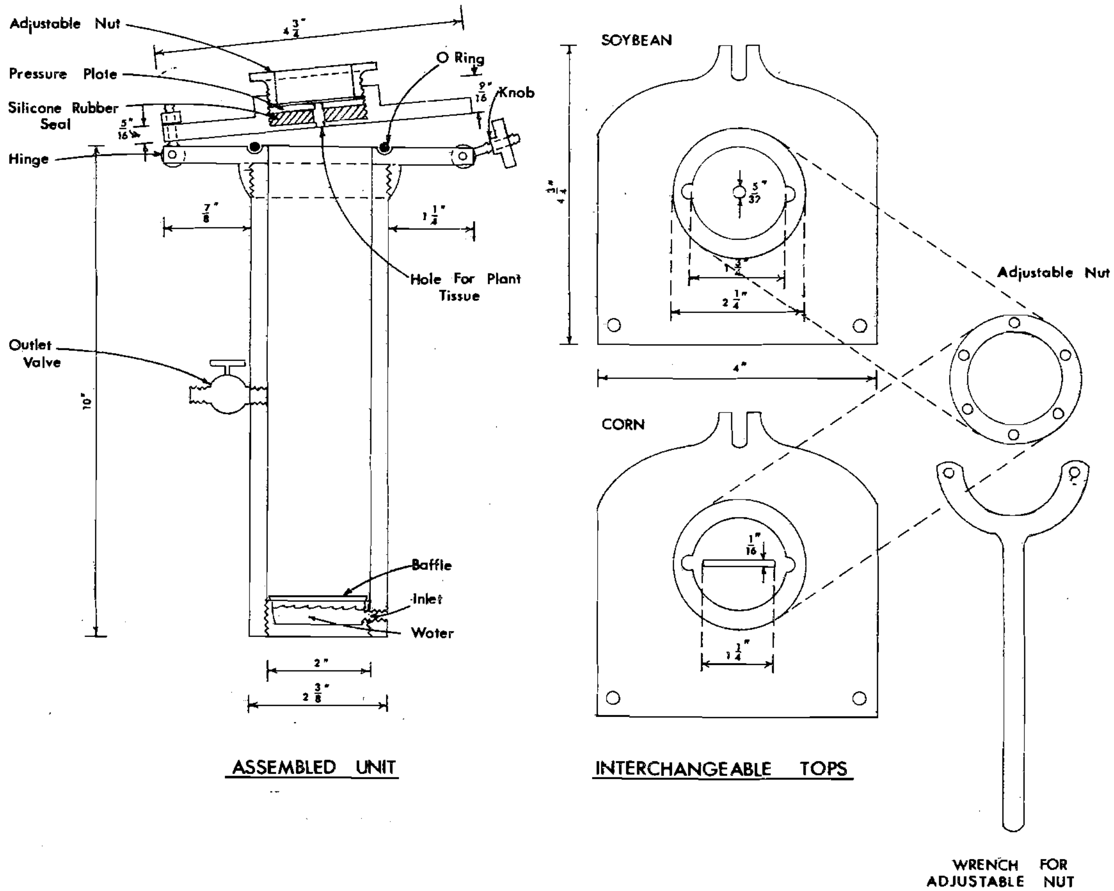

Fig. 3. Construction details of pressure chamber for measuring leaf water status of corn and soybean. Except for adjusting knob, closing knob, pressure plate and bolts for top, entire unit is constructed of structural aluminum.

constructed of stainless steel or brass. The inlet and outlet valves for controlling air pressure are commercially available needle valves made of brass. Gauges are standard items with 300 or 400 psi full scale and 2.5 inch face. A disc baffle is placed above water in the bottom of the chamber so that incoming air is humidified without splashing the tissue. In future versions of the instrument, the gauge which indicates chamber pressure will be mounted on the chamber itself for easy observation. Current design of the instrument permits a range of pressures from 0 to 250 psi to be used.

2. Testing of Pressure Chamber

It is essential that the pressure chamber provides an accurate measurement of the water status of corn and soybean if it is to be useful. To investigate this possibility, values obtained with the instrument have been compared with those from a thermocouple psychrometer (11) known to be highly accurate (1). Agreement was quite good in both corn (13) and soybean (12) and demonstrated that the concentration of the xylem sap, which can be an important source of disagreement between the two methods (2), is low enough to be ignored in both species.

Since the instrument appeared to be accurate enough for field use, a study was conducted of the water status of commercial crops of corn and soybean during the 1971 growing season in fields near Urbana, Illinois. The first half of the season was virtually without rainfall, except for a shower providing 1.1 inch. On July 4, just prior to flowering in both crops, 3.5 inches of rain fell and July 1971 turned out to be one of the wettest months on record in the Champaign-Urbana area. August continued high in soil moisture and large yields were ultimately obtained from both soybean and corn (52 and 140 bushels per acre, respectively). The fields were without irrigation and consequently, water availability to the crop was uncontrolled.

Figure 4 shows that leaf water potentials (1 bar equals 14.7 pounds per square inch measured with the pressure chamber)

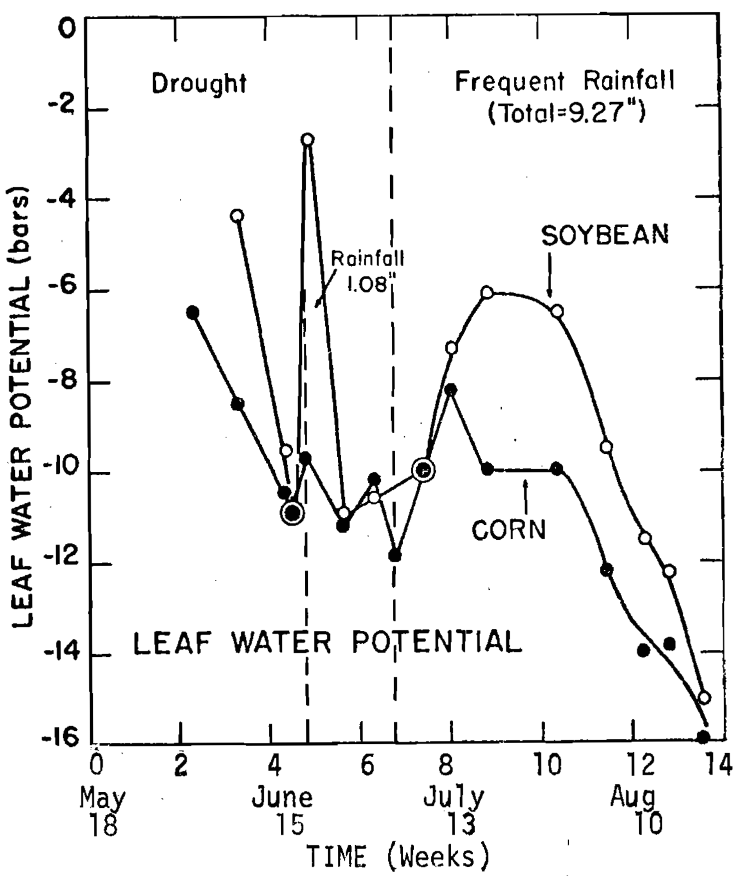

Fig. 4. Leaf water potentials of corn and soybean measured with the pressure chamber in commercial fields during the growing season of 1971. During the first half of the season ("Drought"), 1.08 inches of rain fell and, during the second half ("Frequent Rainfall"), 9.27 inches of rain fell. Reproductive growth of the crops occurred entirely during the second half of the season. Leaf water potentials were measured between 1500 and 1700 hours in leaves that were normal to the incoming radiation and fully illuminated.

generally became lower (more negative, drier) as the season progressed until rain began in July. With moistening of the soil, leaf water potentials rose for 2 weeks, then began falling regardless of soil moisture for the remainder of the season. Measurements were terminated for the season when signs of senescence began to appear in the crops. All measurements were made between 1500 and 1700 hours, when the evaporative demand by the atmosphere was the largest for the day. Leaves were sampled only if they were at the top of the crop, fully illuminated and normal to the incident light.

Throughout the growing season, the pressure chamber remained a sturdy and reliable instrument and was easily used by various personnel. Although leaf tissue was exposed to pressures as high as 235 psi, there was no sign of injury to the leaves or to the portion of each leaf which was in the seal of the top.

The pressure chamber provided values of leaf water potential which generally were expected from the rainfall and meteorological conditions. It showed the severity of crop desiccation long before wilt symptoms appeared in both soybean and corn. As pointed out in a later section, much of crop growth had stopped before wilt symptoms had become visible. Wilt symptoms appeared and growth declined at leaf water potentials which generally were the same as those observed in laboratory studies of the same species. The only exception to this generality occurred in the last third of the growing season, when leaf water potentials declined despite frequent rainfall, and reproductive growth was occurring. In a later section of this report (Fig. 5), data will be given which show that these leaf water potentials predicted photosynthetic rates only 20 to 40% of maximum (6). Yet, rapid reproductive growth occurred and high yields were obtained (52 and 140 bushels per acre in soybean and corn, respectively). The lack of ability of the pressure chamber to predict yield during reproductive growth is not understood at this time.

III. RESPONSE OF LEAF GROWTH, PHOTOSYNTHESIS AND DARK RESPIRATION TO LOW LEAF WATER POTENTIALS

Leaf growth was more sensitive than photosynthesis per unit leaf area to low leaf water potentials in corn, soybean, and sunflower (Fig. 5) when these processes were measured

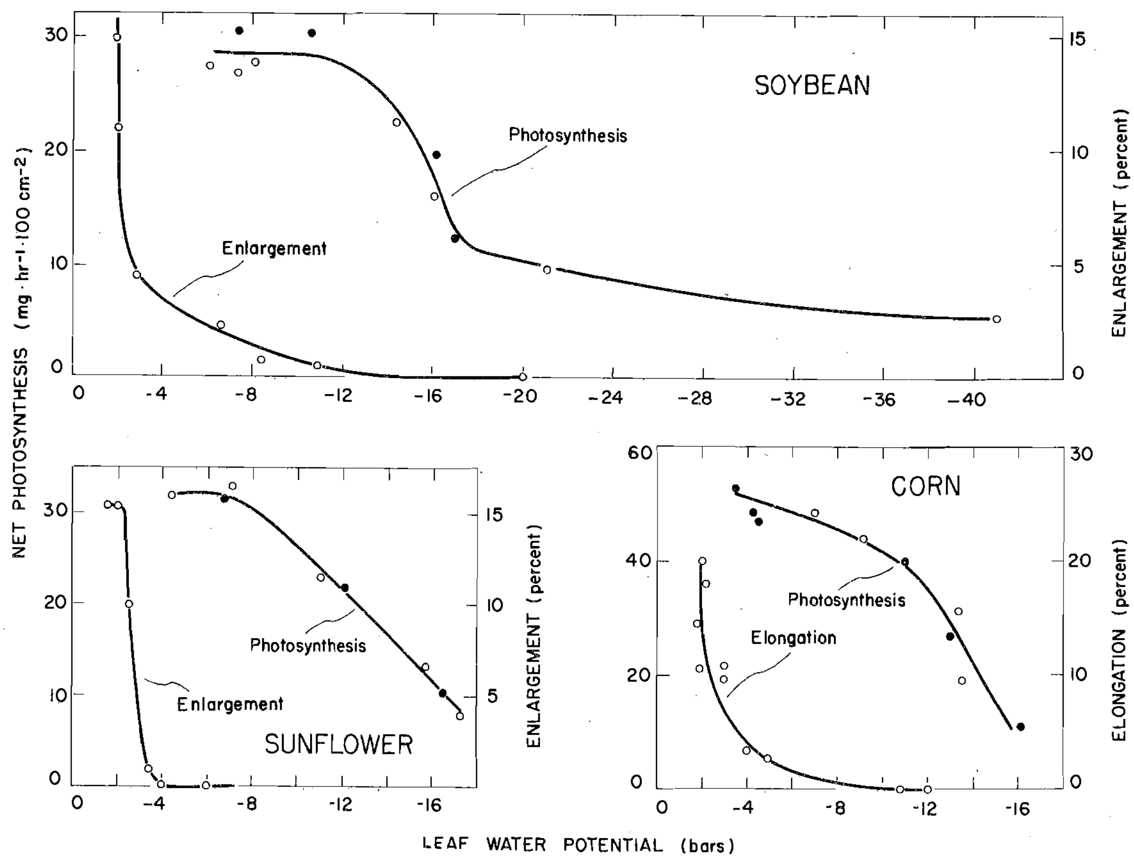

Fig. 5. Leaf growth and net photosynthesis per unit leaf area in corn, soybean, and sunflower plants at various leaf water potentials.

under laboratory conditions. The rates of leaf growth and photosynthesis were measured in intact plants approximately 0.5 to 1 meter high that were in the vegetative phase of growth. The experiments have been outlined in detail (5,6).

Dark respiration responded less to low leaf water potentials than did photosynthesis or leaf growth (6). Thus, differences in plant response to desiccation were probably not attributable to respiration (6).

Photosynthesis in corn was more sensitive than that in soybean (5), probably due to differences in stomatal response to low leaf water potentials. The data in corn suggest that even slight drought is associated with inhibition of photosynthesis in corn.

IV. FIELD SIMULATION OF LEAF ENLARGEMENT AND PHOTOSYNTHESIS IN CORN AND SOYBEAN DURING DROUGHT TO ASSESS IRRIGATION NEED

Leaf enlargement and photosynthesis measured at low leaf water potentials in the laboratory (6) provided a means for simulating leaf enlargement and photosynthesis from leaf water potentials measured in the field. These data permitted recommendations to be developed for irrigation scheduling in corn and soybean in order to maintain growth at a maximum.

Leaf water potentials were measured for a 24 hour period at the height of the drought in the same field used for the data of Fig. 4. A few days later, after over 3.5 inches of rain had fallen, leaf water potentials were measured again during a 24 hour period. With the assumptions that only water limited leaf enlargement and only water and light limited photosynthesis, leaf enlargement and photosynthesis could be simulated. Since the nutrient status of the crops was high and air temperatures were highly favorable for growth and photosynthesis, these were probably reasonable assumptions. Also the plants used in the laboratory were almost identical in size and degree of development to the plants in the field.

Figure 6A shows that leaf water potentials varied diurnally in corn, as expected. The major difference between the measurements before and after the rain was the length of time the plants spent at high water potentials at night. During the drought, the plants spent only an hour or so at leaf water potentials of -1 to -2 bars. After the rain, the same plants remained at -1 to -2 bars for 13 hours. Since leaf growth occurs only at these high water potentials (3,6 and Fig. 5), the length of time for leaf growth was much shorter during the drought than after the rain. Over the 24 hour period, the simulated leaf growth was 2.2 times more rapid after the rain than before the rain (Fig. 6A). The observed height growth of the crop also increased 2.2 fold after the rain. Photosynthesis per unit leaf area was only 0.3 more rapid after the rain than before the rain (Fig. 6A). Thus, leaf growth and height growth were affected similarly and were clearly more affected than photosynthesis by this moderate drought in corn. The story was much the same for soybean (Fig. 6B).

This simulation suggests that if leaf and height growth

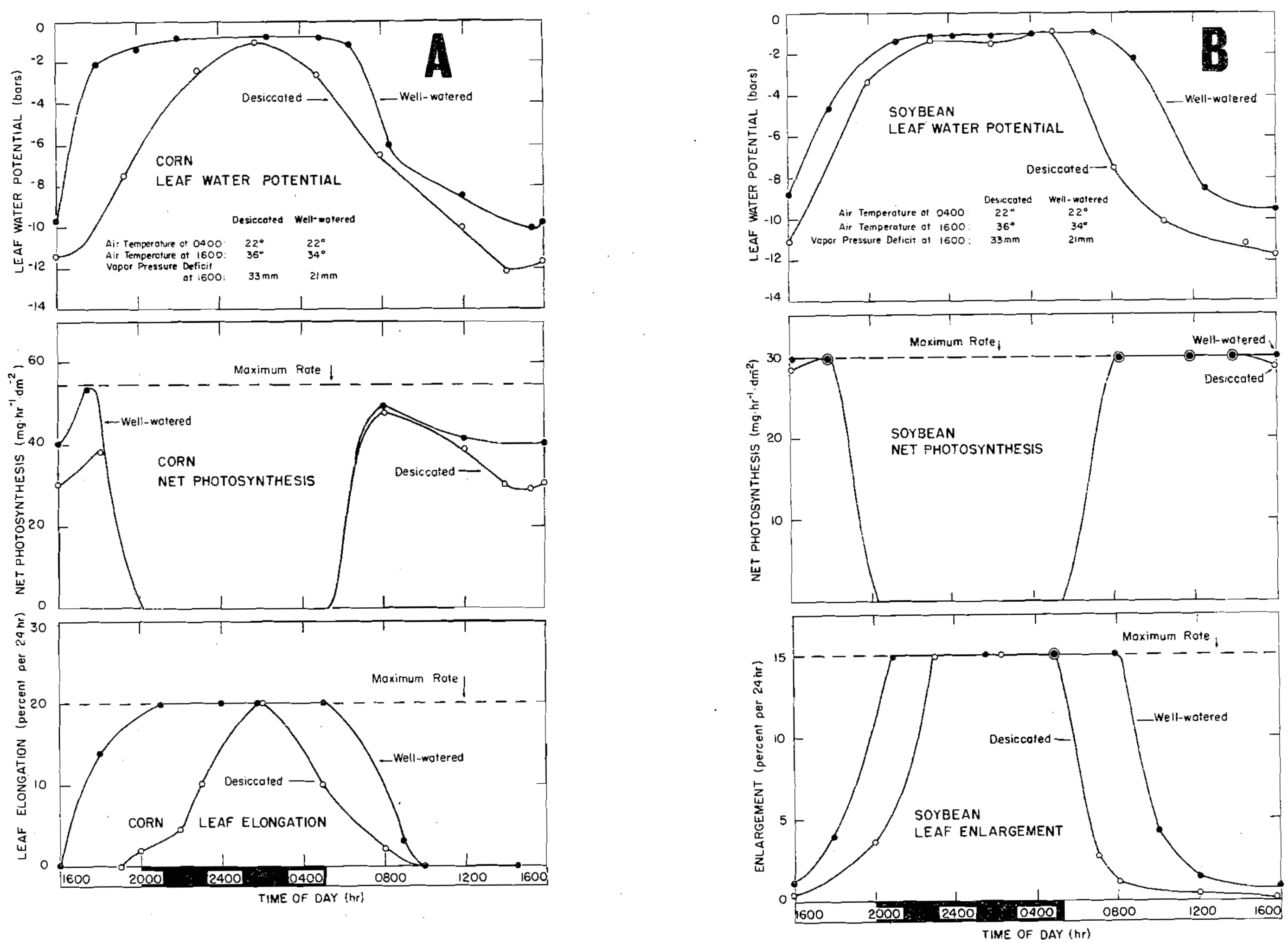

Fig. 6. Leaf water potentials and simulated values for photosynthesis and leaf enlargement in corn (A) and soybean (B) in a 24-hour period during a drought and after a 3.5 inch rainfall in the same field. The simulation was conducted by using the functional dependence of photosynthesis and leaf enlargement on leaf water potential shown in figure 5. Leaf water potentials were measured in the field with the pressure chamber described in this report.

can be maintained, photosynthesis will be occurring at rates close to the maximum as well. The data of Figs. 6A and 6B show that growth could have been maintained if irrigation had been scheduled according to the pressure chamber at exactly sundown in previously illuminated leaves and/or in the illuminated leaves 2 hours after sunup. Water added to soybean and corn whenever leaf water potentials were -2 bars or lower (the pressure readings were 30 psi or higher) at these times would have just maintained maximum leaf growth, photosynthesis, and dark respiration.

Thus, for vegetative growth of soybean and corn, a farmer could plan irrigation by making pressure readings in his crops every few days at these specific times. Irrigation could be conducted until pressure fell below 30 psi and then terminated. In this way, the vegetative development of the crop would be kept continuously high, whereas only a minimum of water would need to be applied.

For the reasons mentioned earlier (Section II, 2), however, this approach probably would not have worked after reproductive growth started.

V. WATER TRANSPORT IN PLANTS

As part of a continuing study of the physical characteristics of water movement in plants, equations were worked out from which the resistance to water movement in plants and plant parts could be obtained. The equations are based on the changes in leaf water potential which occur as a leaf recovers from a water deficiency. The higher the resistance of the pathway to the leaf, the longer it takes the leaf to recover.

This work was the first to demonstrate (9) that there are differences between species with regard to the resistance to water transport in the plant. Soybean appears to have a higher resistance than sunflower, garden bean, or corn when growing vegetatively in soil in pots. The high resistance of soybean is associated with the roots.

The high root resistance in soybean brings about lower leaf water potentials during the day than would occur if resistance were less. There was some indication that there may be differences in varieties in this regard as well.

The root resistance of soybean becomes less when the tissue is infected with the beneficial fungus, Endogone, which makes the root mycorrhizal (16). The beneficial effect of this association is apparently due to an improved nutrient status of the roots as a result of the presence of the fungus, and not due to a direct physical modification of the root by the fungus itself (17).

The plant resistance to water transport is highly important because it ultimately affects the water potential of the leaves in a given environment. The possibility that there may be varietal differences in root resistances and that root resistances might be modified by cultural practices (such as inoculation with Endogone) suggests that further research in this area could be worthwhile.

VI. RESPONSE OF CHLOROPLASTS TO DROUGHT

Studies of photosynthetic metabolism during drought have formed an important part of this work because they may provide a basic understanding of how drought inhibits yield. It is hoped that knowledge of this process might suggest means of avoiding drought effects on crops. Should drought effects be avoidable, the procedures might prove less expensive than irrigation and result in conservation of our water supply.

A number of papers have been published in this area from the laboratory of the principal investigator (5,6,7,8, 10). Consequently, only an overview will be given here.

The rate of photosynthesis is markedly inhibited by plant desiccation (5,6,10 and Fig. 5). The degree of inhibition varies with the species, some species having a range of desiccation which does not affect photosynthesis (soybean) and others being affected by even the slightest desiccation (corn). There are also differences in the extent of desiccation which plants can withstand without tissue death. Soybean will recover completely from leaf water potentials of -41 bars whereas corn begins to show leaf necrosis at leaf water potentials of -18 to -20 bars (5).

Although some of the differences in photosynthetic sensitivity appear to be attributable to stomatal differences (5), this is not always true. Corn appears to be more sensitive photosynthetically than soybean because the stomata close, but sunflower photosynthesis appears to be limited more by the activity of the chloroplasts than by the stomata (7,10). In sunflower, the stomata close, clearly conserving water for the plant (7), but chloroplasts lose activity to a somewhat greater extent, which ultimately limits photosynthesis (10).

Data thus far indicate that the reduction in chloroplast activity in sunflower is apparently due to decreased activity in the "light" reactions of photosynthesis. Oxygen evolution, photosystem II and photosystem I electron transport are all inhibited when the chloroplasts are isolated from desiccated leaves. Ultimately 50 - 80% of activity is lost, but the rest remains as a stable residual activity even in very dry tissue. Cyclic and noncyclic photophosphorylation are inhibited almost totally in these chloroplasts.

The inhibition of chloroplast electron transport can be seen in the intact leaf by measuring leaf photochemical activity (7,10) and is quantitatively predicted by the chloroplast assays (7). The degree of chloroplast inhibition is greater in older plants than in young plants. Inhibition can be reversed by rehydrating the tissue (8) but we have not succeeded in reversing inhibition once the chloroplasts have been isolated. Recovery of the chloroplasts in the tissue appears to be faster in younger tissue than in older tissue, and may be on the order of several minutes after rehydration. Older tissue, however, may never completely regain the photochemical activity of the controls.

Experiments have shown that the free energy changes which occur in the water of the leaf during drought are not responsible for the changes in chloroplast activity which are observed. Rather, chloroplast behavior is correlated more with the concentration of protoplasmic solutes, as though some inhibitory factor were present in the protoplasm and became more concentrated as water was lost by the cells.

The latter correlation suggests the possibility that a solute may interact with chloroplasts directly during drought. We have tested abscisic acid and ribonuclease for possible inhibitory effects on chloroplasts but find none, even though these substances are known to increase in cells as they desiccate.

Further work is needed to clarify possible solute-chloroplast interactions and to determine whether these interactions, if present, can be controlled by cultural practices. Since recovery occurs at the chloroplast level upon irrigation of sunflower (8), it appears that irrigation is a cultural practice which remains beneficial at the chloroplast level. Apparently, only that tissue which has been severely desiccated or is old will be irreversibly affected by drought. The stomata, however, do not recover fully in leaves which have been exposed to a period of severe desiccation (8) and consequently, when the stomata limit photosynthesis, it is probable that rates of photosynthesis will remain below those of plants which have been regularly irrigated.

VII. DISCUSSION AND SIGNIFICANCE OF RESULTS

This work has resulted in a number of accomplishments which are of importance for the effective use of water resources in the U.S. First, a pressure chamber has been developed to quantify the need for irrigation in corn and soybean crops. The instrument can be readily used by individual farmers and water resource planners. Although the technique was tested with corn and soybean, the instrument should be easily used with other crops, such as wheat, cotton, cucumbers, etc. The pressure chamber may be filled with compressed air at automotive service stations, since the required pressures are low, and the instrument will withstand rough treatment. No special skills are required for its use.

Studies with the pressure chamber in corn and soybean showed that a large inhibition of crop growth occurs before visible signs of wilting are apparent. Since rapid growth usually results in the highest efficiency of water use, it is highly important to have a method such as the pressure chamber technique which can tell the farmer or planner the moisture status of crops at any time. With an appropriate knowledge of crop moisture status, the water needs of a farm or region could be quantified. Because agriculture is such a large consumptive user of water, savings derived from such water planning could have considerable impact on national water resources.

A second accomplishment of the work was the establishment of specific recommendations for irrigation based on the use of the pressure chamber. In both corn and soybean crops, irrigation was needed whenever pressure readings were above 30 psi at sundown or 2 hours after sunup in leaves that would normally be exposed to full sunlight. When pressures exceeded this value, leaf and stem growth were inhibited, photosynthesis was often reduced, and dark respiration was ultimately affected.

The work also demonstrated that the labor involved in establishing the irrigation need of a particular field is low with the pressure chamber, since measurements are needed only every few days, and only a few samples need to be taken in fields which are reasonably uniform. The pressure chamber is of inexpensive design ($150-250) and should be within the price range of farmers and water resource planners. In all probability, the price would be recouped after avoiding only 1 or 2 unneeded irrigations.

The metabolic studies which were conducted during this period provided considerable information of value for water resource planning. Studies of photosynthesis during drought and immediately after irrigation showed that there are certain desiccation threshholds which, when exceeded, result in incomplete recovery of the crop. In sunflower, leaf water potentials remained abnormally low and stomata remained somewhat closed for days after irrigation. This work suggests that irrigation after severe drought is far less effective than irrigation after moderate drought.

As a part of this metabolic work, chloroplast studies suggested that metabolic changes due to drought may be associated with solute chloroplast interactions rather than water-chloroplast interactions. If this is true, it may make possible the avoidance of some drought effects by cultural means other than irrigation. This area needs considerably more investigation.

Finally, work with liquid water transport in plants illustrated that there are differences in resistance to flow between species. Furthermore, resistance was affected by the development of mycorrhizal roots and by the nutrient status of the plant. Both of these factors could be incorporated into current cultural practices. The differences between species also raise the possibility of differences between varieties which could then be selected for. Since the resistance to flow has a large effect on the water potential of plant leaves in a given environment, the development of plants with a low resistance to water flow could result in the greater tolerance of a crop for dry conditions and consequently a reduced need for irrigation.

One of the major thoughts which guided this work was that intensive study of the behavior of corn and soybean during drought might suggest some principles of irrigation planning which would be based on the fundamental biology of crops. Thus, these principles might find application beyond corn and soybean. Several findings appear to be in this category. First, leaf enlargement is highly sensitive to desiccation. Second, leaf enlargement responds early enough during desiccation that photosynthetic activity is unlikely to limit growth by enlargement. Third, vegetative development may be maximized by basing irrigation on leaf enlargement. Fourth, certain times during the day appear important because of their high resolution of irrigation need. These times appear to be sundown and 2 hours after sunup, when the transition occurs from night-type to day-type evaporative conditions.

Since corn, soybean, and sunflower followed the above generalities, it appears possible that they may be applied to other crops as well. Although it is still too early to be certain, these guidelines may ultimately be shown to be general enough to be used for other crops without testing each individual crop. But apart from this possibility, the principles which emerged from this work hopefully can provide insight to guide future efforts for developing guidelines with other crops and for optimizing vegetative crop development with low water use.

Despite the data for decision making which the pressure chamber can provide for the individual farmer, two areas remain inadequately explored. The first involves the water strategy a farmer should adopt during a growing season. During vegetative development, corn and soybean often recover from short periods of moderate drought and ultimately give high yields. A good example of this situation occurred in the 1971 growing season described in the present report. Although the reduced crop development during drought increases water use per unit of yield, the farmer might be ahead economically by not irrigating at all. However, for drought which is prolonged and severe, recovery of vigor during vegetative development often does not occur and irrigation would be highly advantageous. Also, for intensive agriculture with limited water, irrigation during even minor drought would probably be worthwhile, since the growing season would be shortened and yield per unit water would be kept high. The cut-off for adopting one strategy versus the other is virtually unknown at this point. Furthermore, the decisions probably would be different for individual cropping requirements.

The second area involves the reproductive development of the crop. The reproductive phase of growth often represents the production of marketable yield but, in the present work, the requirements for maintaining vegetative growth by irrigation could not be applied to reproductive growth. Flowering and fruit fill are the most drought-sensitive aspects of crop development and adequate water is crucial during these periods. Since the economics of agricultural water resource planning will play a large part in the adoption of any advanced methodology, it will be important in the future to develop a quantitative means of assessing irrigation need during the reproductive growth of crops.

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