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RELATIONSHIP TO CROP METABOLISM AND WATER STATUS TO IRRIGATION NEED

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ABSTRACT

RELATIONSHIP OF CROP METABOLISM AND WATER STATUS TO IRRIGATION NEED

Irrigation represents the largest segment of consumptive water use in the U.S. Consequently, improvements in the efficiency of irrigation can have an important effect on the amount of water available for other uses. This research was initiated to determine the physiological limitations to crop yield during drought. The identification of these parameters may provide a way of estimating plant need for irrigation and avoiding unnecessary applications of water.

Maize was grown to maturity, and photosynthesis and translocation of photosynthates were studied when drought occurred during grain development. Both carbon-14 labeling of the photosynthetic products and dry weight determinations indicated that net photosynthesis was substantially reduced whereas translocation was relatively rapid during drought. Furthermore, grain production occurred in proportion to the cumulative photosynthesis for the season. It was concluded that photosynthesis was more limiting than translocation to grain fill under dry conditions and that photosynthetic behavior could be used to reflect the need of maize crops for water.

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PROJECT OBJECTIVES

Agriculture currently consumes more water than the rest of society combined. As world needs for food become larger, it is likely that irrigation and water use planning will become increasingly important for obtaining maximum yields. At the same time, the availability of high quality water will diminish and its energy cost will increase. It is therefore necessary to develop criteria which will optimize the use of water by crops but will leave as much as possible for other uses.

This research was done to help provide criteria that will permit the prediction of the effect of a particular crop water status on the ultimate yield of the crop. Corn was used as the experimental crop because of its relatively high requirement for water and its high cost of production, which makes optimization of irrigation essential.

Specific objectives were:

1. To determine whether changes in rates of photosynthesis or translocation represent key physiological changes controlling yield during drought in the grain-filling stage of crop development.
2. To begin developing yield-physiological factor-water status relationships that may be useful to water planners and agriculturists.

SUMMARY OF ACCOMPLISHMENTS

Both a field experiment and a soil container experiment were conducted with maize growing outdoors. Because of weather problems consisting of spring flooding and an early frost, the field experiment had to be terminated. Consequently, all the data reported below refer to maize plants growing outdoors in large containers of soil.

Methods and Materials

DeKalb XL45 plants were grown in pots containing approximately 17 Kg of dry soil. The hybrid was planted on May 23, emerged on May 29 and pollinated on August 2. To assure the development of a good ear, the plants were fertilized and watered regularly through the pollination stage. At 10 days after pollination three replications of two treatments were imposed for the remainder of the growth cycle: 1) control plants (leaf water potential of -3 to -14 bars) and 2) water deficient plants (leaf water potential of -17 to -20 bars). The water deficient plants were maintained at near constant water potentials by adding 100 ml of water to the pots on days of high evaporative demand.

To observe photosynthesis and translocation, two types of analysis were utilized: 1) whole plant and plant segment dry weights were measured 10, 17, 18, 24, 32, 40, and 51 days after pollination and 2) a single leaf was exposed to radioactive carbon dioxide ($^{14}CO_2$) on the seventh day after initiation of drought. The exposure consisted of injecting lactic acid into a solution of $Na^{14}CO_3$ (activity of 11.1×10^7 dpm) inside a Plexiglas chamber containing the tipward 30.5 cm of the second leaf for 10 minutes. Exposures were conducted at ± 2 hours of solar noon, and plants were harvested and divided into different parts at 1, 4 and 24 hours after the initiation of labeling.

All plant material was dried to a constant weight at 70°C, and tissue for radioactive analysis was ground in a Wiley mill. A 100 mg sample of radioactive tissue was oxidized in a Packard Tri-Carb Sample Oxidizer and counted on a liquid scintillation counter.

Results

Total plant dry weight (net photosynthesis) and the percent of plant dry weight in the grain (translocation of assimilate to the kernels) increased after pollination (Figure 1). An analysis of variance indicated that net photosynthesis was ultimately reduced (to near zero) by moisture deficiency whereas the percentage of dry weight translocated to the grain was not significantly affected. Net photosynthesis was sharply inhibited on the fourteenth day after water was withheld from the soil (Fig. 1). Translocation was identical for the two treatments until the final week (41-51 days after flowering), but even then the differences were not statistically significant (Fig. 1).

An analysis of the carbon-14 data indicated that $^{14}CO_2$ absorption by the second leaf above the ear on the water deficient plants was reduced to 35% of the $^{14}CO_2$ absorption by the well watered plants. Thus, under the conditions of this experiment both the dry weight and $^{14}CO_2$ data support the conclusion that photosynthesis was being reduced by the stress treatment.

Tissue harvested 1 hour after labeling indicates that the rate of translocation out of the exposed leaf of the water deficient plants was initially slower than that from well watered plants (Table 1). However, the percent ^{14}C in the grain after 24 hours was similar for the two treatments. Therefore, it appears that the ultimate translocation of photosynthate to the grain was not appreciably affected by drought in comparison to the production of assimilates on day 7 of the stress period.

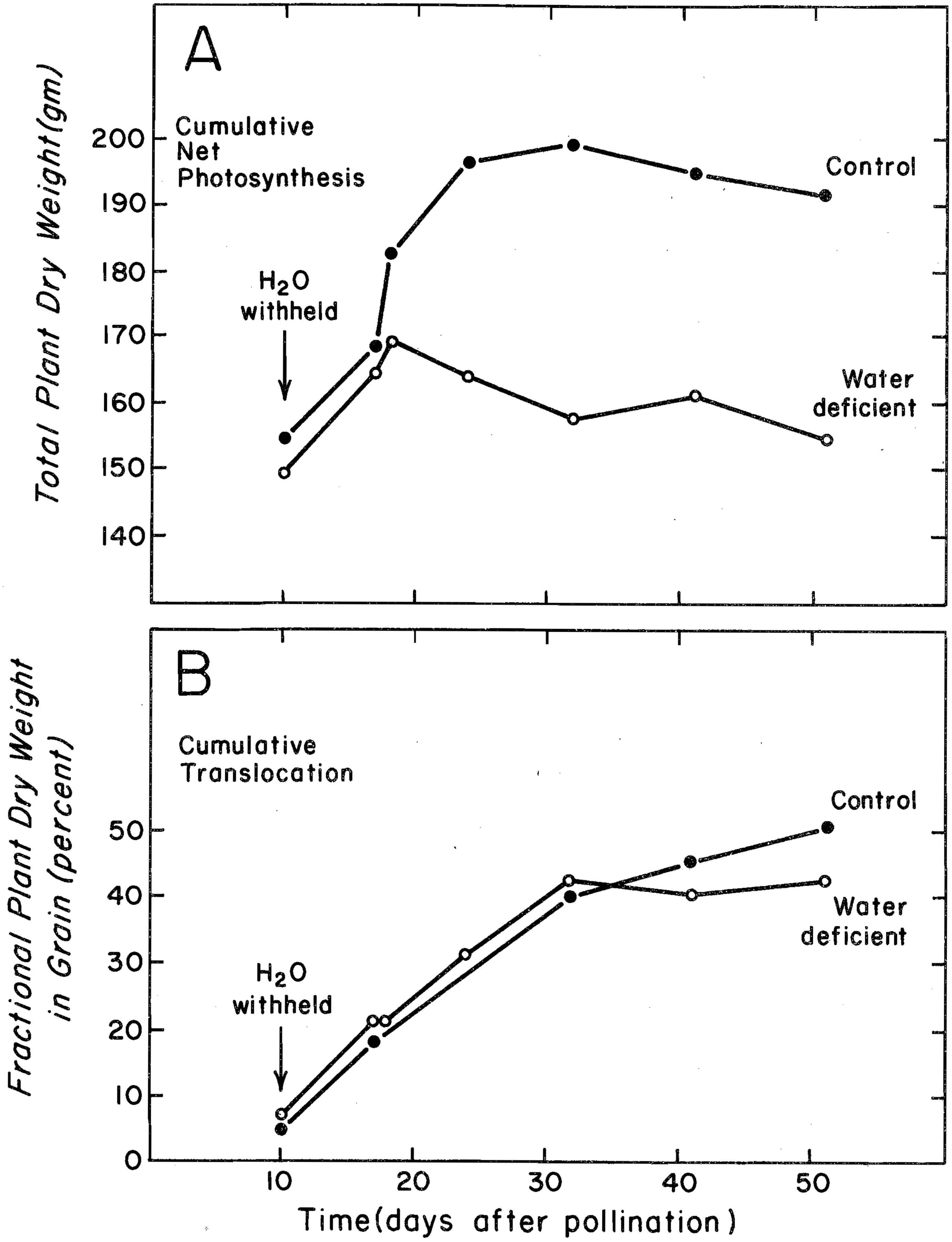

Figure 1. Cumulative net photosynthesis (A) and the translocation of photosynthate to the grain (B) during drought in maize when grain is developing.

Table 1. The distribution of ^{14}C in control and water deficient plants at different times after the initiation of labeling.

	% of total ^{14}C in plant parts					
	1 hour harvest		4 hour harvest		24 hour harvest	
	Control	Deficient	Control	Deficient	Control	Deficient
Upper plant tissue	1.6	0.3	5.2	3.6	2.2	1.3
Exposed leaf	61.7	90.1	52.6	62.2	11.6	24.0
Remainder of exposed leaf & sheath	19.1	7.4	23.2	5.2	3.3	3.7
Ear stalk segment	10.0	1.5	4.6	4.6	4.0	1.1
Grain	1.4	0.2	23.1	11.7	51.0	46.0
Cob	0.5	0.1	10.2	4.5	11.4	11.0
Husk	1.2	0.1	6.4	1.9	6.7	3.5
Lower plant tissue	1.5	0.2	6.4	4.8	5.8	4.5
Root	0.1	0.0	4.5	1.5	4.3	3.0

Movement of the fixed carbon-14 was statistically analyzed by utilizing the percent of: 1) ^{14}C activity remaining in the exposed leaf and 2) ^{14}C activity in the grain. The analysis of variance for percent ^{14}C remaining in the exposed leaf indicated that water deficiency did not significantly reduce the movement of photosynthate out of the leaf. Also, the analysis of percent ^{14}C in the grain indicates that water deficiency did not significantly reduce the cumulative flow of photosynthetic assimilates into the grain.

The leaf water potentials of the ^{14}C labeled control and water deficient plants at harvest time are shown in Figure 2. The water potentials of the stress plants were significantly lower than those of control plants.

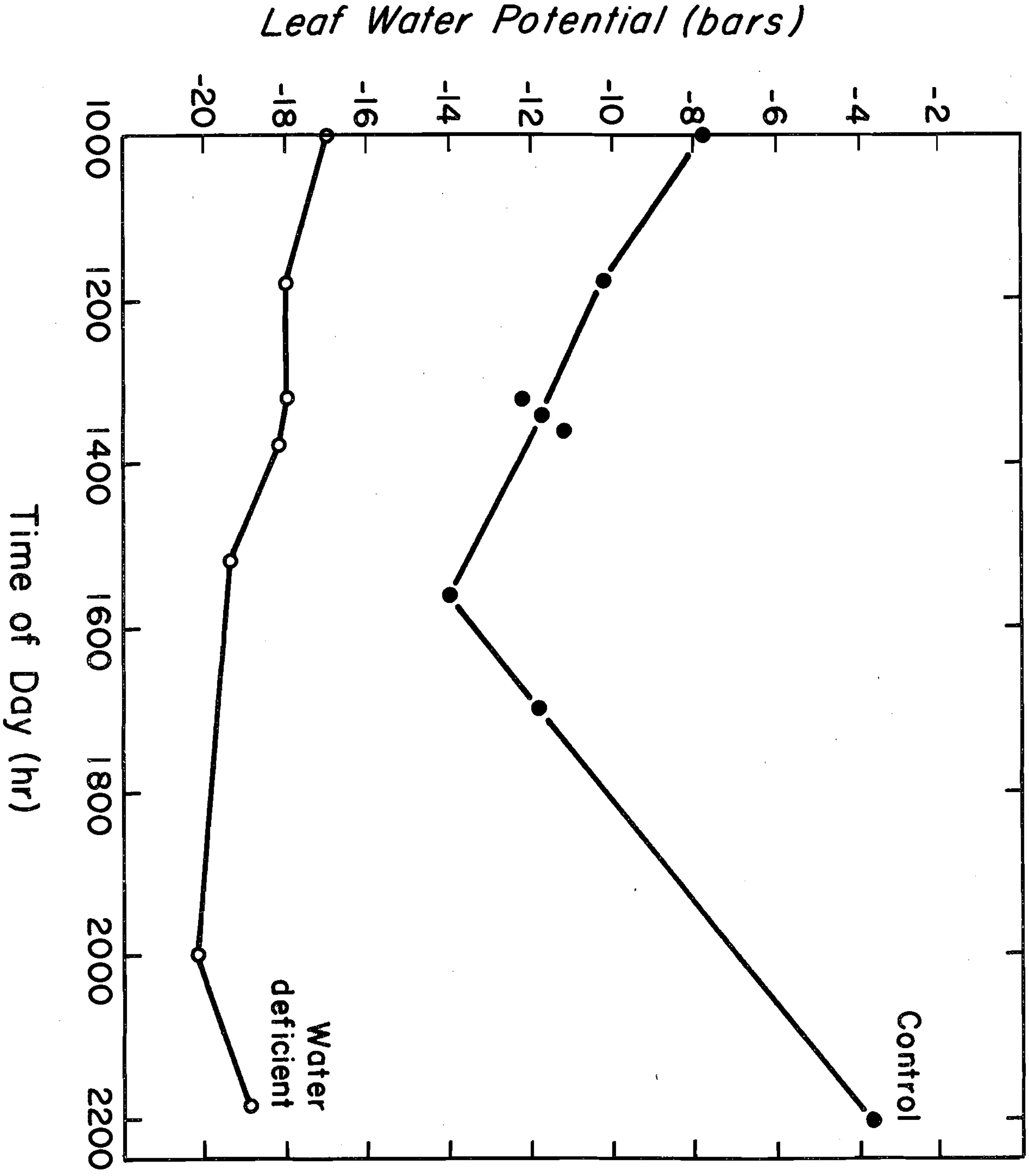

Figure 2. Leaf water potentials during day 7 after the imposition of drought for the plants used in Fig. 1.

Both dry weight data and the carbon-14 data indicate that during early grain fill, well watered plants were utilizing photosynthetic material for both grain fill and the maintenance of plant growth, while the water deficient plants were transporting most of their assimilates to the grain. The water deficient plants then lost their ability to maintain a favorable photosynthetic rate which resulted in little, if any, production of photosynthate for the grain during the last few weeks of grain fill. We can conclude that drought during grain fill was more detrimental to photosynthesis than to translocation.

DISCUSSION

The production of grain yield in crops has been the subject of much study (6). It is clearly affected by the amount of leaf area, the photosynthetic activity of the leaves, the rate of translocation to the grain, source-sink relationships, respiration, hormonal balance and perhaps other unknown factors. These exert major influences at different times during the development of crops, and consequently their relationship to yield is complex.

This research investigates the importance of photosynthesis and translocation to yield during drought because of their central role in grain production. Photosynthesis accounts for most of the dry weight of the plant and translocation is responsible for transporting much of that dry matter to the grain (as much as 50% of the total in maize). During grain fill, leaf development has largely ceased in maize and respiration is only a small fraction of the total carbon exchange of plants.

There is disagreement concerning the involvement of photosynthesis and translocation in the yield reduction caused by drought. Large reductions in photosynthesis occur (3) but their role in reducing grain fill has been unstudied. Translocation is also reduced (2,4,5), but opinions differ as to the cause, which has been attributed to a direct inhibition of the process (2) or a lack of photosynthate available for transport (5).

The present data indicate that photosynthesis is more inhibited than translocation during drought. Two conclusions therefore seem warranted. First, photosynthesis is likely to be more limiting than translocation to grain development. Since leaf growth had ceased by this stage of development and since respiration is considerably less sensitive than photosynthesis to moisture deficiency, photosynthesis is probably the primary limiting process to grain yield in maize subjected to drought.

The second conclusion is that translocation, which proceeded rapidly in spite of near zero photosynthesis, probably transported photosynthetic material laid down prior to the drought. In that way, grain fill continued in spite of a decline in photosynthesis. Since the percentage of photosynthetic material transported to the grain remained virtually the same for both types of plants, translocation was apparently controlled by the total photosynthate accumulated during the growing season. This probably explains why the total photosynthesis during the growing season controlled yield.

It should be pointed out, however, that the well watered plants produced only moderate grain yields in this experiment (perhaps only 2/3 of those expected for field crops). The low yield was probably caused by some factor that adversely affected growth in the soil containers, and it reduced the effects of drought on photosynthesis and translocation. However, had the yield of the well watered plants been higher, the relative response of photosynthesis and translocation would probably have been the same and our conclusions would have remained unaltered.

SIGNIFICANCE OF RESULTS

If photosynthesis represents the rate limiting factor for grain production during drought in maize, then the prediction of the effects of drought on the ultimate yield of crops becomes vastly simplified. In maize, this finding suggests that a knowledge of the integrated (whole season) photosynthetic performance of the crop could predict yield. Since it is possible to measure the water status of crops and since the response of photosynthesis to crop water status is becoming known (for maize, see 1), it should be possible to determine the number of moisture-deficit-days a crop has experienced and calculate the depression in yield.

From this type of prediction, the requirement for irrigation could be quantified for individual fields. A farmer or water resource planner would need to set relative yield limits below which irrigation would be used (for example: irrigation might be applied whenever the number of accumulated moisture-deficit-days depressed relative crop yield below 90% of that for a well watered crop).

The assignment of the yield depression that could be tolerated before irrigation would depend on the cost of irrigation, the availability of water, the economic benefit to the farmer, and the competition for alternate uses of the same water. Consequently, the ultimate use of this approach will be subject to many problems in addition to crop need. However, water conservation in irrigated agriculture cannot proceed with any degree of predictibility unless crop need is known and many of the problems of alternate uses of water and cost-benefit considerations could be accomodated by the approach suggested above.

Although this research indicates that much of the effect of drought on the grain yield of a crop can be predicted from its effects on photosynthesis, there are certain aspects of crop development and agricultural practice that cannot be accomodated by this idea. First, drought that occurs during floral development and flowering can cause reductions in the number of seeds set by the plant in spite of a high availability of photosynthate during the rest of the growth cycle. Investigations of drought effects on the flowering process should therefore be worthwhile. Second, drought often causes secondary effects which result in reductions in yield quite apart from photosynthetic phenomena. Lack of moisture may cause stem weakening and lodging of the crop. Drought also increases the susceptibility of many crops to certain pathogens. Thus, the yield reduction experienced by the farmer may be larger than predicted from the photosynthetic behavior of the crop alone.

These additional problems underscore the need for well-formulated field experiments to supplement the work reported here. With funds from the University of Illinois, we are presently conducting a field experiment based on the present findings. In addition, investigations of the physiological mechanisms of drought response are being conducted in the laboratory with funds from the National Science Foundation. From the field work, we expect the yield reduction to be determined by the loss of photosynthesis plus an additional increment resulting from in-direct effects of drought. Thus, the yield reduction from photosynthesis should represent the minimum to be expected by the farmer. In the laboratory, we will study the cellular mechanisms responsible for the decrease in photosynthesis.

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LITERATURE CITED

1. Boyer, J.S. 1972. Relationship of plant moisture status to irrigation need in corn and soybean crops. Research Report No. 60, University of Illinois Water Resources Center, 2535 Hydrosystems Laboratory, Urbana, Illinois 61801. 35 p.
2. Brevedan, E. R. and H. F. Hodges. 1973. Effects of moisture deficits on ^{14}C translocation in corn (*Zea mays* L.). Plant Physiol. 52: 436-439.
3. Hsiao, T. C. 1973. Metabolic effects of water stress. Ann. Rev. Plant Physiol. 24: 519-570.
4. Roberts, B. R. 1964. Effects of water stress on the translocation of photosynthetically assimilated carbon-14 in yellow poplar. In, "The Formation of Wood in Forest Trees" Pp. 273-288. M. H. Zimmermann, ed., Academic Press, New York.
5. Wardlaw, I. J. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. Austral. J. Biol. Sci. 20: 25-39.
6. Yoshida, S. 1972. Physiological aspects of grain yield. Ann. Rev. Plant Physiol. 23: 437-464.