Response of Metabolism to Low Water Potentials in Plants

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Of the environmental factors which affect crop yield, drought is one of the most frequent and devastating. Although large areas of the world are affected by drought, water for irrigation is increasingly in short supply. Of the water on the earth's surface, 99% is unsuitable for agriculture because it is either frozen or too salty (30). The remaining 1% continues to dwindle because of pollution and the accelerating demands for water by an increasing population. In the USA, for example, the use of water is expected to quadruple in the next 50 years (17). Agriculture currently consumes more water than do all the other users of water combined (30), and is projected to increase its requirements in the future. Yet, the economic product generated from agricultural consumption of water is small, and may be as little as 1/50 of that produced by industrial and municipal users of the same water (30). As a result, in the face of dwindling supplies, the requirements of agriculture for water are growing but are becoming less justifiable on an economic basis.

In this situation, agriculture can remain productive only if it uses water efficiently. Ideally, high efficiency involves the use of a minimum amount of water to maintain vigorous crop growth. Nevertheless, a number of factors make this ideal difficult to attain. There are often large differences in soil characteristics and seasonal and daily variations in rainfall. Consequently, the exact water status of a particular crop is hard to evaluate. Also, the distribution of water to a crop often involves a large water loss and is hindered by the cost of equipment and labor. Nevertheless, since distribution is largely an engineering problem, it is amenable to a number of available approaches. The water status of crops, on the other hand, is far more complex and is little understood.

Probably the most promising approach to the evaluation of crop water status would be to determine the water status of the plants directly during the growing season, interpret the moisture status in terms of the physiological behavior of the crop, and add water only when a yield-inhibiting water status is reached. In this way, the water supply could be adjusted to suit changing conditions. Furthermore, it would be possible to measure when enough water had been added to return the water status of the crop to a favorable level and to determine the additional amounts required to provide soil reserves. Other approaches have been suggested

which generally have been based on changes in soil moisture or meteorological conditions. Direct determination of the water status of the crop should be preferable, however, because it represents the moisture available at the site of growth itself and integrates the effects of soil and climate on the crop.

During the last few years, considerable progress has been made toward developing methods for measuring crop water status. This effort received impetus from the suggestions of Slayter & Taylor (35), who used thermodynamics to describe the energy (in this case, the Gibbs free energy) of water in soils and plants. These workers (35) used the term water potential (ψ_w) for this energy and suggested that it be expressed in units of bars (1 bar = 0.987 atm). The water potentials of plants and soils are usually negative, drier conditions being represented by more negative values. Since energy measurements are uniform regardless of the soil or plant system and are expressed on a thermodynamic basis, they are attractive for describing crop water status because they are quantitative and of general applicability. Water movement in soils and plants is determined by gradients in the free energy of water, and consequently, ψ_w also has the advantage of being directly related to the driving force for water movement. Many of the newer methods are designed to measure this property of plant tissue.

There are two recently developed techniques for measuring ψ_w which are receiving particularly wide usage. The first involves a pressure chamber (4, 33) that can be used in the field and provides measurements of ψ_w in 5 to 10 min in a number of crops. Determinations require single leaves which are removed from the plant and rapidly sealed in the pressure chamber. As the pressure increases, the sap ultimately appears at the cut surface, which extends through a seal to the outside of the chamber. The equilibrium pressure that just returns the sap to the cut surface is approximately equal to ψ_w. The second technique uses a thermocouple psychrometer (3, 13) which is most suitable for the laboratory and provides accurate measurements of ψ_w with small segments of leaf tissue. The apparatus usually requires close control of instrument temperature and depends on calibration with solutions of known ψ_w or, in one particular design which we have found useful, employs a null technique with solutions of known ψ_w on the thermocouple (3, 7, 13). Measurements made with both the pressure chamber and the thermocouple psychrometer are in substantial agreement in most crop tissue (4, 12, 16), although they may disagree somewhat in woody tissue (4, 25). There are two recent reviews of methods for measurement of plant water status (2, 7).

With the availability of methods for evaluation of the water status of crops throughout the growing season, it has become important to understand the significance of a particular water status for crop growth and yield. There are relatively few studies of the physiological behavior of plants at low ψ_w and even fewer that explore the importance of a particular physiological change to the ultimate yield of the crop. Nevertheless, photosynthesis accounts for most of the dry weight of a crop and there is some work which shows that, in well-watered plants, varietal differences in yield can be attributed to differences in the leaf area of the crop or to differences in the photosynthetic activity of a unit of leaf area (18, 20, 28, 31). It is well known that one large effect of low leaf ψ_w is a reduction in photosynthetic activity per unit of leaf area (9, 14, 32, 40). Thus, it seems possible that at least one reason for yield reduction during drought might be a reduction in the rate of photosynthesis for the crop.

The total photosynthesis of plants is determined by both the photosynthetic activity of a unit of leaf and the total leaf area. Studies (6, 8) made of the effect of low leaf ψ_w on photosynthetic activity and leaf growth have shown that leaf growth is more sensitive than photosynthetic activity. When leaf ψ_w dropped from −2 to −4 bars, growth was inhibited by at least 75% in corn, soybean, and sunflower. Photosynthesis per unit leaf area was inhibited by only 10% in corn and unaffected in the other two species. Such a strong inhibition of leaf growth suggests that little growth occurs during the day (6), when leaf ψ_w is rarely above −4 bars even in well-watered plants. Thus, growth occurs primarily at night and appears to be dependent on the length of time the leaf remains at high ψ_w (6).

Since leaf growth was affected before photosynthesis, reductions in photosynthetic activity could not account for the reductions in growth. Dark respiration was even less sensitive than photosynthetic activity (8, 14) to low leaf ψ_w. In these particular experiments, leaf growth was largely a function of cell enlargement and inhibition most likely was due to reduced turgor, which reduces the rate of cell enlargement (6, 8, 15, 22, 23). Cell enlargement requires turgor to be above a minimum before irreversible enlargement occurs (6, 8, 15, 22, 23). Thus, the entire response from maximum to zero rates of growth occurred under conditions of at least some turgor in the leaf and there were no symptoms to reflect that water availability to the plant was affecting leaf growth (6, 8).

These effects suggest that for rapidly growing vegetative plants, one of the first effects of drought is a reduced rate of growth by enlargement. During reproductive growth, however, vegetative development is often practically complete, and it is at this stage that plant yield is most vulnerable to inhibition by desiccation. It is most likely, therefore, that leaf development is an important factor during vegetative growth but that photosynthetic activity or some other factor becomes limiting during reproductive growth.

The reduction in photosynthetic activity per unit of leaf is usually attributed (9, 14, 32, 34, 38, 40) to stomatal closure. Differences in photosynthetic response to low ψ_w have been described for different species and have been attributed to differences in stomatal behavior (9). For example, in corn, stomata appeared to shut partially whenever leaf ψ_w decreased below −3.5 bars (9). For soybean, desiccation had no effect on stomata until ψ_w

decreased to −11 bars (9). In both species, depressions in photosynthesis and closure of stomata occurred simultaneously. Thus, there is the possibility that differences in stomatal behavior exist between species. If similar differences are present within a single species, they may offer an opportunity for plant breeders.

Although stomatal closure began when a decline in photosynthesis was observed and leaf diffusive resistances initially increased enough to account for the effects of low ψ_w on photosynthesis in corn and soybean, such evidence may not indicate that photosynthesis would be limited by stomatal closure in all higher plants. This was illustrated recently in an experiment with sunflower (10). The experiment was based on the idea that if stomatal closure limits photosynthesis, it should be possible to reverse the effect by enriching the air around the plant with CO_2. However, in sunflower, increasing the external concentration of CO_2 had no effect after the plant became desiccated and the stomata closed partially (10). The diffusive resistance (r_l) of the leaf (which was largely a result of stomatal apertures) remained constant during the changes in CO_2 concentration, so that the CO_2 supply in the leaf must have increased when the supply outside the leaf increased. Consequently, some process other than stomatal closure limited photosynthesis in these plants.

The lack of limitation of photosynthesis by stomatal closure suggests a change at the chloroplast level. Measurements of leaf photochemical activity (determined at limiting light intensities) showed an inhibition of the same magnitude as that occurring under high light conditions (10). Furthermore, oxygen evolution in chloroplasts isolated from these leaves was similarly inhibited (11). Other work in our laboratory has shown that noncyclic photophosphorylation, cyclic photophosphorylation, and electron transport through photosystems I and II are reduced at ψ_w below −10 bars. These effects appear to be influenced by the age of the plant, with inhibition becoming more severe at a particular desiccation level in older plants. Other work has shown that desiccation has little effect on the chloroplast enzymes of the carboxylative, or dark, phase of photosynthesis (24). Thus, there is a general inhibition of a number of parts of the light reactions of photosynthesis, and it is most likely that photosynthesis is controlled by this inhibition rather than by stomatal closure or the dark phase of photosynthesis during drought in sunflower. Although chloroplast changes have been observed to a certain extent in species other than sunflower (21, 29), too little is currently known to determine whether they also limit photosynthesis under high light during drought.

It is always possible in work of this sort to conclude mistakenly that effects observed with isolated chloroplasts represent effects that occur in intact leaves. For example, desiccation may predispose the chloroplasts to loss of some essential cofactor during isolation, or the flaccid tissue may have yielded more of a particular type of chloroplast than did turgid tissue. However, the correspondence of leaf photochemical activity with chloroplast oxygen evolution (11) indicates that intact leaf and chloroplast behavior were similar in sunflower with regard to electron transport. Nevertheless, the results with photophosphorylation by chloroplasts remain to be demonstrated in intact tissue.

What brings about these changes in cell metabolism? Although much of electron transport and photophosphorylating activity were lost in sunflower chloroplasts at ψ_w of −17 bars, half the original water was still in the leaf. Furthermore, the mole fraction of the water had declined only from 0.99 to 0.98, and the total quantity of solute in the leaf had remained approximately constant. On a dry weight basis, the water content of the leaf under the severest desiccation levels was about 300% of the dry weight of the leaf. By contrast, seeds from the same plant would survive water contents as low as 10-15% of the dry weight of the seed.

In an effort to understand the sensitivity of leaf metabolism to desiccation, we have been conducting experiments with sunflower chloroplasts, where effects are largely associated with membrane systems (the thylakoid membranes), and with nitrate reductase, which represents a soluble cytoplasmic enzyme known to be quite sensitive to leaf desiccation (1, 24). The most attractive hypothesis was that drought might interact with metabolism because of changes in ψ_w or one of its components, which could act directly on membranes or enzyme systems and result in inhibition of certain aspects of metabolism, as suggested by Kramer (27). This might be visualized according to the ideas of Klotz (26), who suggested that changes in the free energy of water could result in changes in the aqueous environment immediately surrounding enzymes or next to membranes. Walter & Stadelmann (41) suggested a somewhat similar idea but emphasized the importance of cell hydration as measured by the osmotic potential.

The water potential of leaves of small plants is determined primarily by three types of forces:

$$\psi_w = \psi_p + \psi_s + \psi_m$$

where p, s, and m represent the effects of pressure, solute, and matric forces, respectively. Matric potentials are generally small enough to be ignored in sunflower (5). Thus, if ψ_w affected chloroplast activity, it probably acted through changes in ψ_p, ψ_s, or both.

In the chloroplast membrane system, the hypothesis of direct interaction with ψ_w was attractive because inhibition occurred so rapidly (11) after a decrease in ψ_w that it was difficult to separate the two (Fig. 1). Furthermore, chloroplasts appeared to recover rapidly when the activity of photosystem II was measured. To test whether ψ_w was involved, ψ_p and ψ_s were measured as leaves became desiccated. In sunflower leaves, ψ_p decreased dramatically as ψ_w decreased (Fig. 2). After ψ_w had decreased below −10 bars, ψ_s began to change

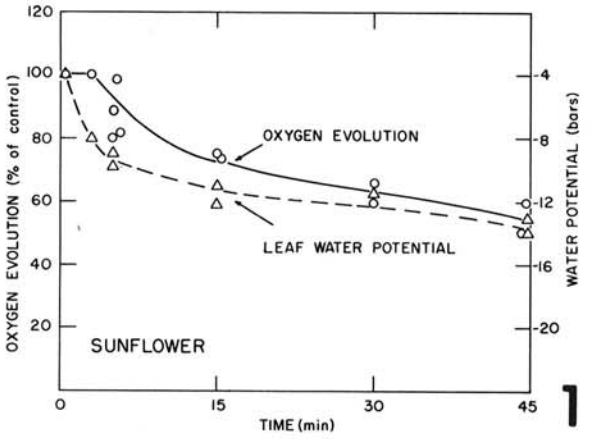

Fig. 1. Changes in oxygen evolution of sunflower chloroplasts and in the water potential of the half-leaves from which the chloroplasts were isolated as a function of time. Oxygen evolution was measured in the presence of 88 μM 2,4-dichloroindophenol as electron acceptor. Controls were chloroplasts from undesiccated leaf-halves. Control activity was 35-55 μmoles O_2 hr^{-1} mg Chl^{-1}.

appreciably. However, most of the decline in photochemical activity (and therefore in the chloroplasts) occurred at ψ_w below −10 bars, when ψ_p was zero (Fig. 2).

The data of Fig. 2 suggest that leaf photochemical activity was unaffected by ψ_p but that it was correlated with leaf ψ_s. However, if ψ_s affected chloroplast activity, it should have been possible to duplicate the effects of desiccation by exposing chloroplasts to various concentrations of osmoticum in vitro. Fig. 3 shows that chloroplasts isolated from both well-watered and desiccated leaf tissue showed little inhibition in various concentrations of sorbitol, an osmoticum routinely used in assays for chloroplast activity. There was no tendency for any similarity of activity in chloroplasts from well-watered and desiccated tissue when ψ_s of the assay medium was high (−2.4 bars) or low (−24 bars). Thus, the ψ_s associated with sorbitol solutions did not reproduce the effects of desiccation. Although sorbitol represents only one of a wide range of solutes which might have been used to control ψ_s in vitro, it should have reproduced the ψ_s occurring in vivo in sunflower leaves regardless of the solutes in the leaf. Nevertheless, since solutes could interact directly with the chloroplast system, it is probable that the sorbitol experiments did not reproduce possible solute-chloroplast interactions occurring in vivo. Thus, ψ_s may not affect chloroplasts enough to explain the effects of drought in sunflower, but the possibility for solute-chloroplast interactions remains open.

Since neither ψ_p nor ψ_s appeared to interact directly with chloroplasts, it is possible that there was some indirect response to desiccation which resulted in a change in the concentration of a substance that in turn affected chloroplast activity. One such change which has been described recently is the increase in levels of abscisic acid (ABA) shortly after leaves have been desiccated (43, 44). It seemed possible that this compound might affect chloroplast activity since applications of plant hormones to leaves can bring about changes in photosynthetic activity (42). Table 1 shows that sunflower leaves incubated in ABA for 1 or 3 hr showed no inhibition of noncyclic or cyclic photophosphorylation when chloroplasts were isolated from the leaves. Chloroplasts incubated directly in ABA also showed no response. Thus, ABA levels seemed to have little effect on chloroplast activity in sunflower.

In contrast to the chloroplast membrane system, changes in the enzyme system [nitrate reductase (NR)] did not occur rapidly when leaf ψ_w changed. Fig. 4 shows that NR activity in corn was unaffected 1.5 hr after desiccation even though leaf ψ_w had decreased to −12 to −14 bars. After 1.5 hr, NR activity declined slowly and after 24 hr it was only 15% of the original activity (Fig. 5). These results suggest that direct inactivation of NR by low ψ_w was negligible and that some other factor had changed which in turn brought about a decrease in NR activity. Such a factor might have been an increase in the rate of degradation of the enzyme or a decrease in the rate of synthesis of the enzyme as a result of leaf desiccation.

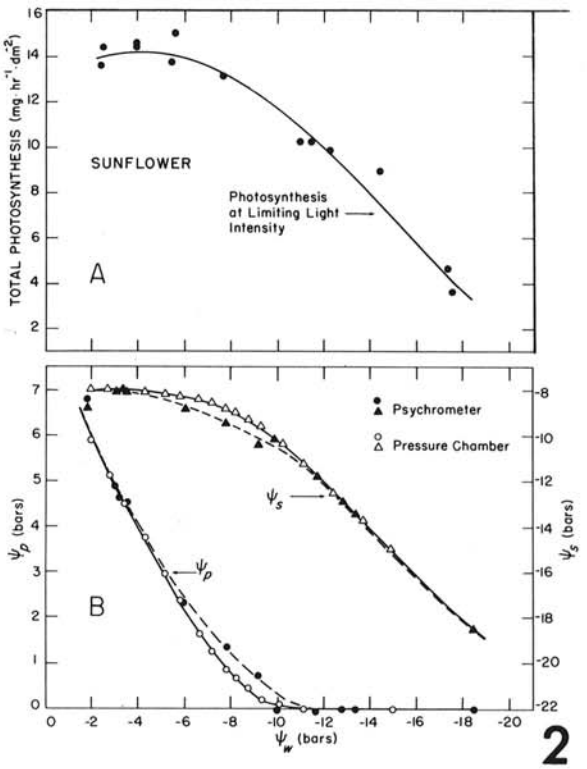

Fig. 2. A) Changes in the photochemical activity of intact leaves (measured at low light), and **B)** changes in turgor and leaf osmotic potential as a function of leaf water potential.

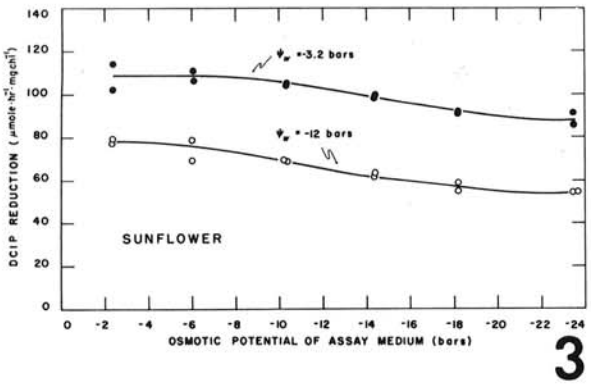

Fig. 3. Activity of sunflower chloroplasts assayed in sorbitol solutions with various osmotic potentials. Chloroplasts were isolated from a leaf-half with a water potential of −3.2 bars and from the opposite leaf-half after desiccation to a water potential of −12 bars. Activity was measured as the quantity of 44 μM 2,4-dichloroindophenol reduced in 1 min of saturating light. The osmotic potential of the leaf tissue from which the chloroplasts were isolated was −8 and −12 bars in the tissue with a water potential of −3.2 and −12 bars, respectively.

TABLE 1. Effect of abscisic acid (ABA) on cyclic and noncyclic photophosphorylation in chloroplasts isolated from well-watered sunflower leaves

Treatment[a]	% Cyclic	% Noncyclic
Chloroplasts assayed in ABA	100	100
Tissue floated in ABA 1 hr	100	88
Tissue floated in ABA 3 hr	112	110

[a] Treatments consisted of floating leaf tissue on solutions containing ABA (10^{-4} M) and sodium phosphate buffer (10 mM; pH 6.5) for 1 or 3 hr and assaying in ABA-free medium, or assaying chloroplasts in assay medium plus ABA (10^{-6} M) but without prior exposure of the tissue to ABA. Data represent averages of two replications. Control activities: cyclic phosphorylation = 1,560-2,200 μm ATP hr^{-1} mg Chl^{-1}; noncyclic photophosphorylation = 900-1,360 μm ATP hr^{-1} mg Chl^{-1}.

Figure 5 shows that the kinetics of degradation of NR in well-watered tissue exposed to an inhibitor of cytoplasmic protein synthesis, cycloheximide, were similar to the kinetics of degradation of NR in desiccated tissue without the inhibitor. Thus, the in vivo degradation of NR during desiccation was not significantly different from that in well-watered tissue. However, the percentage of polyribosomes in the tissue was reduced during desiccation (Fig. 6). This suggests that the capacity for protein synthesis was reduced during desiccation, since it is known that polyribosomes are correlated with the capacity of plant tissue to synthesize protein (19, 36, 37). Reductions in the percentage of polyribosomes always preceded the reduction in NR activity. Furthermore, rewatering the tissue brought about recovery of NR activity only in the absence of cycloheximide and only if the percentage of polyribosomes had increased.

These results suggest that extractable enzyme activity in leaves may be affected more by synthesis of new proteins during desiccation than by direct inactivation of enzyme molecules by ψ_w or by increased degradation of active enzyme. If this is true, enzymes which normally have a short half-life (such as NR) would likely be most susceptible to reduced activity during desiccation (1). On the other hand, enzymes such as ribonuclease, which are often associated with senescence, appear to be synthesized during desiccation (39) and, although the role of ribonuclease is unknown, there is the possibility that there is a shift in synthesis to different proteins at the same time there is a general reduction in protein synthesis during desiccation.

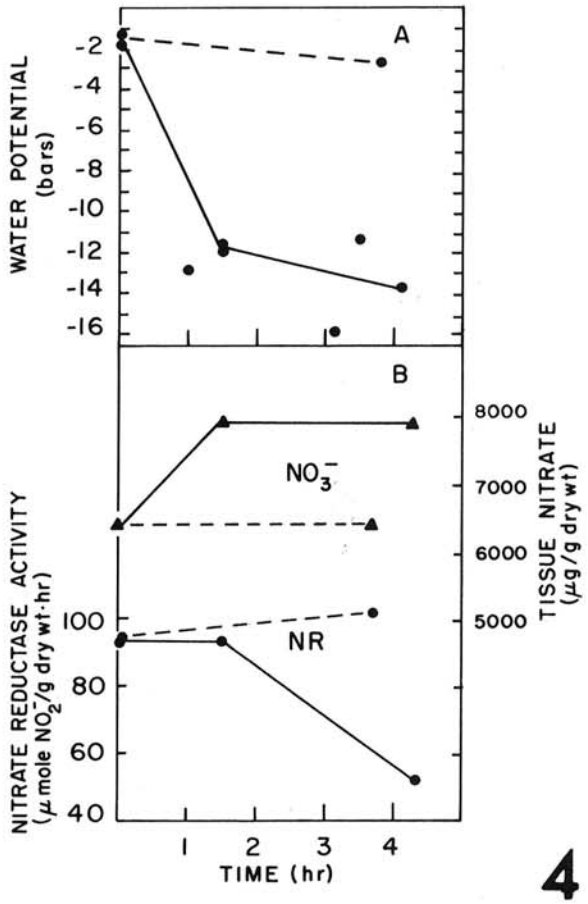

Fig. 4. A) Leaf water potential, and B) leaf nitrate content and leaf nitrate reductase (NR) activity, in corn as a function of time. Corn shoots were excised and desiccated under growth conditions (———). Controls were excised and placed in water (– – – –). The increase in nitrate in the desiccated tissue occurred as a result of translocation of nitrate from stems to leaves before assay of the leaves in the excised shoots.

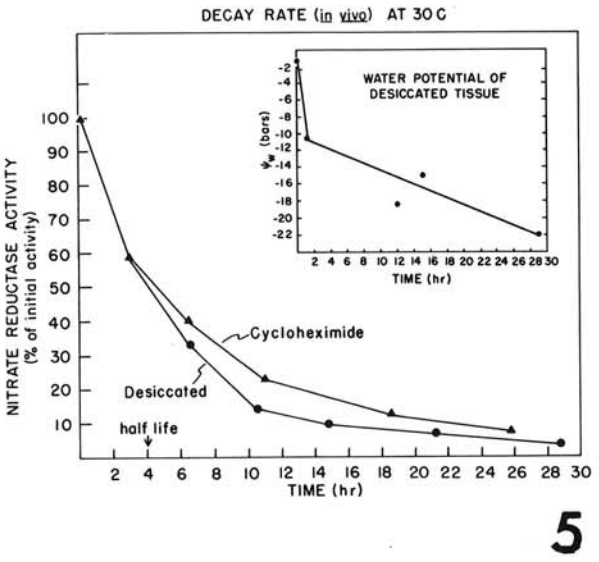

Fig. 5. Decay of nitrate reductase in well-watered corn leaves treated with cycloheximide and in desiccated corn leaves untreated with cycloheximide. The leaves treated with cycloheximide were pretreated for 3 hr. The progress of ψ_W is shown in the inset for the desiccated leaves. Initial activity was 80 μmoles NO_2^- hr^{-1} g dry $weight^{-1}$

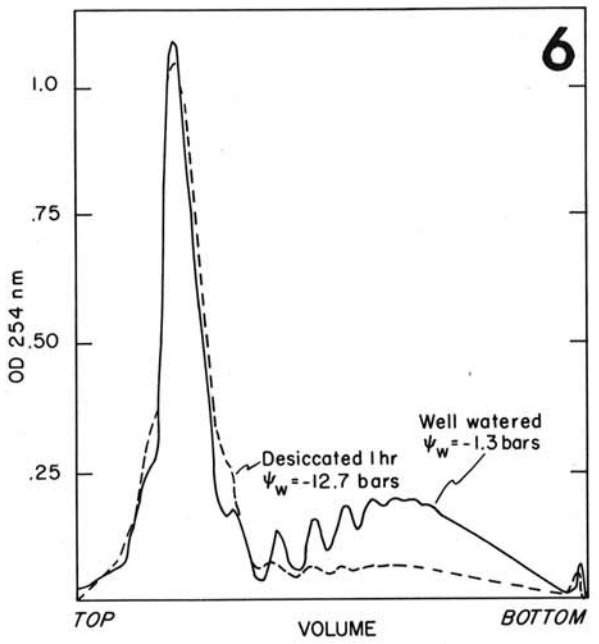

Fig. 6. Sucrose gradient profiles of ribosomes in excised leaves from 8-day-old corn seedlings. Half the leaves were desiccated for 1 hr and the other half were not desiccated. The major peak represents the monoribosomes, and all the peaks to the right of the monoribosome peak represent polyribosomes. The percentage of polyribosomes has been shown to be correlated with the rate of nitrate reductase synthesis by the tissue (36, 37). The large decline in polyribosomes after 1 hr precedes the decline in nitrate reductase activity (see Fig. 4).

Thus, in neither the chloroplast membrane system nor the cytoplasmic enzyme system do changes in ψ_W appear to be directly responsible for the response of the system to desiccation. It is much more likely that the changes are indirect results of other cellular responses to desiccation. Ultimately, of course, some system within the cell must respond relatively directly to desiccation in such a way that large portions of metabolism are affected. At this point, however, these directly sensitive portions of metabolism are unknown. Nevertheless, the above results raise the possibility that there may be only a few of them, rather than a general sensitivity of all of metabolism. An understanding of the directly sensitive parts of the living system and the mechanism of the action of desiccation on these central points is one of the most exciting areas for future work. Hopefully, the knowledge of the way in which desiccation brings about metabolic changes will ultimately suggest ways to avoid the effects of drought on crop yield.

LITERATURE CITED

1. BARDZIK, J. M., H. V. MARSH, JR., & J. R. HAVIS. 1971. Effects of water stress on the activities of three enzymes in maize seedlings. Plant Physiol. 47:828-831.
2. BARRS, H. D. 1968. Determination of water deficits in plant tissue. *In* T. T. Kozlowski [ed.]. Water deficits and plant growth, Vol. I. Academic Press, New York. 368 p.
3. BOYER, J. S. 1966. Isopiestic technique: measurement of accurate leaf water potentials. Science 154:1459-1460.
4. BOYER, J. S. 1967. Leaf water potentials measured with a pressure chamber. Plant Physiol. 42:133-137.
5. BOYER, J. S. 1967. Matric potentials of leaves. Plant Physiol. 42:213-217.
6. BOYER, J. S. 1968. Relationship of water potential to growth of leaves. Plant Physiol. 43:1056-1062.
7. BOYER, J. S. 1969. Measurement of the water status of plants. Annu. Rev. Plant Physiol. 20:351-364.
8. BOYER, J. S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at low leaf water potentials. Plant Physiol. 46:233-235.
9. BOYER, J. S. 1970. Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. Plant Physiol. 46:236-239.
10. BOYER, J. S. 1971. Nonstomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. Plant Physiol. 48:532-536.
11. BOYER, J. S., & B. L. BOWEN. 1970. Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials. Plant Physiol. 45:612-615.
12. BOYER, J. S., & S. R. GHORASHY. 1971. Rapid field measurement of leaf water potential in soybean. Agron. J. 63:344-345.
13. BOYER, J. S., & E. B. KNIPLING. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. Proc. Nat. Acad. Sci. USA 54:1044-1051.
14. BRIX, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant. 15:10-20.

15. CLELAND, R. 1959. Effect of osmotic concentration on auxin-action and on irreversible and reversible expansion of Avena coleoptile. Physiol. Plant. 12:809-825.
16. DE ROO, H. C. 1969. Leaf water potentials of sorghum and corn estimated with the pressure chamber. Agron. J. 61:969-970.
17. EIPPER, A. W. 1970. Pollution problems, resource policy, and the scientist. Science 169:11-15.
18. EL-SHARKAWY, M. A., & J. D. HESKETH. 1964. Effect of stomatal differences among species on leaf photosynthesis. Crop Sci. 4:619-621.
19. EVINS, W. H., & J. E. VARNER. 1972. Hormonal control of polyribosome formation in barley aleurone layers. Plant Physiol. 49:348-352.
20. FISCHER, R. A., & G. D. KOHN. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. Aust. J. Agr. Res. 17:281-295.
21. FRY, K. E. 1970. Some factors affecting the Hill reaction activity in cotton chloroplasts. Plant Physiol. 45:465-469.
22. GREEN, P. B. 1968. Growth physics in Nitella: A method for continuous in vivo analysis of extensibility based on a micromanometer technique for turgor pressure. Plant Physiol. 43:1169-1184.
23. GREEN, P. B., R. D. ERICKSON, & J. BUGGY. 1971. Metabolic and physical control of cell elongation rate. In vivo studies in Nitella. Plant Physiol. 47:423-430.
24. HUFFAKER, R. C., T. C. RADIN, G. E. KLEINKOPF, & E. L. COX. 1970. Effects of mild water stress on enzymes of nitrate assimilation and of the carboxylative phase of photosynthesis in barley. Crop Sci. 10:471-474.
25. KAUFMANN, M. R. 1968. Evaluation of the pressure chamber technique for estimating plant water potential of forest tree species. Forest Sci. 14:369-374.
26. KLOTZ, I. 1958. Protein hydration and behavior. Science 128:815-822.
27. KRAMER, P. J. 1969. Plant and soil water relationships. McGraw-Hill Book Co., New York. 482 p.
28. MURAMOTO, H., J. D. HESKETH, & M. A. EL-SHARKAWY. 1965. Relationship among rate of leaf area development, photosynthetic rate, and rate of dry matter production among American cultivated cotton and other species. Crop Sci. 5:163-166.
29. NIR, I., & A. POLJAKOFF-MAYBER. 1967. Effect of water stress on the photochemical activity of chloroplasts. Nature 213:418-419.
30. PETERSON, M. L. 1971. U.S. land and water resources–research needs. *In* C. A. Black, G. E. Van Riper, W. C. Barrows, & R. F. Holland [ed.]. Agronomy in a changing world and research needs for the seventies. Amer. Soc. Agron. Spec. Bull. 19. American Society of Agronomy, 677 South Segoe Road, Madison, Wis. 53711. 65 p.
31. PUCKRIDGE, D. W. 1971. Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of crop communities. Aust. J. Agr. Res. 22:1-9.
32. SCHNEIDER, C. W., & N. F. CHILDERS. 1941. Influence of soil moisture on photosynthesis, respiration, and transpiration of apple leaves. Plant Physiol. 16:565-583.
33. SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, & E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science 148:339-346.
34. SHIMSHI, D. 1963. Effect of soil moisture and phenylmercuric acetate upon stomatal aperture, transpiration, and photosynthesis. Plant Physiol. 38:713-721.
35. SLATYER, R. O., & S. A. TAYLOR. 1960. Terminology in plant- and soil-water relations. Nature 187:922-924.
36. TRAVIS, R. L., R. C. HUFFAKER, & J. L. KEY. 1970. Light induced development of polyribosomes and the induction of nitrate reductase in corn leaves. Plant Physiol. 46:800-805.
37. TRAVIS, R. L., & J. L. KEY. 1971. Correlation between polyribosome level and the ability to induce nitrate reductase in dark-grown corn seedlings. Plant Physiol. 48:617-620.
38. TROUGHTON, J. H., & R. O. SLATYER. 1969. Plant water status, leaf temperature, and the calculated mesophyll resistance to carbon dioxide of cotton leaves. Aust. J. Biol. Sci. 22:815-828.
39. TVORUS, E. K. 1970. Effect of drought and temperature increase on ribonuclease activity in plants. Fiziol. Rast. 17:787-794.
40. VAADIA, Y., F. C. RANEY, & R. M. HAGAN. 1961. Plant water deficits and physiological processes. Annu. Rev. Plant Physiol. 12:265-292.
41. WALTER, H., & E. STADELMANN. 1968. The physiological prerequisites for the transition of autotrophic plants from water to terrestrial life. Bioscience 18:694-701.
42. WAREING, P. F., M. M. KHALIFA, & K. J. TREHARNE. 1968. Rate-limiting processes in photosynthesis at saturating light intensities. Nature 220:453-457.
43. WRIGHT, S. T. C., & R. W. P. HIRON. 1969. (+)–Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. Nature 224:719-720.
44. ZEEVART, J. A. D. 1971. (+)–Abscisic acid content of spinach in relation to photoperiod and water stress. Plant Physiol. 48:86-90.