Photosynthesis at Low Water Potentials

J. S. Boyer

Phil. Trans. R. Soc. Lond. B 1976 **273**, 501-512
doi: 10.1098/rstb.1976.0027

Phil. Trans. R. Soc. Lond. B. **273**, 501–512 (1976) [501]
Printed in Great Britain

Photosynthesis at low water potentials

By J. S. Boyer
Departments of Botany and Agronomy, University of Illinois, Urbana, Illinois 61801, *U.S.A.*

Low leaf water potentials result in large reductions in photosynthesis. In higher plants, the reductions are caused both by decreases in the photosynthetic activity of a unit of leaf and in the production of new leaf surface. Photosynthetic activity declines because of decreased stomatal opening and the inhibition of chloroplast activity, either of which may control photosynthesis depending on which is more limiting at low leaf water potentials. The production of new leaf area is highly sensitive to water deficits and is usually reduced before photosynthetic activity decreases. This may be attributed to the high responsiveness of leaf enlargement to turgor, which expands the cells. When low leaf water potentials are prolonged, leaf senescence often occurs and the quantity of existing leaf area may decline.

There is evidence that translocation is less sensitive than photosynthesis to low leaf water potentials. Consequently, grain yield, which depends on both photosynthesis and translocation, is more likely to be limited by photosynthesis than translocation. Since substantial translocation to the grain may occur from parts of the plant other than the leaves during desiccation, the total photosynthate accumulated during the growing season is more important than that produced during the grain-filling period alone when plants have had low water potentials.

Introduction

In this review, I will discuss the effects of low water potentials on the photosynthesis of higher plants. Because of the wide nature of the subject, allied topics such as the effects of desiccation on lower plants or the effects of osmotica will not be treated, although they may be important in themselves and often are significant for agriculture.

Drought is probably the most inhibitory unpredictable aspect of the environment encountered by a plant during its life cycle. Agricultural production may be reduced virtually to zero during a prolonged spell without water, and native vegetation may show extreme adaptations for protection against drought. At one point in the life cycle, the adaptation to drought becomes a common problem for all seed-bearing plants, since the protection of the embryo against the lethal effects of desiccation during seed maturation and dormancy is essential for the propagation of species.

Unfortunately, the metabolic events that lead to these inhibitions and adaptations are relatively unknown and most attempts to study drought-induced changes in metabolism have involved descriptions of the events rather than analyses of their molecular control (see Hsiao 1973 for a recent review). One of them, the drought-induced change in photosynthesis, has been shown to be particularly dramatic, and much interest in the subject has occurred because of the obvious importance of photosynthesis for agricultural production.

Effects of low water potentials on photosynthetic activity

Probably the first to describe desiccation effects on photosynthetic activity was Kreusler (1885). By the time Pfeffer (1900) wrote his extensive treatise on plant physiology, therefore, he was able to say ‘A slight diminution of turgidity sufficient to close the stomata will render the absorption of carbon dioxide extremely difficult, and hence may markedly diminish the assimilatory activity...'. Nevertheless, only a few studies were published during the 50 years after the work of Kreusler (1885), and consequently Pfeffer (1900) and those reviewers that followed (cf. Miller 1938) had little to go on.

Virtually all the work that was done in the first half of this century agrees that even modest desiccation can have large inhibitory effects on photosynthetic activity (Thoday 1910; Iljin 1923; Brilliant 1924; Dastur 1924, 1925; Wood 1929; Heinicke & Childers 1935; Schneider & Childers 1941; Allmendinger, Kenworthy & Overholser 1943; Verduin & Loomis 1944; Loustalot 1945; Simonis 1947, 1952; Kozlowski 1949; Scarth & Shaw 1951; Bormann 1953; Bourdeau 1954; Upchurch, Peterson & Hagan 1955; Ashton 1956). There was little agreement about the role of the stomata, however, since most of these workers did not follow stomatal behaviour, and those that made the attempt (Thoday 1910; Heinicke & Childers 1935; Schneider & Childers 1941; Verduin & Loomis 1944; Loustalot 1945; Kozlowski 1949; Scarth & Shaw 1951) frequently monitored transpiration rather than stomatal behaviour. Stomatal closure and transpiration were often uncorrelated with photosynthesis, particularly during the early phases of desiccation. Indeed, Scarth & Shaw (1951) considered reductions in photosynthesis to *cause* initial changes in stomatal aperture rather than the reverse.

Recent work that measured photosynthesis as a function of leaf water status has confirmed the inhibition of the process, although stomatal measurements were not made (El-Sharkawy & Hesketh 1964; Strain 1970; Chen, Mederski & Curry 1971; Ghorashy *et al.* 1971; Bazzaz, Paape & Boggess 1972; Oechel, Strain & Odening 1972; Beardsell, Mitchell & Thomas 1973; Bazzaz 1974).

With the publication by Gaastra (1959) of a means of quantifying stomatal resistances by relatively simple measurements, the techniques and measurement parameters for following stomatal changes became more commonly understood. Soon after, a number of studies were done that attempted to quantify the stomatal contribution to photosynthetic inhibition during desiccation. Shimshi (1963) showed that stomatal apertures were reduced but concluded that a nonstomatal factor also limited photosynthesis at low soil moisture levels. Gale, Kohl & Hagan (1966) provided evidence of a similar sort and suggested that the so-called mesophyll resistance, which Gaastra (1959) introduced to account for nonstomatal effects of CO_2 diffusion within the leaf on photosynthesis, probably increased during desiccation. Similar conclusions were reached by Troughton (1969), Boyer (1970*a*) and Hansen (1971) using the analysis of Gaastra (1959). Moldau (1972) and Slatyer (1973), with similar measurements, concluded that stomata may account for much of the limitation of photosynthesis, however.

Others correlated the rate of transpiration or the diffusive resistance to water loss with the rate of photosynthesis by the leaves at low water potentials (Brix 1962; Baker & Musgrave 1964; Willis & Balasubramaniam 1968; Driessche, Conner & Turnstall 1971; Kriedemann & Smart 1971; Beadle *et al.* 1973; Frank, Power & Willis 1973; Harris 1973; Johnson, Frey & Moss 1974; Regehr, Bazzaz & Boggess 1975; O'Toole 1975). Two of these are notable for the high resolution which their measurements provided. Brix (1962) showed an almost perfect correspondence between transpiration and photosynthesis as leaf water potentials changed. Willis & Balasubramaniam (1968) showed a similar phenomenon, although close inspection of their data reveals significant changes in leaf diffusive resistances before changes in photosynthesis occurred during the early parts of desiccation and recovery. Both papers stated that the stomata are likely to exert the major control over photosynthesis at low leaf water potentials.

Barrs (1968) used an interesting approach by studying photosynthesis and transpiration when the stomata had been induced to cycle. The correspondence between photosynthesis and transpiration was close in leaves of cotton, pepper, and sunflower and he concluded that the stomata accounted for virtually all the effects of desiccation on photosynthesis. The mesophyll, or nonstomatal, resistance was therefore considered to be negligible. Unfortunately, he did not measure leaf temperature, and the correlation between transpiration and photosynthesis could have represented enzymatic control just as well as stomatal control of photosynthesis.

Regardless of the exact mechanism controlling photosynthesis and transpiration, the bulk of the measurements clearly show that the two are correlated in desiccated tissue. There are a few exceptions, particularly during the early phases of desiccation and recovery, but across a wide range of desiccation levels, the correlation has been amply documented. The correlation can be useful for those wishing to estimate the photosynthetic capability of crops indirectly from measurements of transpiration or from the diffusive resistances of the stomata. Indeed, the data suggest that modellers and meteorologists who are able to estimate transpiration from physical inputs may also be able to estimate many desiccation effects on photosynthesis, at least by taking certain precautions and using certain controls.

Nevertheless, in spite of its potential usefulness, the parallelism between photosynthesis and transpiration remains only a correlation, and one with several bothersome exceptions. In order for stomatal closure to have an effect on both transpiration and photosynthesis, photosynthesis must be limited at least partially by the rate of CO_2 diffusion through the stomata. Then, and only then, will closure of the stomata actually cause a decrease in the rate of photosynthesis. With the exception of the initial experiments of Gaastra (1959), none of the work cited heretofore has shown that CO_2 actually limited the rate of photosynthesis under all the conditions of the experiments. Thus, it is possible that the correlation between transpiration and photosynthesis was often fortuitous and those instances where there were exceptions provide evidence that stomatal closure may not have completely controlled photosynthesis. As a result, the conclusions regarding the stomatal contribution to the photosynthetic inhibition by drought need re-evaluation.

There are a few recent papers that address this problem more broadly. Wardlaw (1967) showed that in dim light, photosynthesis continued to be inhibited in desiccated wheat. Since photosynthesis is most likely to be limited by light rather than CO_2 under these conditions, one would expect the inhibitory effects of desiccation to disappear if only stomatal effects were involved. Unfortunately, stomatal behaviour was not monitored in this work. Boyer & Bowen (1970) did a more extensive study of leaf photosynthesis in dim light and were able to show a large response to low leaf water potentials even though photosynthesis was proportional to light intensity, and clearly was limited by light and not CO_2. These results can be explained only by an alteration at the chloroplast level.

In another study, Boyer (1971*a*) showed that the response of photosynthesis to CO_2 (200–400 cm^3/m^3 in the external air) was undetectable under low light and also was lacking under high light in desiccated leaves of sunflower. He monitored the diffusive resistance of the stomata and showed that the stomata could not account for the effects he saw. Furthermore, photosynthesis remained inhibited under limiting light intensities. The response of light-limited photosynthesis was as large as that of the changes in the diffusive resistance of the stomata during desiccation and therefore could have permitted large nonstomatal effects on photosynthesis.

Troughton & Slatyer (1969), in an excellent study, recognized the complicating effects of stomatal diffusion and circumvented them by forcing air directly through the leaves of cotton. They worked at low O_2 concentrations (to reduce respiration effects) and low CO_2 levels (which assured CO_2 limitation of photosynthesis) and were able to detect no response of photosynthesis to desiccation. Nevertheless, by working at low CO_2 concentrations (100 cm^3/m^3 and less), they could have overlooked biochemical effects on photosynthesis that would appear at more normal CO_2 concentrations.

Redshaw & Meidner (1972) did a similar experiment but at higher CO_2 concentrations (average = 240 cm^3/m^3) and found large effects on net photosynthesis in tobacco. These workers did not inhibit respiration, however,

Using another approach, Graziani & Livne (1971) stripped the epidermis from tobacco leaves. During severe desiccation, the leaves showed a considerable loss in photosynthetic activity.

It therefore seems that there may be nonstomatal effects on photosynthesis in addition to the stomatal effects at low leaf water potentials. With the exception of the work of Troughton & Slatyer (1969), who used conditions that might have caused them to overlook certain kinds of nonstomatal effects, all these recent studies demonstrated significant and quite large changes in photosynthetic activity that could not be attributed to stomatal closure.

In view of the *in vivo* evidence for the nonstomatal effects of low leaf water potentials, it is logical to expect that chloroplast changes might occur at the same time as the stomata closed at low leaf water potentials. Some calculations of chloroplast Hill activity on a chlorophyll basis from the data of Todd & Basler (1965) show that Hill activity was reduced in chloroplasts isolated from severely wilted leaves. Nir & Poljakoff-Mayber (1967) and Fry (1970) showed the same phenomenon in chloroplasts from severely desiccated leaves. Chloroplasts severely desiccated *in vitro* had lower Hill activity than non-desiccated chloroplasts (Santarius & Heber 1967). Santarius (1967) showed a decrease in the ATP and NADPH contents of severely desiccated tissue, and Wilson & Huffaker (1964) demonstrated a decline in phosphorylated intermediates during desiccation, although the quantity of inorganic phosphate remained stable.

Since most of this work involved desiccation that was apparently severe, it was not clear whether the subcellular changes were correlated with the effects of moderately low water potentials or merely reflected the large changes that would be expected as the cells became irreversibly damaged.

In an effort to answer this question, Boyer & Bowen (1970) assayed for oxygen evolution in chloroplasts isolated from sunflower leaves having a wide range of water potentials. Oxygen evolution (which later was identified to be a measure of photosystem 2 activity (Potter & Boyer 1973, Keck & Boyer 1974)) decreased as soon as photosynthesis in the whole leaves began to be affected. Over the entire range of leaf water potentials, there was a correlation between chloroplast activity and photosynthesis that was as strong as that for transpiration rate or stomatal aperture (Boyer & Bowen 1970). A demonstration that leaf photosynthesis under light-limited conditions was inhibited by about the same amount as chloroplast photosystem 2 (one of the 'light-reactions') suggested that the changes in isolated chloroplasts were also occurring *in vivo* (Boyer & Bowen 1970).

Subsequently, Keck & Boyer (1974) explored the extent to which other partial reactions of photosynthesis were inhibited in isolated chloroplasts. Photosystems 1 and 2, whole chain electron transport, and cyclic and noncyclic photophosphorylation were inhibited when chloroplasts were isolated from leaves having low water potentials and assayed under conditions that were identical for all treatments. Therefore, desiccation of the tissue before isolation had caused chloroplast changes that could be detected after isolation. Since the effects on electron transport appeared in chloroplasts from tissue having water potentials that corresponded to those causing effects on photosynthesis *in vivo*, these workers suggested that an inhibition of electron transport is probably important during early desiccation. Since decreases in photophosphorylation became severe at very low leaf water potentials, they suggested that the low activity of photophosphorylation may be more important than that of electron transport during extreme desiccation.

In addition to the effects of low leaf water potentials on the photochemical portion of photosynthesis, there also are changes in some of the enzymes of the 'dark' reactions. Ribulose 1,5-diphosphate carboxylase activity is reduced when assays are performed on extracts from desiccated leaves (Huffaker, Radin, Kleinkopf & Cox 1970; Jones 1973; Lee, Campbell & Paulsen 1974; Johnson *et al.* 1974; O'Toole 1975). When the inhibition is compared with the inhibition of photosynthesis *in vivo*, however, none of these studies demonstrated an effect large enough to account completely for the inhibition of photosynthesis in the intact leaf (Jones 1973; Lee *et al.* 1974; Johnson *et al.* 1974; O'Toole 1975). Phosphoenolpyruvate carboxylase and ribulose-5-phosphate kinase also showed too little change to be completely limiting (Huffaker *et al.* 1970; Shearman, Eastin, Sullivan & Kinbacher 1972). Plaut (1971) found little effect of high sorbitol concentrations on extracted ribulose 1,5-diphosphate carboxylase and ribulose 5-phosphate kinase, although he observed an inhibition when the assays were conducted in isolated but intact chloroplasts. Unfortunately, the assays in the intact plastids were dependent on endogenous ATP, and a decrease in photophosphorylation (Keck & Boyer 1974) could have accounted for his results, a problem he recognized (Plaut 1971). Plaut & Bravdo (1973) could show an inhibition of CO_2 fixation in chloroplasts isolated from intact leaves.

Taken together, the chloroplast and low leaf studies show that the inhibition of photosynthesis by low leaf water potentials involves both stomatal and chloroplast effects occurring simultaneously. Rates of photosynthesis apparently may be limited by one or the other or perhaps by a combination of both according to the conditions and the particular species involved. In general, stomatal effects are likely to be important in bright light, since there is a large CO_2 flux to the chloroplasts. Carboxylation activities are unlikely to affect photosynthesis to a large degree under these conditions. As radiation decreases, chloroplast effects should become increasingly predominant, however. Photochemical aspects of chloroplast activity would probably be quite important, since there are such large changes in the partial reactions of the 'light' portion of photosynthesis. The exact radiation levels at which they would become important would depend on how severe the reduction in photochemical activity is relative to that for the stomata or other factors.

Extensive measurements show that desiccation affects the rate of dark respiration (Schneider & Childers 1941; Upchurch *et al.* 1955; Brix 1962; Kaul 1966; Flowers & Hanson 1969; Boyer 1970*b*; Bell, Koeppe & Miller 1971; Miller, Bell & Koeppe 1971; Koeppe, Miller & Bell 1973). In certain cases, desiccation causes an initial rise in the rate of respiration (Schneider & Childers 1941; Upchurch *et al.* 1955; Brix 1962; Kaul 1966), and in principle, the rise in respiration could cause a decrease in net photosynthesis. However, the rise is small and ultimately a decline occurs. In many species only a decline is observed. Therefore, a rise in dark respiration at low leaf water potentials is unlikely to account for decreases in net photosynthesis.

Light-induced respiration or photorespiration appears to decrease as leaf water potentials decrease (Boyer 1971*a*). Thus, it too is unlikely to account for decreases in net photosynthesis.

Most of these conclusions are based on experiments done by withholding water from the soil. By comparison, there is relatively little work on the reverse – the recovery of desiccated plants after resupplying water to the soil. Brix (1962) showed that the recovery of photosynthesis and transpiration followed similar kinetics, and the recovery time could be decreased if the plant roots were excised under water. Willis & Balasubramaniam (1968) also showed a general correspondence between photosynthesis and transpiration during recovery. Boyer (1971*b*) found that rates of photosynthesis often did not return immediately to control levels even though leaf water potentials did, and after-effects of desiccation could be seen several days later, particularly in tissue that was mature during desiccation. The photochemical activity of the chloroplasts recovered readily under these conditions (Boyer 1971*b*; Potter & Boyer 1973) but the stomata frequently did not open fully in spite of leaf water potentials that had returned to control levels (Boyer 1971*b*).

The recovery experiments shed no new light on how photosynthesis is limited by desiccation but they suggest that the chloroplast changes are reasonably reversible, at least by comparison with the stomatal changes. If anything, then, it would appear that a period of exposure to low leaf water potentials causes photosynthesis to be subsequently more limited by stomatal diffusion. The end result is a tendency for water use per unit photosynthesis to be less after recovery than before low water potentials occur.

Effects of low water potentials on leaf production

The production of leaves represents the production of photosynthetic surface for most plants. As a result, it is an important contributor to photosynthesis on a whole plant basis. As leaf water potentials decrease, leaf production is reduced because of effects on leaf initiation occurring in the meristem and effects on cell enlargement. The rate of leaf initiation may become slower or cease altogether (Husain & Aspinall 1970) and there is evidence that cell division may be reduced (Terry, Waldron & Ulrich 1971; Kirkham, Gardner & Gerloff 1972; Meyer & Boyer 1972; McCree & Davis 1974). In general, cell enlargement seems to be more sensitive than cell division (Meyer & Boyer 1972), although Kirkham *et al.* (1972) describe an early effect of osmotic solutions on cell division.

The exceptional sensitivity of leaf enlargement to low leaf water potentials can be seen in the data of Boyer (1968, 1970*b*) and Acevedo, Hsiao & Henderson (1971), who showed that enlargement proceeded at a rate 25% of the control rate or less when leaf water potentials decreased to −0.4 MPa (−4 bar) in maize, soybean, and sunflower (Boyer 1968, 1970*b*) or −0.6 MPa in maize (Acevedo *et al.* 1971). Photosynthetic activity was unaffected at these water potentials (Boyer 1970*b*).

This degree of sensitivity is enough to cause large decreases in leaf growth in midday when water potentials are often below −0.4 to −0.6 MPa, even in well watered plants. Acevedo *et al.* (1971) show, however, that short periods of decreased leaf enlargement are reversible, and rapid enlargement resumes at night (Boyer 1968). On the other hand, when inhibition lasts for several days, leaf enlargement may ultimately resume but at less than the control rate (Boyer 1970*b*). This suggests that the normal diurnal changes in leaf desiccation are likely to cause reversible effects on leaf growth but desiccation for prolonged periods can cause an inhibition that is only partially reversible.

In certain field situations, leaves never attain water potentials as high as −0.4 to −0.6 MPa. Examples are the leaves of plants adapted to saline soils or the leaves at the tops of tall trees.

They grow, however, and this suggests that they are capable of adjusting in some way so that enlargement is less affected than in those cases described by Boyer (1968, 1970*b*) and Acevedo *et al.* (1971).

Meyer & Boyer (1972) described a form of adaptation that may be involved in the adjustment of cell enlargement to withstand drier conditions. They showed that soybean hypocotyls, which carry on rapid cell division and elongation, can compensate for low tissue water potentials by permitting solute accumulation in the elongating cells. This provides an internal osmotic compensation that parallels decreases in water potential so that turgor remains high. The overall effect was to reduce the responsiveness of cell enlargement to changes in tissue water potentials. When the tissue was deprived of this mechanism, tissue elongation became much more sensitive to low water potentials. Greacen & Oh (1972) have shown a similar phenomenon for roots, and Goode & Higgs (1973) and Biscoe (1972) report that it may occur in leaves.

In addition to the effects of low water potentials on the production of new leaf area, low leaf water potentials may cause the loss of existing leaf area. As desiccation becomes prolonged, leaf senescence occurs and in some species may be particularly rapid. Figure 1*c* shows the quantity of viable leaf area in maize when leaf water potentials remained constant at −1.8 to −2.0 MPa during most of the grain-filling period. All leaves had senesced 30 days after the plants reached low leaf water potentials. The uppermost leaves, which are the largest contributors to grain-fill, began to senesce 10–14 days after leaf water potentials had decreased to −1.8 to −2.0 MPa.

The early senescence of leaf area in maize represents an irreversible loss of photosynthetic capability by the crop. In this particular case, it occurred late enough in the growing season so that a substantial amount of grain was still produced (see below), albeit at the expense of previous photosynthate.

It is important to note that the metabolic changes that bring on senescence can occur rapidly in maize. Among the earliest are dramatic rises in the activity of hydrolytic enzymes, such as ribonuclease (Sacher 1973). Within 4–5 h, ribonuclease activity increases in maize leaves having low water potentials (Morilla, Boyer & Hageman 1973). By contrast, nitrate reductase, which is active during rapid growth and decreases during senescence, displays a dramatic decrease in activity within this time (Morilla *et al.* 1973). The metabolic conditions that bring about these changes are unknown but it is clear that they can ultimately lead to a significant alteration in the leaf area of crops.

Significance of inhibited photosynthesis for grain production at low leaf water potentials

Although photosynthesis is reponsible for the accumulation of the bulk of the dry mass of plants, and dry matter yield is reduced when plants are subjected to low leaf water potentials, there are few studies of how the inhibition of photosynthesis relates to the reduction in yield that ultimately occurs (Salter & Goode 1967). This is a particularly important problem in grain crops, where the development of the grain and translocation of photosynthate to the grain also affect grain production.

In an effort to provide some information about this question, a recent experiment was conducted by the author and Dr H. G. McPherson at the Climate Laboratory in Palmerston North, New Zealand. The intent of the experiment was to subject maize to low leaf water potentials during the early grain-filling period (soon after flowering and pollination had been completed) and hold the potentials constant while the metabolic response and productivity of the plants were observed. Since maize must accumulate 40 to 50 % of the total plant dry mass during the grain-filling period, this provided an opportunity to study the effects of low leaf water potentials and photosynthate deprivation on the grain-filling process without the complications of vegetative development.

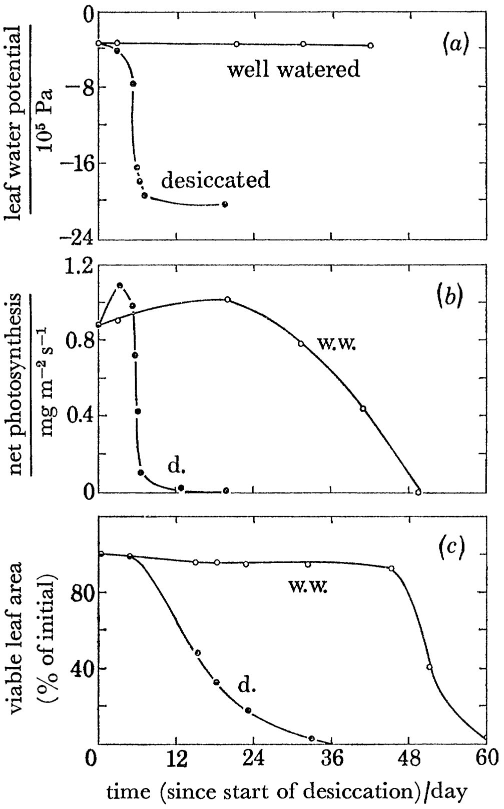

FIGURE 1. (*a*) Leaf water potential, (*b*) net photosynthesis, and (*c*) viable leaf area of maize during the grain-filling period. Desiccation was initiated by withholding water from the soil shortly after pollination had been completed, and low leaf water potentials were maintained by adding small amounts of water ($\frac{1}{7}$ that of the controls) for the remainder of the growing season. Data from McPherson & Boyer (unpublished).

Figure 1 shows that photosynthesis virtually ceased when leaf potentials decreased to −1.8 to −2.0 MPa. The plants remained inactive photosynthetically for the remainder of the season (figure 1*b*) and leaf senescence proceeded rapidly (figure 1*c*). Table 1 shows that the shoot dry matter accumulated during the desiccation period was reduced to 21 % of that accumulated by the controls. However, in spite of this, grain yield was 47 % of the control grain yield. Clearly, considerable dry mass had to be contributed by other parts of the shoot and represented photosynthate that had accumulated before the desiccation period. Indeed, grain yield was a relatively constant fraction of the dry weight that had accumulated for the whole season (table 1). Thus, photosynthesis had a large effect on grain yield, but it was the total season photosynthesis that was important rather than just that which occurred during grain fill.

Of course, since the ear continued to fill at low leaf potentials even though photosynthesis was virtually undetectable, translocation must have been capable of occurring (cf. figure 1 and table 1). This suggests that translocation to the grain is considerably less sensitive than photosynthesis to low leaf water potentials. The ability to translocate dry matter to the grain in spite of an inhibition of current photosynthesis has also been observed in wheat (Wardlaw 1967) and is probably a noteworthy mechanism for assuring the survival of a species under dry conditions.

Table 1. Dry matter production by maize that was desiccated for most of the grain-filling period

(The plants were the same as those shown in figure 1. Data represent averages for 10–12 plants ± 1 standard deviation.)

	well watered	desiccated	
	grams per plant	grams per plant	percent of well watered
A grain yield	133 ± 21	62.2 ± 4.0	47
B total shoot			
1 dry matter production, whole season	310 ± 24	154 ± 7	50
2 dry matter production, desiccation period	199 ± 24	42.5 ± 13	21
ratio			
A/B1	0.43	0.40	
A/B2	0.67	1.46	

References (Boyer)

Acevedo, E., Hsiao, T. C. & Henderson, D. W. 1971 Immediate and subsequent growth responses of maize leaves to changes in water status. *Pl. Physiol.* **48**, 631–636.

Allmendinger, D. F., Kenworthy, A. L. & Overholser, E. L. 1943 The carbon dioxide intake of apple leaves as affected by reducing the available soil water to different levels. *Proc. Am. Soc. Hort. Sci.* **42**, 133–140.

Ashton, F. M. 1956 Effects of a series of cycles of alternating low and high soil water contents on the rate of apparent photosynthesis in sugar cane. *Pl. Physiol.* **31**, 266–274.

Baker, D. N. & Musgrave, R. B. 1964 The effects of low level moisture stresses on the rate of apparent photosynthesis in corn. *Crop Sci.* **4**, 249–253.

Barrs, H. D. 1968 Effect of cyclic variations in gas exchange under constant environmental conditions on the ratio of transpiration to net photosynthesis. *Physiologia Pl.* **21**, 918–929.

Bazzaz, F. A. 1974 Ecophysiology of *Ambrosia artemisiifolia*: a successional dominant. *Ecology* **55**, 112–119.

Bazzaz, F. A., Paape, V. & Boggess, W. R. 1972 Photosynthetic and respiratory rates of *Sassafras albidum*. *For. Sci.* **18**, 218–222.

Beadle, C. L., Stevenson, K. R., Neumann, H. H., Thurtell, G. W. & King, K. M. 1973 Diffusive resistance, transpiration, and photosynthesis in single leaves of corn and sorghum in relation to leaf water potential. *Can. J. Pl. Sci.* **53**, 537–544.

Beardsell, M. F., Mitchell, K. J. & Thomas, R. G. 1973 Effects of water stress under contrasting environmental conditions on transpiration and photosynthesis in soybean. *J. exp. Bot.* **24**, 579–586.

Bell, D. T., Koeppe, D. E. & Miller, R. J. 1971 The effects of drought stress on respiration of isolated corn mitochondria. *Pl. Physiol.* **48**, 413–415.

Biscoe, P. V. 1972 The diffusive resistance and water status of leaves of *Beta vulgaris*. *J. exp. Bot.* **23**, 930–940.

Bormann, F. H. 1953 Factors determining the role of loblolly pine and sweetgum in early old-field succession in the Piedmont of North Carolina. *Ecol. Monographs* **23**, 339–358.

Bourdeau, P. 1954 Oak seedling ecology determining segregation of species in Piedmont oak-hickory forests. *Ecol. Monographs* **24**, 297–320.

Boyer, J. S. 1968 Relationship of water potential to growth of leaves. *Pl. Physiol.* **43**, 1056–1062.

Boyer, J. S. 1970*a* Differing sensitivity of photosynthesis to low leaf water potentials in corn and soybean. *Pl. Physiol.* **46**, 236–239.

Boyer, J. S. 1970*b* Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. *Pl. Physiol.* **46**, 233–235.

Boyer, J. S. 1971*a* Nonstomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. *Pl. Physiol.* **48**, 532–536.

Boyer, J. S. 1971*b* Recovery of photosynthesis in sunflower after a period of low leaf water potential. *Pl. Physiol.* **47**, 816–820.

Boyer, J. S. & Bowen, B. L. 1970 Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials. *Pl. Physiol.* **45**, 612–615.

Brilliant, B. 1924 Le teneur en eau dans les feuilles et l'energie assimilatrice. *Compt. Rend. Acad. Sci.* (*Paris*) **178**, 2122–2125.

Brix, H. 1962 The effect of water stress on the rates of photosynthesis and respiration in tomato plants and loblolly pine seedlings. *Physiologia Pl.* **15**, 10–20.

Chen, L. H., Mederski, H. J. & Curry, R. B. 1971 Water stress effects on photosynthesis and stem diameter in soybean plants. *Crop Sci.* **11**, 428–431.

Dastur, R. H. 1924 Water content, a factor in photosynthesis. *Ann. Bot.* **38**, 779–788.

Dastur, R. H. 1925 The relation between water content and photosynthesis. *Ann. Bot.* **39**, 769–786.

Driessche, R. van den, Conner, D. J. & Turnstall, B. R. 1971 Photosynthetic response of brigalow to irradiance, temperature and water potential. *Photosynthetica* **5**, 210–217.

El-Sharkawy, M. A. & Hesketh, J. D. 1964 Effects of temperature and water deficit on leaf photosynthetic rates of different species. *Crop Sci.* **4**, 514–518.

Flowers, T. J. & Hanson, J. B. 1969 The effect of reduced leaf water potential on soybean mitochondria. *Pl. Physiol.* **44**, 939–945.

Frank, A. B., Power, J. F. & Willis, W. O. 1973 Effect of temperature and plant water stress on photosynthesis, diffusion resistance, and leaf water potential in spring wheat. *Agron. J.* **65**, 777–780.

Fry, K. E. 1970 Some factors affecting the Hill reaction activity in cotton chloroplasts. *Pl. Physiol.* **45**, 465–469.

Gaastra, P. 1959 Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. *Mededel. Landbouhogeschool Wageningen* **59**, 1–68.

Gale, J., Kohl, H. C. & Hagan, R. M. 1966 Mesophyll and stomatal resistances affecting photosynthesis under varying conditions of soil, water and evaporation demand. *Isr. J. Bot.* **15**, 64–71.

Ghorashy, S. R., Pendleton, J. W., Peters, D. B., Boyer, J. S. & Beuerlein, J. E. 1971 Internal water stress and apparent photosynthesis wtih soybeans differing in pubescence. *Agron. J.* **63**, 674–676.

Goode, J. E. & Higgs, K. H. 1973 Water, osmotic and pressure potential relationships in apple leaves. *J. Hort. Sci.* **48**, 203–215.

Graziani, Y. & Livne, A. 1971 Dehydration, water fluxes, and permeability of tobacco leaf tissue. *Pl. Physiol.* **48**, 575–579.

Greacen, E. L. & Oh, J. S. 1972 Physics of root growth. *Nature New Biol.* **235**, 24–25.

Hansen, G. K. 1971 Photosynthesis, transpiration and diffusion resistance in relation to water potential in leaves during water stress. *Acta Agric. Scand.* **21**, 163–171.

Harris, D. G. 1973 Photosynthesis, diffusion resistance and relative water content of cotton as influenced by induced water stress. *Crop Sci.* **13**, 570–572.

Heinicke, A. J. & Childers, N. F. 1935 The influence of water deficiency on photosynthesis and transpiration of apple leaves. *Proc. Am. Soc. Hort. Sci.* **33**, 155–159.

Hsiao, T. C. 1973 Plant responses to water stress. *A. Rev. Pl. Physiol.* **24**, 519–570.

Huffaker, R. C., Radin, T., Kleinkopf, G. E. & Cox, E. L. 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.

Husain, I. & Aspinall, D. 1970 Water stress and apical morphogenesis in barley. *Ann. Bot.* **34**, 393–408.

Iljin, W. S. 1923 Der Einfluss des Wassermangels auf die Kohlenstoff-assimilation durch die Pflanzen. *Flora* **116**, 360–378.

Johnson, R. R., Frey, N. M. & Moss, D. N. 1974 Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. *Crop Sci.* **14**, 728–731.

Jones, H. G. 1973 Moderate-term water stresses and associated changes in some photosynthetic parameters in cotton. *New Phytol.* **72**, 1095–1105.

Kaul, R. 1966 Effect of water stress on respiration by wheat. *Can. J. Bot.* **44**, 623–632.

Keck, R. W. & Boyer, J. S. 1974 Chloroplast response to low leaf water potentials. III. Differing inhibition of electron transport and photophosphorylation. *Pl. Physiol.* **53**, 474–479.

Kirkham, M. B., Gardner, W. R. & Gerloff, G. C. 1972 Regulation of cell division and cell enlargement by turgor pressure. *Pl. Physiol.* **49**, 961–962.

Koeppe, D. E., Miller, R. J. & Bell, D. T. 1973 Drought-affected mitochondrial processes as related to tissue and whole plant responses. *Agron. J.* **65**, 566–569.

Kozlowski, T. T. 1949 Light and water in relation to growth and competition of Piedmont forest tree species. *Ecol. Monographs* **19**, 207–231.

Kreusler, U. 1885 Ueber eine Methode zur Beobachtung der Assimilation und Athmung der Pflanzen und über einige diese Vorgänge beeinflussende Momente. *Landw. Jahrb.* **14**, 913–965.

Kriedemann, P. E. & Smart, R. E. 1971 Effects of irradiance, temperature, and leaf water potential on photosynthesis of vine leaves. *Photosynthetica* **5**, 6–15.

Lee, K. C., Campbell, R. W. & Paulsen, G. M. 1974 Effects of drought stress and succinic acid-2,2-dimethylhydrazide treatment on water relations and photosynthesis in pea seedlings. *Crop Sci.* **14**, 279–282.

Loustalot, A. J. 1945 Influence of soil moisture conditions on apparent photosynthesis and transpiration of pecan leaves. *J. Agric. Res.* **71**, 519–532.

McCree, K. J. & Davis, S. D. 1974 Effect of water stress and temperature on leaf size and on size and number of epidermal cells in grain sorghum. *Crop Sci.* **14**, 751–755.

Meyer, R. F. & Boyer, J. S. 1972 Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. *Planta* **108**, 77–87.

Miller, E. C. 1938 *Plant physiology*. New York: McGraw-Hill Book Company.

Miller, R. J., Bell, D. T. & Koeppe, D. E. 1971 The effects of water stress on some membrane characteristics of corn mitochondria. *Pl. Physiol.* **48**, 229–231.

Moldau, K. H. 1972 Effects of a water deficit and the light regime on photosynthetic activity of leaves. *Sov. Plant Physiol.* **19**, 970–975.

Morilla, C. A., Boyer, J. S. & Hageman, R. H. 1973 Nitrate reductase activity and polyribosomal content of corn (*Zea mays* L.) having low leaf water potentials. *Pl. Physiol.* **51**, 817–824.

Nir, I. & Poljakoff-Mayber, A. 1967 Effect of water stress on the photochemical activity of chloroplasts. *Nature, Lond.* **213**, 418–419.

Oechel, W. C., Strain, B. R. & Odening, W. R. 1972 Tissue water potential, photosynthesis, ^{14}C-labeled photosynthate utilization, and growth of the desert shrub *Larrea divaricata* Cav. *Ecol. Monographs* **42**, 127–141.

O'Toole, J. C. 1975 Photosynthetic response to water stress in *Phaseolus vulgaris* L. Ph.D. dissertation, Cornell University, Ithaca, New York.

Pfeffer, W. 1900 *The physiology of plants*. Vol. I. Pg. 338 (English translation). Oxford: Clarendon Press.

Plaut, Z. 1971 Inhibition of photosynthetic carbon dioxide fixation in isolated spinach chloroplasts exposed to reduced osmotic potentials. *Pl. Physiol.* **48**, 591–595.

Plaut, Z. & Bravdo, B. 1973 Response of carbon dioxide to water stress. *Pl. Physiol.* **52**, 28–32.

Potter, J. R. & Boyer, J. S. 1973 Chloroplast response to low leaf water potentials. II. Role of osmotic potential. *Pl. Physiol.* **51**, 993–997.

Redshaw, A. J. & Meidner, H. 1972 Effects of water stress on the resistance to uptake of carbon dioxide in tobacco. *J. exp. Bot.* **23**, 229–240.

Regehr, D. L., Bazzaz, F. A. & Boggess, W. R. 1975 Photosynthesis, transpiration, and leaf conductance of *Populus deltoides* in relation to flooding and drought. *Photosynthetica* **9**, 52–61.

Sacher, J. A. 1973 Senescence and postharvest physiology. *A. Rev. Pl. Physiol.* **24**, 197–224.

Salter, P. J. & Goode, J. E. 1967 *Crop responses to water at different stages of growth*. Farnham Royal, Bucks, England: Commonwealth Agricultural Bureaux.

Santarius, K. A. 1967 Das Verhalten von CO_2-Assimilation, NADP- und PGS-Reduktion und ATP-Syntheses intakter Blattzellen in Abhängigkeit vom Wassergehalt. *Planta* **73**, 228–242.

Santarius, K. A. & Heber, U. 1967 Das Verhalten von Hill-Reaktion und Photophosphorylierung isolierter Chloroplasten in Abhängigkeit vom Wassergehalt. II. Wasserentzug uber $CaCl_2$. *Planta* **73**, 109–137.

Scarth, G. W. & Shaw, M. 1951 Stomatal movement and photosynthesis in *Pelargonium*. II. Effects of water deficit and of chloroform: photosynthesis in guard cells. *Pl. Physiol.* **26**, 581–597.

Schneider, W. G. & Childers, N. F. 1941 Influence of soil moisture on photosynthesis, respiration, and transpiration of apple leaves. *Pl. Physiol.* **16**, 565–583.

Shearman, L. L., Eastin, J. D., Sullivan, C. Y. & Kinbacher, E. J. 1972 Carbon dioxide exchange in water stressed sorghum. *Crop Sci.* **12**, 406–409.

Shimshi, D. 1963 Effect of soil moisture and phenylmercuric acetate upon stomatal aperture, transpiration, and photosynthesis. *Pl. Physiol.* **38**, 713–721.

Simonis, W. 1947 CO_2-Assimilation und Stoffproduction trocken gezogener Pflanzen. *Planta* **35**, 188–224.

Simonis, W. 1952 Untersuchungen zum Durreeffekt. I. Mitteilung. Morphologische Struktur, Wasserhaushalt, Atmung und Photosynthese feucht und trocken gezogener Pflanzen. *Planta* **40**, 313–332.

Slatyer, R. O. 1973 Effects of short periods of water stress on leaf photosynthesis. In *Symposium on Plant Response to Climatic Factors* (ed. R. O. Slatyer). UNESCO, Proceedings of the Uppsala Symposium.

Strain, B. R. 1970 Field measurements of tissue water potential and carbon dioxide exchange in the desert shrub *Prosopis julifera* and *Larrea divaricata*. *Photosynthetica* **4**, 118–122.

Terry, N., Waldron, L. J. & Ulrich, A. 1971 Effects of moisture stress on the multiplication and expansion of cells in leaves of sugar beet. *Planta* **97**, 281–289.

Thoday, D. 1910 Experimental researches on vegetable assimilation and respiration. VI. Some experiments on assimilation in the open air. *Proc. R. Soc. Lond.* B **82**, 421–450.

Todd, G. W. & Basler, E. 1965 Fate of various protoplasmic constituents in droughted wheat plants. *Phyton* **22**, 79–85.

Troughton, J. H. 1969 Plant water status and carbon dioxide exchange of cotton leaves. *Australian J. Biol. Sci.* **22**, 289–302.

Troughton, J. H. & Slatyer, R. O. 1969 Plant water status, leaf temperature, and the calculated mesophyll resistance to carbon dioxide of cotton leaves. *Australian J. Biol. Sci.* **22**, 815–827.

Upchurch, R. P., Peterson, M. L. & Hagan, R. M. 1955 Effect of soil-moisture content on the rate of photosynthesis and respiration in ladino clover (*Trifolium repens* L.). *Pl. Physiol.* **30**, 297–303.

Verduin, J. & Loomis, W. E. 1944 Absorption of carbon dioxide by maize. *Pl Physiol.* **19**, 278–293.

Wardlaw, I. F. 1967 The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. *Australian J. Biol. Sci.* **20**, 25–39.

Willis, A. J. & Balasubramaniam, S. 1968 Stomatal behavior in relation to rates of photosynthesis and transpiration in *Pelargonium. New Phytol.* **67**, 265–285.

Wilson, A. M. & Huffaker, R. C. 1964 Effects of moisture stress on acid-soluble phosphorus compounds in *Trifolium subterraneum. Pl. Physiol.* **39**, 555–560.

Wood, J. G. 1929 The relation between water content and amount of photosynthesis. *Australian J. Exptl Biol. Med. Sci.* **6**, 127–131.