Comparisons of Photosynthetic Responses of *Xanthium strumarium* and *Helianthus annuus* to Chronic and Acute Water Stress in Sun and Shade

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ABSTRACT

We have examined the effects of mild, chronic water stress and acute water stress on two water stress sensitive plants, *Xanthium strumarium* and *Helianthus annuus*. Using a combination of the leaf disc O$_2$ electrode to measure the light responses of photosynthesis and 77 K fluorescence to monitor damage to the primary photochemistry, we have found the following: (a) The CO$_2$ saturated rate of photosynthesis at high light is the most water stress sensitive parameter measured. (b) The apparent quantum yield (molecules O$_2$ per molecule photons) was slightly, if at all, affected by mild water stress ($=-1.5$ megapascals). (c) Severe water stress ($<-1.5$ megapascals) reduced the quantum yield of photosynthesis regardless of whether the stress was applied in sun or shade. The light independent reduction of quantum yield was not associated with a reduction in 77 K fluorescence ($F/Fe$) indicating that the quantum yield reduction was not the result of damage to primary photochemistry. (d) The diel fluctuation in 77 K fluorescence seen in sun-exposed control leaves was greatly exaggerated in water stressed leaves because of enhanced decline in 77 K fluorescence in the morning. The rate of recovery was similar in both control and water stressed leaves. Shaded leaves showed no change in 77 K fluorescence regardless of whether water stress was imposed or not. (e) The water stress sensitive plants used in these experiments did not recover from acute water stress severe enough to reduce the quantum yield or chronic water stress which lasted long enough that light dependent damage to primary photochemistry occurred.

The effects of water stress on photosynthesis in leaves are generally considered to involve both stomatal closure and effects on the biochemical process of photosynthesis (7). Boyer (8) showed that high external CO$_2$ concentrations did not reverse the effect of water stress on photosynthesis, establishing the fundamental importance of inhibition of biochemical processes. Biochemical effects of water stress on leaf photosynthesis in *vivo* have been examined using quantitative analytical gas exchange methods. Jones (13), for example, observed a decrease in time in both the initial slope and CO$_2$ saturated portion of the curve relating assimilation to intercellular CO$_2$ partial pressure in cotton leaves exposed to mild, controlled water stress. Similar results have been reported for a range of cultivated and wild species subject to slowly applied water stress (10, 19, 26, 27, 29).

Changes in the apparent quantum yield were among the earliest reported biochemical responses of leaf photosynthesis to water stress (8, 9). Mohanty and Boyer (18) measured a decrease in absorbed quantum yield following water stress, in leaves and in chloroplasts, supporting earlier hypotheses that water stress affected photochemical activity (8). Rapidly applied water stress in sunflower reduces quantum yields, and this change is independent of light intensity during stress (28). Slowly applied stress in Nerium oleander reduces quantum yield (19) and is associated with a light dependent reduction in primary photochemistry (77 K fluorescence) as well as in electron transport (6).

We have examined some of these aspects of biochemical inhibition of photosynthesis using a leaf disc O$_2$ electrode which permits quantum yield measurement at CO$_2$ saturation and 77 K fluorescence analysis (1, 2, 5, 30). We studied both sustained (chronic) mild water stress and brief severe (acute) water stress. We studied acutely stressed leaves to determine the primary lesion caused by water stress. We also studied chronically stressed leaves to investigate the interaction between light and water stress. Our experiments indicate that species differ in response of biochemical photosynthetic properties to water stress and that initially, these responses are independent of changes in primary photochemistry and light or dark during stress. An abstract of these data is in press (3).

MATERIALS AND METHODS

Plant Material. *Helianthus annuus* L. var mammoth (CH Lilly, Portland, OR), and *Xanthium strumarium* L. (Chicago strain, seed from JAD Zeevaart, Michigan State University, East Lansing, MI) were grown in potting mix (compost:sand:perlite = 2:1:1 by volume) in a temperature controlled glasshouse (26°C d/18°C night; full sunlight = 1500 to 1800 µmol quanta m$^{-2}$ s$^{-1}$) with supplemental lighting (approx 1 µmol quanta m$^{-2}$ s$^{-1}$) to extend daylight to 18 h. Plants were watered twice daily and fertilized three times weekly with 200 ml Hoagland nutrient solution. After 4 weeks a uniform population of plants was selected and fully expanded leaves of the same age were tagged for experimental manipulation. Aging effects and shade acclimation were sometimes observed, but not always. Control plants were included in all experiments to distinguish shade acclimation and aging effects from water stress effects.

Sustained (Chronic) Mild Water Stress Treatments. Water stress was imposed by withholding water. Plants were subsequently maintained at leaf water potentials just above wilting by...
frequent additions of small quantities of water 2 to 4 times daily for 6 to 10 d. In early experiments, separate plants were placed under shade cloth (15% transmission) and others were kept in sun. However, it proved difficult to maintain equal water potentials so the following experimental design was used. One fully expanded leaf on a plant was placed in a shade screen envelope, open on two sides, which transmitted an average of 22% incident PAR. Spot measurements during experiments showed that water potentials of shaded and unshaded leaves were within ±0.07 MPa and there was no consistent difference in leaf temperature. Leaf temperatures in the well ventilated greenhouse ranged between 22 and 28°C in sun and shade throughout the day in irrigated and water stressed plants. In this design leaves were compared on the same plant, but separate plants were required for each photosynthetic measurement.

**Brief Severe (Acute) Water Stress Treatments.** In these experiments water was withheld entirely for the duration and plants were allowed to desiccate until leaves failed to recover on rewatering. When water was withheld, one fully expanded leaf was placed in a shade envelope and another equivalent leaf on the same plant was tagged and supported horizontally on a wire frame. Control leaves did not need to be supported. Predawn and midday water potentials were determined on the same leaves of the same plant. Wilting occurred at predawn water potentials of –1.0 to 1.2 MPa in both species and wilted leaves declined over 2 to 3 d to –2.0 to –2.5 MPa before they became necrotic. In all of the acute water stress experiments, plants experienced cloudless summer days in the temperature controlled glasshouse (maximum 1800 μmol photons m⁻² s⁻¹). Another set of experiments was designed to check the relationship between change in quantum yield and 77 K fluorescence in acutely water stressed Xanthium. In these experiments water was withheld until midday wilting became evident. Then plants were taken into the laboratory each evening, water potential measured next morning, and leaf discs taken for fluorescence and quantum yield measurement. Fluorescence was measured before the quantum yield was determined, then measured again after quantum yield had been determined by subsampling the disc used in the O₂ electrode. The plant was returned to bright light after the initial sampling, and other discs taken for fluorescence measurement at intervals. In another experiment, detached leaves of Helianthus were kept in very weak light (1 μmol photons m⁻² s⁻¹) and allowed to desiccate in air, or kept with petiole in water. Fluorescence and photosynthetic properties were measured at intervals.

**Measurements of Photosynthesis and 77 K Fluorescence.** The apparent quantum yield and the CO₂ saturated rates of photosynthesis at high light and 25°C were measured by O₂ exchange using a Hansatech leaf disc electrode system (Decagon Devices, Pullman, WA) (11) fitted with a quartz iodide light source, as described by Walker and Osmond (30) and Adams et al. (1). Unless otherwise specified, leaf discs were taken from leaves of control or water stressed plants at noon, about 1 h after transferring plants from the glasshouse to the laboratory. At the same time another disc was taken from the same leaf and used for measurement of 77 K fluorescence at 692 nm using a device similar to that described by Bowles and Björkman (24) modified as described elsewhere (2). Leaf discs were dark adapted in the fluorescence cuvette for 10 min and then chilled in liquid N₂ for 5 min before fluorescence transients were measured. Data are reported as the ratio of variable fluorescence (Fₘ) to maximum fluorescence (Fₜ). Variable fluorescence was obtained by subtracting the instantaneous fluorescence (Fₛ) from Fₜ. In some experiments, the daily course of changes in fluorescence kinetics was measured.

Apparent quantum yield was calculated as the slope of the light response curve for those measurements taken at less than 100 μmol m⁻² s⁻¹. No correction for leaf absorbance was made. Quantum yields measured by the leaf disc electrode are approximately 30% higher than those measured at CO₂ saturation using CO₂ gas exchange techniques (24, 30). We measured apparent quantum yield of the same, unstressed Xanthium leaf, first by CO₂ exchange, then in the O₂ electrode. At an intercellular CO₂ concentration of 880 μbar CO₂ in 190 μbar O₂ we obtained a value of 0.060 mol CO₂ mol⁻¹ photons and in the O₂ electrode at approximately 50,000 μbar CO₂ and 150 μbar O₂ we obtained a value of 0.084 mol O₂ mol⁻¹ photons in red light. Similar results have been obtained using Phaseolus leaves. When corrected for leaf absorbance and the lower overall photochemical efficiency of white light, the O₂ electrode method gives quantum yields very close to the theoretical expectation of 0.125 mol O₂ mol⁻¹ photons in red light based on NADPH requirements (5, 12). The O₂ electrode method also provides a quick and convenient method for evaluation of the whole light response curve.

These experiments describe one of the first comparisons of the effects of water stress on both in vivo photosynthetic metabolism and photochemical activity by analysis of 77 K fluorescence emission. This latter technique, previously used to analyze effects of water stress on the primary photochemistry of a water stress tolerant plant, Nerium oleander (6), has been extensively evaluated recently using models of primary photochemistry developed on the basis of in vitro studies (4, 17).

**Water Potential and Other Measurements.** Leaf water potentials were measured predawn, at midday, and at dusk at intervals throughout each experiment on the leaf from which a leaf disc was taken for photosynthetic measurements, and on other leaves on the plant using a pressure bomb (Soil Moisture Corporation, Santa Barbara, CA). Pressure-volume curves were determined on leaves similar to those used for photosynthetic and fluorescence measurements and changes in cell osmotic pressures were calculated as described by Richter et al. (25).

**RESULTS**

*Sustained ( Chronic) Mild Water Stress in Sun or Shade.** Helianthus plants were allowed to dry down in full sunlight for 3 d until predawn water potential decreased from –0.25 MPa to –0.67 MPa. From pressure volume curves with similar leaves it was estimated that the osmotic pressure increased from 0.83 to 0.88 MPa. Some pots were then transferred to the shade treatment. Over the next 6 d the predawn water potential of stressed plants averaged –0.55 MPa with a maximum daily excursion to –0.95 MPa in sun and –0.85 MPa in the shade. The estimated osmotic pressures were 0.95 and 0.92 MPa, respectively. The effects of this treatment on photosynthetic O₂ exchange and on 77 K fluorescence were measured at intervals during this period. The light and CO₂ saturated rate of photosynthesis was reduced by about 30% 3 d after the treatment began (Fig. 1). In a similar experiment, the apparent quantum yield was depressed slightly (about 20%) after 6 d, independent of sun or shade treatment during water stress (Table I). A midday depression of 77 K fluorescence (Fₘ/Fₜ) was observed in control and water stressed leaves in the sun, but not in shaded leaves. This depression was greater in water stressed leaves than in controls, but Fₘ/Fₜ was fully restored to dawn levels by late afternoon.

These experiments were repeated with Xanthium and Helianthus using the shade envelope technique which ensured better control of leaf water potential of sun exposed and shaded leaves on the same plant. Predawn leaf water potentials of controls averaged –0.25 MPa. Water stressed plants were maintained at –1.05 ± 0.06 MPa throughout and leaves did not wilt in these experiments. For Xanthium it was estimated that the osmotic pressure increased from 0.88 to 1.10 and for Helianthus the changes were estimated by stress to be from 0.86 to 0.95 MPa. The somewhat greater, but still mild water stress in these experiments again had a large effect on the CO₂ saturated rate of photosynthesis at high light (Figs. 2, 3).

In Xanthium after 4 d without water in the sun there was a 40% decline in maximum photosynthesis and over the subse-
Table 1. Effects of Sustained Mild Water Photosynthesis Stress on Apparent Quantum Yield and 77 K Fluorescence (Fv/Fm) in Leaves of Helianthus

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Photosynthesis</th>
<th>Apparent quantum yield</th>
<th>Fv/Fm*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>μmol m⁻² s⁻¹</td>
<td>mol O₂ mol⁻¹ photons</td>
<td>ratio</td>
</tr>
<tr>
<td>Control sun</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 d</td>
<td>38.4</td>
<td>0.105</td>
<td>0.85</td>
</tr>
<tr>
<td>6 d</td>
<td>39.4</td>
<td>0.105</td>
<td>0.85</td>
</tr>
<tr>
<td>Water stress sun</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 d</td>
<td>30.2</td>
<td>0.090</td>
<td>0.86</td>
</tr>
<tr>
<td>6 d</td>
<td>25.6</td>
<td>0.086</td>
<td>0.86</td>
</tr>
<tr>
<td>Water stress shade</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 d</td>
<td>37.3</td>
<td>0.105</td>
<td>0.86</td>
</tr>
<tr>
<td>6 d</td>
<td>27.2</td>
<td>0.086</td>
<td>0.86</td>
</tr>
</tbody>
</table>

* Range of values, lowest being observed at about 1300 h.

FIG. 1. Effect of sustained mild water stress on light response curve for photosynthetic O₂ exchange at CO₂ saturation in Helianthus leaves. Controls before (○) and after (●) 3 d and separate water stressed plants after 3 d in the sun (△) or shade (▲).

FIG. 2. Effect of sustained mild water stress in sun or shade on the light response curves for leaf photosynthetic O₂ evolution at CO₂ saturation in Xanthium. Shaded leaves on same plant in shade envelope. Controls before (○) and after 9 d (■); treated plants after 4 d (○) and 9 d (●) at -1.05 MPa.
Much the Fm inasion by the observed during sustained Xanthium indicated same fluorescence by ured independent light quickly than techniques used plants deprived plants water envelopes possible with plants. It excursion in reduction by quantum Xanthium. Controls Shaded leaves lianthus. Shaded leaves were before (-1.1 MPa) on CO2 Saturated Photosynthesis (at 600 μmol photons m-2 s-1), Apparent Quantum Yield and 77 K Fluorescence in Leaves of Xanthium in Sun or Shade

<table>
<thead>
<tr>
<th>Treatment, Time</th>
<th>Photosynthesis</th>
<th>Quantum Yield</th>
<th>Fluorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control 3 d</td>
<td>42.8</td>
<td>0.098</td>
<td>0.84</td>
</tr>
<tr>
<td>Sun 6 d</td>
<td>36.6</td>
<td>0.093</td>
<td>0.81</td>
</tr>
<tr>
<td>Control 3 d</td>
<td>32.5</td>
<td>0.101</td>
<td>0.82</td>
</tr>
<tr>
<td>Shade 6 d</td>
<td>27.3</td>
<td>0.089</td>
<td>0.81</td>
</tr>
<tr>
<td>Stress 3 d</td>
<td>33.5</td>
<td>0.097</td>
<td>0.82</td>
</tr>
<tr>
<td>Sun 6 d</td>
<td>16.0</td>
<td>0.068</td>
<td>0.82</td>
</tr>
<tr>
<td>Stress 3 d</td>
<td>22.5</td>
<td>0.097</td>
<td>0.82</td>
</tr>
<tr>
<td>Shade 6 d</td>
<td>14.7</td>
<td>0.082</td>
<td>0.79</td>
</tr>
</tbody>
</table>

reduction in apparent quantum yield in Xanthium was not accompanied by a decrease in Fv/Fm of early morning 77 K fluorescence. In Helianthus, there was little change in apparent quantum yield or Fv/Fm of early morning 77 K fluorescence. An excursion in Fv/Fm throughout the day was observed in control plants. It was greatest in water stressed plants in the sun and least in plants in the shade.

Rapidly Applied (Acute) Water Stress in Sun or Shade. The techniques used above were applied to Xanthium and Helianthus plants which experienced acute, terminal water stress. Xanthium plants deprived of water wilted in 4 to 5 d (leaf water potential -1.2 MPa) and were kept without water for a further 2 to 3 d (leaf water potential -1.8 to -2.5 MPa). Wilted leaves kept in shade envelopes during these treatments became necrotic more quickly than those in full sunlight and so measurements were not possible with shade leaves. Preliminary experiments with Xanthium indicated that acute water stress caused a substantial light independent depression of quantum yield in air, as measured by CO2 exchange, without effects on early morning 77 K fluorescence (data not shown). Studies in the O2 electrode system showed that acute water stress treatment produced much the same effects on CO2 saturated photosynthesis as high light as observed during sustained mild water stress (Fig. 4; cf. Fig. 2). However, the decline in photosynthesis at -2.3 MPa was accompanied by a substantial decline in quantum yield (Fig. 4).

Control Xanthium leaves in the sun displayed a diurnal excursion in Fv/Fm, but not in shaded leaves (Fig. 5). With progressive acute water stress the magnitude of the diurnal excursion in Fv/Fm increased and the level of recovery in the afternoon declined. Much the same response to acute stress was observed in Helianthus (Fig. 6). In these experiments, Helianthus did not attain water potentials as low as Xanthium before the leaves became necrotic. Leaves at -1.8 MPa or lower water potential did not recover when plants were rewated. The fluorescence properties

![Fig. 3. Effect of sustained mild water stress in sun or shade on the light response curves for leaf photosynthetic O2 evolution at CO2 saturation in Helianthus. Shaded leaves on same plant in shade envelope. Controls before (□) and after 9 d (●); treated plants after 3 d (○) and 7 d (○) at -1.05 MPa.](image)

![Fig. 4. Effect of acute water stress in the sun on the light response curve for leaf photosynthetic O2 evolution at CO2 saturation in Xanthium.](image)
of control and water stressed *Helianthus* leaves are shown in Figure 7. The diel depression in $F_v/F_m$ observed previously in chronic, mild water stress (Table I) was exaggerated in acutely stressed *Helianthus* and was greater in sun than shade, both in control and stressed leaves (Fig. 7). In severely water stressed leaves kept in room light (20 μmol photons m$^{-2}$ s$^{-1}$) there was no diel change in $F_v/F_m$, but in sunlight $F_v/F_m$ was depressed from 0.85 to 0.55. Most of this depression was reversible, and at dawn the next day $F_v/F_m$ returned to 0.81.

The question of whether the extent of light dependent depression of $F_v/F_m$ was due to a change in onset or recovery processes was examined by comparing high water potential and low water potential leaves on intact plants of *Xanthium* and in detached leaves of *Helianthus*. Pots of well watered and acutely water stressed *Xanthium* plants were taken to the laboratory in the evening and $F_v/F_m$ measured early next morning. Figure 8a shows that there was little difference in fluorescence at the outset, but after exposure to sunlight (1300 μmol photons m$^{-2}$ s$^{-1}$) for several hours, the stressed leaves showed more rapid decline in $F_v/F_m$. On return to the laboratory light (16 μmol photons m$^{-2}$ s$^{-1}$) there was a rapid increase in $F_v/F_m$ of the stressed leaves, but overall the rate of recovery of $F_v/F_m$ was similar to controls. Much the same response was found in acutely stressed detached leaves of *Helianthus* (Fig. 8b). In these, the decline of $F_v/F_m$ in sunlight was much more rapid. The rapid initial increase in $F_v/F_m$ of the stressed leaves was again observed, but overall recovery was slower, possibly because very low light (1 μmol photon m$^{-2}$ s$^{-1}$) was used.

A summary of photosynthetic response to acute water stress has been presented in Figure 9. The rate of CO$_2$ saturated photosynthesis (measured at 600 μmol photons m$^{-2}$ s$^{-1}$) is much

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**Fig. 7.** Diel changes in 77 K fluorescence in leaves of *Helianthus* exposed to acute water stress in sun (C) or shade (○). In the treatment shown at −2.00 MPa, leaves were kept in deep shade (20 μmol photons) or sun.

**Fig. 8.** Time course of changes in 77 K fluorescence in control and acutely water stressed leaves of (a) intact *Xanthium* plants and (b) detached leaves of *Helianthus* allowed to desiccate in air in very weak light (1 μmol photons m$^{-2}$ s$^{-1}$).

**Fig. 6.** Effect of acute water stress in the sun on the light response curve for leaf photosynthesis at CO$_2$ saturation in *Helianthus*.
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more responsive to decreasing leaf water potential (Fig. 9a) than is apparent quantum yield or fluorescence. Apparent quantum yield declines slightly until about -1.7 MPa, and then precipitously in Xanthium (Fig. 9b). In detached leaves of Helianthus kept in very weak light (1 μmol photon m⁻² s⁻¹) there was absolutely no change in $F_0/F_m$ of 77 K fluorescence, even at the lowest water potentials measured before leaves became crisp (Fig. 9c). Water stressed leaves of intact plants of Helianthus or Xanthium also showed very little influence of stress on early morning values of $F_0/F_m$.

**DISCUSSION**

Our experiments confirm that with water stress sensitive plants such as Xanthium and Helianthus, the primary effects of water stress are on maximum photosynthetic activity, measured at CO₂ saturation and high light. Such effects have been observed repeatedly using conventional gas exchange analysis (8, 13, 26, 27, 29). At limiting CO₂ (26, 27, 29) or limiting light (this study) nonlethal water stress has little effect on photosynthesis. On the basis of contemporary models of photosynthetic biochemistry in vivo, these results indicate effects of water stress on the maximum capacity for regeneration of RuBP for photosynthetic CO₂ fixation (27, 29).

In these experiments with Xanthium and Helianthus, and other experiments with a desert annual Eriogonum inflatum (22), quantum yield was much less sensitive to water stress than was light and CO₂ saturated photosynthesis. Quantum yield was depressed by water stress in these water stress sensitive plants independent of light, but only by severe stress subsequent to wilting, from which the leaves did not recover. CO₂ saturated photosynthesis at high light is markedly depressed before wilting occurs. The inhibition of photosynthesis resulting from osmotic stress of cells and protoplasts depends on the degree of volume change induced by the stress (14, 27). In contrast, intact leaves show substantial reductions in photosynthetic rate with very small changes in estimated osmotic pressure, an indicator of volume changes.

Studies of chloroplasts isolated from water stressed Helianthus leaves (16) indicated that electron transport and photophosphorylation were very sensitive to water stress. However, subsequent studies with (27) and protoplasts (15) indicate that electron transport is not affected by low water potential. Strong biochemical evidence has been adduced for effects of water stress on the conformation and activity of chloroplast coupling factor (15, 20, 27, 31).

The effect of water stress on photophosphorylation could explain most of the results obtained in this study. Mild water stress could reduce the maximum capacity for photophosphorylation. When photosynthesis is limited by light or CO₂, the capacity for photophosphorylation would still be sufficient and so the effect of mild water stress would only be apparent at saturating CO₂ and high light. More severe water stress could damage the coupling factor enough to cause uncoupling, as was observed with osmotically stressed cells (27). This uncoupling would cause a reduced quantum yield under severe water stress.

If the reduced quantum yield seen after acute stress resulted from uncoupling of photophosphorylation from electron transport rather than light dependent damage to PSI, then it is expected that the reduced quantum yield would occur independent of light regime during stress and that low temperature fluorescence would be unaffected.

Severe water stress evidently predisposes leaves to light dependent changes in primary photochemistry. Water stress exaggerates the light dependent diel depression of $F_0/F_m$ in both Xanthium and Helianthus. On the basis of his analysis of this reversible quenching of PSI and PSII fluorescence emission in leaves of sun plants, Björkman (4) concludes that it is associated with stimulation of the rate constant for nonradiative energy dissipation in the pigment bed. This quenching may reflect the operation of regulatory and protective processes. The fact that severe water stress exaggerates this reversible quenching may imply that regulation is impaired and/or the requirement for protection is greater. Successive cycles of this diel change lead to progressively lower values of $F_0/F_m$ each morning. That is, recovery seems to be incomplete, even though the rate of recovery is comparable. Water stress thus seems to enhance the rate of damage to primary photochemistry in acutely water stressed leaves.

It now remains to survey the light dependence of the above catena of water stress effects on photosynthetic biochemistry in vivo and assess the potential significance of photoinhibition. The initial depression of light and CO₂ saturated photosynthesis during chronic mild water stress and in acute water stress in Xanthium and Helianthus (and Eriogonum (22)) seems to be independent of light regime during the stress. This conclusion cannot be stated with absolute security because shade acclimation and the ontogeny of leaf senescence are both accompanied by a
decrease in this parameter. We cannot envisage an experimental design which would eliminate these additional interactions as factors in our comparison of shade and sun. Shade acclimation and onotogenetic effects on leaf photosynthesis are not normally associated with changes in apparent quantum yield, unless nutritional complications arise (21). Sustained mild (chronic) water stress leads to a light dependent depression of quantum yield which accompanies the depression of CO₂ and light saturated photosynthesis in Xanthium. In some experiments with Xanthium (not shown) the light dependent decline in quantum yield was large but usually plants stressed for periods long enough to demonstrate a substantial light dependent decline in quantum yield senesced before reproducible results could be obtained. This was especially true for stressed leaves in the shade. In Helianthus we were unable to demonstrate a substantial light dependent inhibition of quantum yield, confirming previous observations (28). The light dependent attenuation in diel changes in 77 K fluorescence which is observed in severely stressed leaves may presage photoinhibition. However, it is a terminal and insignificant part of photosynthetic responses to these water stress sensitive plants. Leaves which display these effects will not recover from their water stress experience.

In water stress tolerant Nerium oleander, light and CO₂ saturated photosynthesis, as well as quantum yield, are reduced in response to water stress under natural conditions (6). Comparisons of the 77 K fluorescence of the upper and lower surfaces of leaves during the onset of water stress show that these changes are accomplished by light dependent inhibition of F₄/F₆ (6). These changes in F₄/F₆ can be simulated, at high water potential, by artificially sealing the epidermis and forcing internal recycling of CO₂ in photorespiration. We suspect these changes may differ in time constants, but not in kind, from the light dependent changes studied in CO₂ deprived leaves of water stress sensitive or tolerant species at high water potential (23). We believe that these studies indicate that light dependent damage to primary photochemistry is a long-term consequence of impaired photosynthetic carbon metabolism but that it is not the primary lesion in photosynthesis caused by water stress of mesophytic plants.

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LITERATURE CITED

28. SHARP RE, JS BOYER 1986 Inhibition of photosynthesis at low water potentials in sunflower: lack of photoinhibitory effects. Plant Physiol 82: 90–95