

Relative Sensitivity of Photosynthetic Assimilation and Translocation of ^{14}C Carbon to Water Stress¹

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ABSTRACT

The relationship between photosynthesis and translocation rate changes as affected by water stress intensity and stage of plant development was evaluated in cotton and sorghum, representing a C_3 and a C_4 photosynthetic type, respectively. Photosynthetic rates were reduced as midday leaf water potentials declined from -14 to -27 bars in both species. Sorghum maintained higher photosynthesis and translocation rates compared to cotton at comparable leaf water potentials; however, the rate of change per bar decline in water potential was greater in sorghum than in cotton. Photosynthetic rates were reduced with increasing water stress prior to any significant change in translocation rates suggesting that photosynthesis is the more sensitive of the two processes. Severe water stress, corresponding to leaf water potentials of -27 bars, did not completely inhibit either photosynthesis or translocation.

Disagreement exists as to the relative sensitivity of photosynthesis and translocation to water stress. Several studies have concluded that translocation is more sensitive to water deficits than is photosynthesis (6, 7). In contrast to these conclusions, others (11, 13, 14, 19, 20) have suggested that photosynthesis is more sensitive to water stress than translocation. Wardlaw (19) has indicated that the effect of water stress on the translocation process is related to the availability of photosynthate more so than by a direct effect on the translocation process mechanism *per se*.

The objective of this study was to define the relationship between leaf water status, photosynthesis, and translocation of current assimilate as a function of photosynthetic type (C_3 versus C_4) and growth stage.

MATERIALS AND METHODS

Sorghum (*Sorghum bicolor* L. Moench) and cotton (*Gossypium hirsutum* L. cv. SP 37) were chosen for study due to differences in photosynthetic types (C_4 versus C_3) and growth habits (determinate versus indeterminate). Two sorghum hybrids (ATX378 \times TX7000 and ASC35 \times SC599-6) were selected due to differences in leaf senescence characteristics under water stress. The hybrid ATX378 \times TX7000 represents a genotype in which the lower leaves readily senesce during grain filling. Of the 16 total leaves produced this hybrid will retain from 5 to 8 leaves during grain filling depending upon the intensity and duration of the water stress. The hybrid ASC35 \times SC599-6 represents a more nonsenescent type. Of the 16 leaves it produces, 10 to 12 leaves will be retained during grain filling depending upon stress level.

Experiments were conducted in the glasshouse during the fall and spring and field studies were conducted during the normal summer growing season. Glasshouse environmental conditions averaged 30/20 C temperatures on a day/night basis with a photoperiod of 11.5 to 12 h of sunlight. Light intensity at the leaf surface generally exceeded $1,500 \mu\text{E m}^{-2} \text{s}^{-1}$ at midday. Experimental plants were grown in large containers ($4 \times 2 \times 1$ m) filled with fine sandy loam soil (fine loamy, mixed thermic Aridic Paleustoll). One container served as the control representing the nonstressed condition. A second container was used to allow stress to develop during the period of maximum vegetative development prior to the beginning of flowering. A third container was allowed to develop stress during the period of maximum reproductive development (15-25 days after flowering). Field plots were established on a clay loam soil type (fine, mixed, thermic family of Torrertic Paleustoll) approximately 1 m deep underlain by a calcic horizon. Populations were 18 to 20 plants m^{-2} for sorghum and 10 plants m^{-2} for cotton in both glasshouse and field experiments. Irrigation water was supplied to the control plants whenever the midday Ψ_w of the uppermost, fully expanded leaf declined 2 bars from normal midday minimum (-14 bars for sorghum, -15 bars for cotton).

Photosynthetic rates of individual leaves were determined using

Photosynthetic rate reductions due to increasing water stress have been observed in a variety of plant species. Stomatal effects are usually considered to be the first and major limitation to CO_2 fixation, although inhibitions at the chloroplast level have been proposed (5, 10). Under semiarid field conditions, stomatal closure is not evident in fully illuminated cotton leaves even at Ψ_w^2 approaching -30 bars; however, photosynthesis is severely reduced (1, 2). In this same environment, stomatal regulation is observed only prior to flowering in sorghum's response to increasing water stress (1). Photosynthetic rates of individual leaves of sorghum are significantly reduced prior to any measurable increase in stomatal resistance. After the leaf has attained maximum size no evidence of stomatal closure exists in response to increasing water stress; however, photosynthetic rates are severely affected (12, and unpublished data of Krieg).

Leaf photosynthesis may be affected by accumulation of photosynthate due to effects on translocation or utilization of the assimilate (16, 18). Inhibition of assimilate translocation by water stress has been observed in a number of plant species (6, 7, 11, 13). Wardlaw (19, 20) has indicated that the major effect of water stress on translocation is to delay and reduce the rate of transfer of sugars from the assimilating tissue to the conducting tissue. The velocity of transport within the conducting tissue is not affected by water stress.

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² Abbreviation: Ψ_w : leaf water potential.

a $^{14}\text{CO}_2$ fixation technique (15). However, we used 0.2 ml of 70% HClO_4 and 0.2 ml of 30% H_2O_2 for tissue digestion and bleaching. Translocation rates were determined using the techniques described by Hofstra and Nelson (8). Photosynthesis and translocation measurements were obtained at two stages of plant development which were 7 to 10 days after panicle initiation for sorghum and during flower bud development for cotton and 20 to 25 days after flowering in each species during rapid fruit development. Data were obtained from the uppermost collared leaves during panicle development (corresponded to 8th through 10th leaves initiated), and the first leaf below the flag leaf during grain filling in sorghum. In cotton, the uppermost fully expanded leaves on the main stem and leaves subtending reproductive structures on the sympodial branches were used. Photosynthesis and translocation rate measurements were conducted between 1200 and 1300 h (CDT). The light intensity on the leaf surface generally exceeded $1,900 \mu\text{E m}^{-2} \text{s}^{-1}$ in the field and $1,500 \mu\text{E m}^{-2} \text{s}^{-1}$ in the greenhouse at the time physiological measurements were made. Each data point represents the mean of at least three different plants. All data were analyzed for statistical significance using Duncan's New Multiple Range Test and regression analysis (17).

RESULTS AND DISCUSSION

Field-grown plants and glasshouse-grown plants responded similarly to water stress intensity; therefore, the derived relationships are based upon pooled data from both growth environments. Although many studies have revealed significant differences in the physiological responses of different plant species between field and greenhouse environments, we believe that the major reason these plants responded similarly in the two environments was due to the high incident radiation level at the plant surface and probably more importantly to the volume of soil available to each plant which approximated field conditions. The plants were allowed to develop stress slowly and thus comparably to that experienced under field conditions. The glasshouse-grown plants were in excess of 90% of their field-grown counterparts in terms of leaf number and leaf area and in development and size of reproductive organs.

Photosynthetic rates of cotton leaves were reduced an average of 26% prior to flowering by a water stress differential of 11 bars and by 39% due to a differential of 13 bars during the boll-filling stage of development (Table I). The differences indicated that the boll-filling stage was more sensitive to water stress or that the slight difference in Ψ_w of the stressed plants between the two growth stages resulted in the pronounced decline. Calculating the change in photosynthetic rate on the rate of change in Ψ_w resulted in no significant growth stage effect for leaves on the main axes (monopodial leaves) but significant effects for the leaves on the sympodial branches which were more sensitive during the boll-filling stage of growth. Stomatal resistance was not significantly affected by the intensity of water stress encountered and remained in the 2 s cm^{-1} range for leaf resistance, similar to our previous results (1, 2).

Photosynthetic rates of the different leaf types varied with stage of development (Table I). During flower bud development, photosynthetic rates of the leaves on the main axis appeared to be greater than leaves on the sympodial branches. However, during the boll development period, the pattern was reversed and sympodial leaves had higher photosynthetic rates. Since the developing fruit receives most of its assimilate from the nearest leaf (4), the increased demand probably had a marked influence on the activity of the sympodial leaf.

Photosynthetic rates of sorghum were significantly greater than cotton at all growth stages and comparable levels of Ψ_w (Table II). Somewhat contrary to the results obtained for cotton concerning the relative sensitivity of the two growth stages, sorghum photosynthetic rates were reduced 37% prior to flowering at a stress differential of 9 bars, and 24% with a 6-bar differential during the grain-filling stage of development. Calculated on the basis of rate of change in photosynthesis per unit change in Ψ_w no significant growth stage effect existed (4% reduction or $2 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ reduction in photosynthetic rate per bar decline in Ψ_w). Significant genotype differences were apparent in the photosynthetic rate response to water stress in sorghum in that the senescent hybrid (ATX378 \times TX7000) changed at a rate of $2.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ per bar decline, and the nonsenescent sorghum (ASC35 \times SC599-6) changed at a rate of $1.8 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$

Table I. Photosynthetic Rates of Cotton Leaves as a Function of Growth Stage, Leaf Type, and Water Stress Intensity

Growth Stage	Leaf Type	Photosynthetic Rate		Reduction in Photosynthetic Rate Due to Water Stress		
		Nonstressed ¹	Stressed ¹	%	%/bar	$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ per bar
		$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$				
Prior to flowering	Monopodial	44.0 ab ²	3.18 d	27	2.5	1.1
	Sympodial	38.4 c	27.6 de	26	2.2	0.9
During boll development	Monopodial	39.7 bc	25.2 e	38	2.7	1.0
	Sympodial	47.0 a	27.9 de	40	3.1	1.5

¹ Nonstressed plants had midday Ψ_w of -14 to -15 bars; stressed plants had an average Ψ_w of -26 bars prior to flowering and -28 bars during boll development.

² Means followed by the same letter are not significantly different ($P < 0.05$) using Duncan's new multiple range test (17).

Table II. Photosynthetic Rates of Sorghum Leaves as a Function of Growth Stage, Genotype, and Water Stress Intensity

Growth Stage	Genotype	Photosynthetic Rate		Reduction in Photosynthetic Rate Due to Water Stress		
		Nonstressed ¹	Stressed ²	%	%/bar	$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ per bar
		$\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$				
Prior to flowering	ATX378 \times TX7000	59.3 a ²	37.3 cd	37	4.1	2.4
	ASC35 \times SC599-6	55.8 ab	35.2 d	37	3.4	1.8
During grain filling	ATX378 \times TX7000	55.0 ab	40.5 c	25	4.2	2.5
	ASC35 \times SC599-6	49.1 b	38.1 c	23	3.8	1.8

¹ Nonstressed plants had midday Ψ_w of -16 bars, stressed plants had average midday Ψ_w of -26 bars prior to flowering and -24 bars during grain filling.

² Means followed by the same letter are not significantly different ($P < 0.05$) using Duncan's new multiple range test (17).

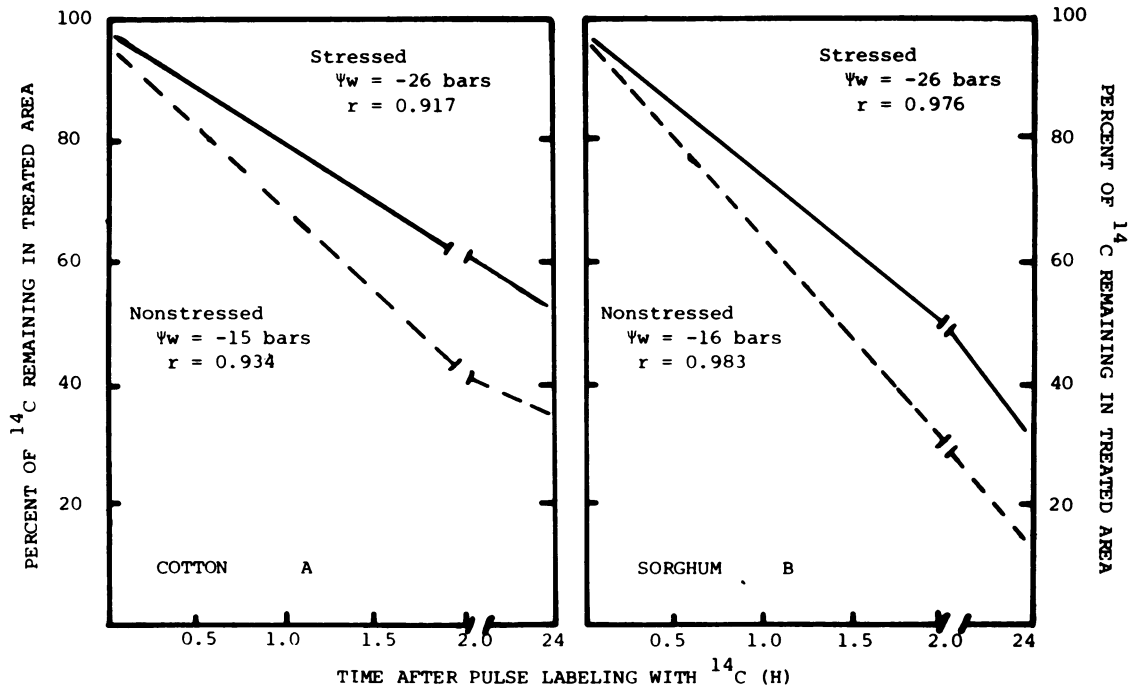


FIG. 1. Water stress effect on the translocation of ¹⁴C from individual leaves of cotton (A) and sorghum (B).

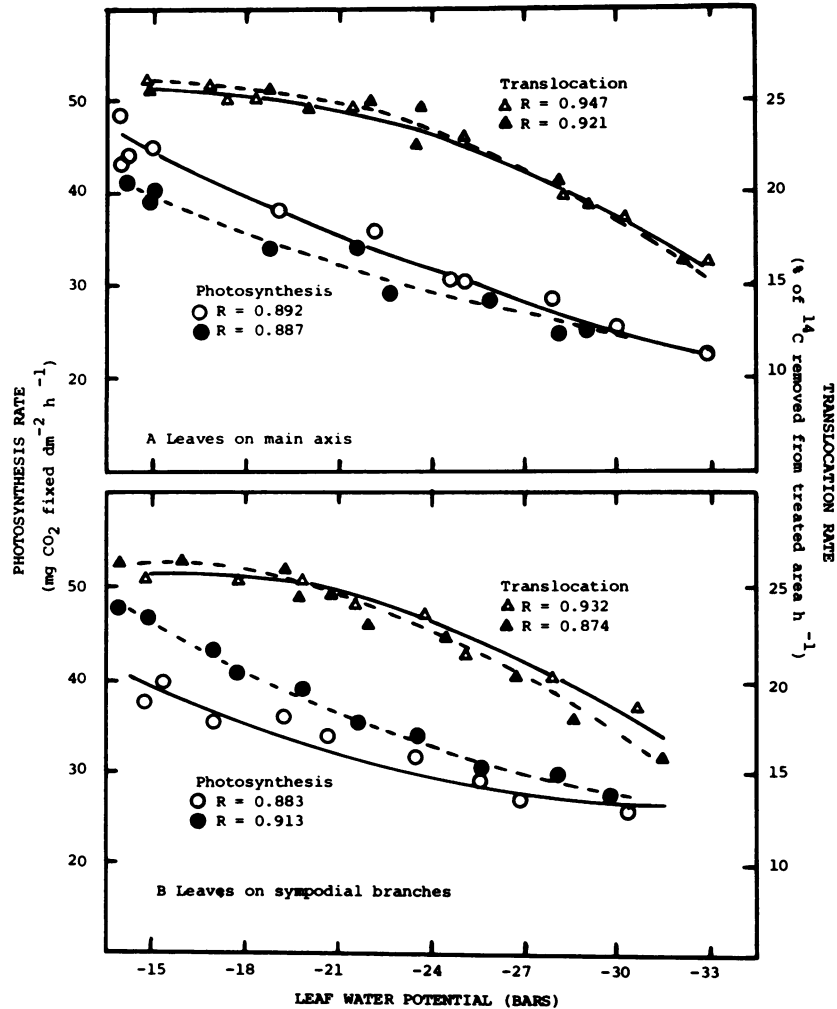


FIG. 2. Response of photosynthesis and translocation rates to increasing water stress in cotton as a function of leaf type (A: leaves on main axis; B: leaves on sympodial branches), and growth stage (○, △: flower bud development; ●, ▲: boll-filling period).

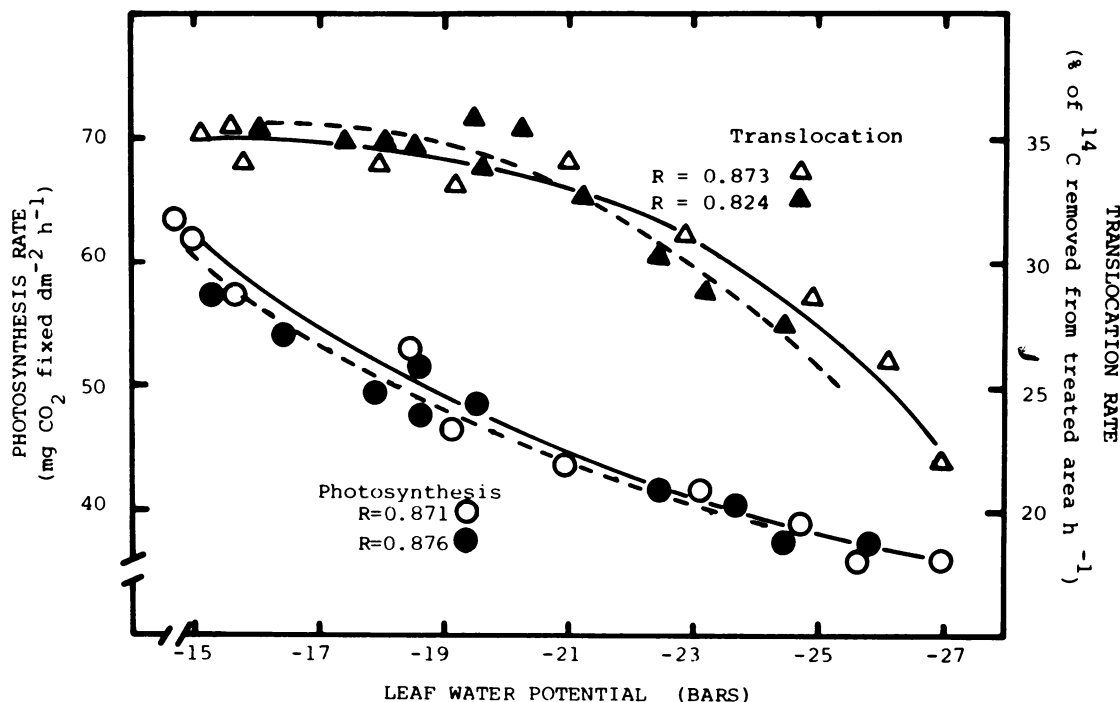


FIG. 3. Response of photosynthesis and translocation rates to increasing water stress in sorghum as a function of growth stage (○, △: panicle differentiation; ●, ▲: grain filling).

per bar. Although stomatal resistance of sorghum does increase prior to flowering at the stress intensities encountered, the consistent change in the photosynthetic rate response to water stress at both growth stages strongly suggests that stomatal resistance was not the primary cause of the observed response.

Translocation of current assimilate from various source leaves of the two species followed a pattern similar to that observed in other species (8, 9) in that a rapid linear phase existed for about 2 h after pulse labeling followed by a slower curvilinear phase (Fig. 1). The translocation rate during the linear phase was significantly affected by species and water stress. Under nonstressed conditions ($\Psi_w = -14$ to -15 bars), cotton translocated current assimilate at a rate of 26% per h, whereas sorghum translocated at a rate of 35% per h. Water stress ($\Psi_w = -26$ bars) reduced the translocation rate to 19% per h for cotton and 24% per h for sorghum. No significant differences were observed due to leaf type or growth stage in the translocation response of cotton to water stress. However, significant growth stage effects were observed in sorghum. The data plotted in Figure 1 for sorghum represent the response prior to flowering. During rapid grain filling no statistically significant reductions existed; however, the mean rate was reduced to 29% by water stress. The lack of a significant reduction could have been due to the difference in stress intensity between the two growth stages. Leaf water potentials differed by only 6 bars during grain filling whereas a 9-bar differential existed between nonstressed and stressed plants during the preflowering period.

The data obtained at specific levels of stress did not allow the differentiation of the two physiological systems as to relative sensitivity to water stress. During the field experiment, the rate of change in each process was monitored during a drying cycle in each growth stage for each species. In both cotton and sorghum, photosynthetic rates declined as stress intensified prior to any measurable reduction in translocation rates. In cotton, leaf type \times growth stage interactions were observed in the photosynthetic rate response but not in the translocation rate response. Prior to flowering, leaves on the main axis had higher photosynthetic rates under nonstressed conditions and were more severely affected by

water stress than were the same leaf types during the boll-filling stage of development (Fig. 2A). The opposite pattern existed for leaves on sympodial branches (Fig. 2B). The rate of translocation of current assimilate from each leaf type was reduced as Ψ_w approached -24 bars irrespective of stage of development.

The Ψ_w resulting in a 10% reduction in the photosynthetic rate of cotton was -18 to -20 bars. As water stress intensified from -24 to -30 bars the rate of reduction in the translocation rate exceeded that of the photosynthetic rate decline.

In sorghum, essentially the same phenomenon was observed (Fig. 3). Photosynthesis declined at a rate of $3.5 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ per bar within the range of -15 to -20 bars. From -20 to -27 bars the rate of decline was approximately $1.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ per bar. No significant difference due to growth stage was apparent. Translocation rate was not altered until Ψ_w declined to -21 bars similar to the response in cotton. The translocation rate declined at a rapid rate from -22 bars to -27 bars.

The velocity of assimilate transport in the translocation stream was also measured as a function of stress intensity with the results indicating no significant effects similar to the findings of Wardlaw (19, 20). The results strongly suggest that the CO_2 assimilation process is more sensitive to water stress than is the translocation of the current assimilate in these two plant species representing C_3 and C_4 photosynthetic types. The results of this series of experiments confirm the previous conclusions (11, 13, 14, 19, 20) and extend the findings across growth stages, environments (glasshouse and field), and a wider range of Ψ_w . Brevedan and Hodges (6) and Hartt (7) came to a different conclusion as to the relative sensitivity of photosynthesis and translocation to water stress. However, their interpretation may be biased by stress intensity or by partitioning differences due to stress and therefore does not clearly differentiate photosynthesis and translocation of current assimilate from the source leaf.

Based upon the results presented herein, it is our conclusion that the CO_2 assimilation process is affected first and more severely by water stress than is the translocation process. The rate of translocation is ultimately affected but the reduction is closely related to the amount of photosynthate available for translocation.

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