Photosynthetic Recovery From Drought in Relation to Stress Effects on Leaf Osmotic Potential and Nitrogen Content

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Summary

A field study was conducted at Córdoba, Spain to evaluate photosynthetic (Pn) recovery after drought in relation to stress effects on specific leaf weight (SLW), leaf nitrogen (N) content, and leaf osmotic potential. Upper (sun) leaves of droughted plants had significantly higher SLW and leaf N per unit leaf area than upper leaves of control (irrigated) plants, but comparisons among lower shaded leaves showed no significant treatment effect on these parameters. Substantial osmotic adjustment was observed at all leaf positions in droughted plants, and osmotic potentials were most negative in upper leaves. Photosynthesis per unit leaf dry weight of upper leaves of droughted plants recovered to about 50% of control values 1 day after irrigation, while Pn calculated on a per unit leaf area basis showed almost complete recovery in the same time period. This contrast was associated with the SLW response to drought and concentration of N (and presumably photosynthetic enzymes) per unit area in upper leaves of droughted plants. Recovery of leaves lower in the plant canopy was slower, but 10 days after irrigation, Pn per unit leaf area, Pn per unit leaf N, and leaf water potential components of both upper and lower leaves recovered to control values.

Introduction

The decline in Pn of sunflower as soil water deficits develop is usually accompanied by a decline in stomatal conductance (Rawson and Constable, 1980; Turner et al., 1978), although recent evidence indicates that non-stomatal factors such as ribulose-1,5-bisphosphate regeneration (Gimenez et al., 1992) and chloroplast dysfunction (Matthews and Boyer, 1984) may be involved. Wise et al. (1990) found no evidence of permanent damage to the photosynthetic apparatus due to low Ψ_L imposed in the field. They emphasized the ability of sunflower to acclimate to the diurnal cycling in Ψ_L under both irrigated and non-irrigated field conditions. Our observations in preliminary field experiments suggested considerable capacity for recovery of photosynthetic activity after drought in this crop species, particularly in upper leaves that intercept the bulk of incoming solar radiation and are therefore most important in terms of carbon and water economy of the plant. The primary objective of this study was to examine the water relations and photosynthetic response of mature field-grown sunflower plants to a drought and recovery cycle. The response of upper and lower leaf positions was also compared.

Materials and Methods

The experiments were conducted on a deep sandy-loam Typic Xerofluvent soil at the Agricultural Research Center of Córdoba, Spain (38° N, 4° W) in 1991. Sunflower (cv. Sungro 380) was sown on 22 February and plants were thinned to 7 plants m^{-2} at the 4-leaf stage. Prior to sowing, the plots were fertilized with urea (156 kg N ha^{-1}), and Trifluralin herbicide was applied for weed control. Frequent light sprinkler irrigations were applied to the entire experimental area until treatments were imposed at 54 days after emergence.

WET treatments were trickle-irrigated (2 liter h^{-1} emitters, 0.3 m apart in the row) with an amount equal to the estimated crop evapotranspiration of the previous day. DRY plots received no water for several 10 - 20 day periods, with each dry period followed by a short recovery period with irrigation. The research reported here was conducted during the final drought-recovery cycle, where DRY plots were reirrigated on 11 June. Treatments were arranged in a randomized, complete block design with four replications and three guard rows between each plot.

All measurements were taken at midday (13:00 - 15:00) on fully expanded leaves in the upper (full sun) and lower (partial shade) sections of the plant canopy. Nodal positions selected sometimes differed between treatments because of slightly delayed development in the DRY plots. Net photosynthesis was determined with a portable "closed" leaf gas exchange system (LI-COR 6200, Lincoln NE USA) at saturating light intensity (> 1500 $\mu E\ m^{-2}\ s^{-1}$ photosynthetic photon flux density). Adjacent plants were pulled back in the early morning so that leaves to be measured could acclimate to full sunlight for at least 4 h. Leaves measured for Pn were collected, dried at 70° C for 48 h, weighed, and saved for later total N analysis using a micro-Kjehldal procedure.

Immediately after Pn measurements, leaves from the same plants at nodes one above or below those used for Pn, were measured for leaf water potential (Ψ_L) with a pressure bomb. These leaves were then wrapped in aluminum foil, placed in an ice chest maintained between 5 - 10° C, and transported to the laboratory within 1 h where they were frozen and stored at -10° C. The leaves were later thawed to room temperature for measurement of osmotic potential (Ψ_o) using a thermocouple psychrometer (Decagon Devices, Pullman, WA USA). Leaf pressure potential (Ψ_p) was calculated as the difference between Ψ_L and Ψ_o.

Results

Midday Ψ_L in the DRY treatment declined to -1.96 MPa just prior to reirrigation on 11 June (Table 1). This was 1.0 MPa more negative than the control, WET, treatment. There was little indication of recovery of Ψ_L 1 day after reirrigation (12 June). The Ψ_o was more negative in DRY than WET treatments, and within the DRY treatment, Ψ_o was more negative in upper than lower leaves. A slight positive turgor pressure was observed in upper, but not lower, leaves of the DRY treatment 1 day after reirrigation. However, Ψ_p of both upper and lower leaves were significantly lower in DRY than WET plots at this time. At 10 days after reirrigation, Ψ_L, Ψ_o, and Ψ_p in the DRY treatment completely recovered to control values, regardless of leaf position.

Specific leaf weight was significantly higher in the DRY compared to WET treatment upper leaves at the end of the drought period, 11 June (Table 2), but this was not observed in the lower leaves at this time. Leaf N per unit leaf dry weight was higher in the WET treatment for both upper and lower leaves. However, the increase in SLW of upper leaves of droughted plants tended to concentrate leaf N on a per unit leaf area basis, and N per unit leaf area was significantly higher in upper leaves of the DRY compared to the WET treatment. After 10 days of recovery, both upper and lower leaves of the DRY treatment showed significantly higher leaf N per unit leaf area.

Table 1. Total leaf water potential (Ψ_L), osmotic potential (Ψ_o) and calculated turgor pressure ((Ψ_p) of upper and lower leaves in the canopy, measured at midday (13:00-15:00), in irrigated and dry treatments. Symbols *, **, ***, and NS indicate statistically significant at .05, .01, .001, or not significant, respectively.

			Water Potential (MPa)		
Date	Leaf Position	Treatment	Ψ_L	Ψ_o	Ψ_p
June 11	Upper	Irrig.	-0.96		
		Dry	-1.96		
			(***)		
June 12 (1 day after irrigation)	Upper	Irrig.	-0.97	-1.44	0.47
		Dry-reirrig.	-1.90	-2.00	0.10
			(***)	(**)	(**)
	Lower	Irrig.	-0.82	-1.02	0.20
		Dry-reirrig.	-1.88	-1.72	-0.16
			(***)	(***)	(*)
June 21 (10 days after irrigation)	Upper	Irrig.	-1.12	-1.46	0.34
		Dry-reirrig.	-1.20	-1.56	0.36
			(NS)	(NS)	(NS)

Table 2. Specific leaf weight (SLW) and leaf nitrogen per unit leaf dry weight and per unit leaf area for leaves in the upper (sun) and lower (shaded) positions of irrigated and dry treatments. The symbols *, **, ***, and NS indicate statistically significant at .05, .01, .001, and not significant, respectively.

			SLW	Leaf Nitrogen	
Date	Leaf Position	Treatment	(mg cm^{-2})	(μgN mg^{1})	(μgN cm^{-2})
June 11	Upper	Irrig.	6.30	37.3	234.1
		Dry	8.27	33.2	274.4
			(***)	(*)	(**)
	Lower	Irrig.	5.16	34.1	175.7
		Dry	5.89	29.9	175.5
			(NS)	(**)	(NS)
June 21	Upper	Irrig.	7.97	34.8	277.7
(10 days after irrigation)		Dry-reirrig.	9.17	33.2	303.6
			(*)	(NS)	(*)
	Lower	Irrig.	6.18	31.0	192.3
		Dry-reirrig.	8.12	32.2	261.8
			(**)	(NS)	(*)

Table 3. Net photosynthesis calculated on a per unit leaf dry weight, leaf nitrogen, and leaf area basis. All measurements were taken at midday (13:00-15:00) at saturating light intensity (photon flux density > 1500 μ E $m^{-2}s^{-1}$). Symbols *, **, ***, and NS indicate statistically significant at .05, .01, .001, and not significant, respectively.

			Photosynthesis Per Unit:		
Date	Leaf Position	Treatment	Leaf Dry Wt. (μmol $g^{-1}s^{-1}$)	Leaf Nitrogen (μmol $gN^{-1}s^{-1}$)	Leaf Area (μmol $m^{-2}s^{-1}$)
June 11	Upper	Irrig.	0.53	14.3	33.5
		Dry	0.16	4.8	13.1
			(***)	(***)	(***)
	Lower	Irrig.	0.44	13.1	23.0
		Dry	0.04	0.9	2.7
			(***)	(***)	(***)
June 12	Upper	Irrig.	0.56		34.3
		Dry-reirrig.	0.32		27.8
			(***)		(NS)
	Lower	Irrig.	0.47		23.5
		Dry-reirrig.	0.12		6.9
			(***)		(***)
June 21	Upper	Irrig.	0.47	13.3	36.9
		Dry-reirrig.	0.45	13.4	40.6
			(NS)	(NS)	(NS)
	Lower	Irrig.	0.39	12.7	24.5
		Dry-reirrig.	0.39	12.00	31.5
			(NS)	(NS)	(NS)

Photosynthetic rate of upper leaves in the DRY treatment at the end of the drought period was about 30 - 40% of the control, regardless of basis of expression of Pn (Table 3). Lower leaves were more affected, with Pn rates in the DRY treatment about 10% of the control. One day after reirrigation of the DRY treatment, Pn per unit leaf area showed almost complete recovery in the upper leaves (no statistically significant treatment effect). In contrast, Pn expressed on a per unit leaf dry weight basis remained significantly lower than the control. Lower leaves recovered more slowly than upper leaves, but by ten days after reirrigation, Pn of both lower and upper leaves had completely recovered.

Discussion and Conclusions

These results indicate that under field conditions where drought is imposed gradually, leaf osmotic adjustment and an increase in N (and presumalbly photosynthetic enzymes) per unit leaf area allow for rapid recovery of Pn per unit leaf area when stress is relieved. The increase in

N per unit leaf area was associated with a higher SLW in leaves of droughted plants, and not an increase in N concentration per unit leaf dry weight. The capacity of sunflower for osmotic adjustment (Turner et al., 1978) and an increase in SLW due to drought (Wise et al., 1990) have been previously observed, but not directly related to photosynthetic recovery after relief of stress.

Rawson and Constable (1980) reported that lower leaves fixed relatively less CO_2 during water stress, and that lower leaves were the first to wilt. We also observed more wilting and slower Ψ_p recovery in lower leaves, and measurements of water potential components indicated this discrepancy was due to more solute accumulation (osmotic adjustment) in upper compared to lower leaves. The SLW and increase in N per unit leaf area responses to drought were also more pronounced in upper compared to lower leaves of the plant canopy. Upper leaves, since they intercept the majority of incoming solar radiation and are younger, will have more potential contribution to photosynthetic capacity and growth during recovery.

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