

TIMING OF WATER STRESS EFFECTS ON YIELD COMPONENTS IN SUNFLOWER

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Abstract

Two inbred sunflower (*Helianthus annuus* L.) lines were grown in sand-nutrient solution culture at a density of 4.5 plants/square meter and exposed to water stress at one of each of five phenological stages between floral initiation and start of linear embryo growth. Oil yield per plant was significantly ($P=0.05$) reduced by stress at all stages examined. The relative changes in the components of yield (cypsela/head, cypselae weight, oil content) varied with timing of stress. Embryo growth could be described by a lag phase + linear growth phase model. Stress affected rate of embryo growth rather than duration of growth, and reduction in oil content in plants stressed at anthesis or later was not attributable to changes in the proportion of pericarp. Intensive utilization of pre-anthesis assimilate for cypselae filling appeared to be limited to treatments stressed at anthesis or later. Maximum leaf area was a poor predictor of yield, but a strong ($r=0.95$, $n=22$) association was found between oil yield per plant and post-anthesis leaf area duration. This relationship appears to integrate effects of stress on leaf area, post-anthesis dry weight partitioning and embryo oil content.

Introduction

In Argentina there has been a tendency towards a shift in the sunflower crop area towards regions of lesser water availability because of competition with other cropping systems such as wheat - soybean relay cropping. We are involved in an on-going effort to define water availability patterns in these more marginal areas and to identify plant characteristics which may contribute to tolerance to water stress; with the aim of optimizing the match between water availability, plant characteristics and management strategies. As part of this programme, we have examined the effects of brief exposures to water stress at one each of five phenological stages between inflorescence initiation and embryo filling on the yield and its components in two inbred sunflower lines, B14 and R16.

Materials and Methods

Plants were grown at Junín, Provincia de Buenos Aires, Argentina, in two successive seasons (1981-82, 1982-83) in sand-nutrient solution culture (Hall et al., 1980) under a polyethylene film roof which excluded about 25% of photosynthetically active radiation. Each plant grew in a 35-l container full of coarse sand, containers were arranged in 66-cm rows to give a density of 4.5 plant/square metre. There was a separate shelter for each cultivar, and each plot of 170 containers was surrounded by a further two guard rows. Treatment positions were randomized within each plot. Stress was applied at the stages shown in Fig. 1 by interrupting the regular watering regime. Start of visible stress was taken as the day of appearance of afternoon wilting (ca. 16.00 hours), and during the visible stress period plants received a daily watering equivalent to 25% of control plant evapotranspiration. At the end of the stress period plants were returned to normal watering regime until the end of the season. Slightly different guidelines for stress application were used in 1981-82, resulting in more severe stress than that obtaining the second year.

Observations on the progress of inflorescence and floret development were made on dissected apices, leaf areas were determined from thrice-weekly measurements of leaf width and length, and eight plants per treatment harvested for dry weight determinations at anthesis and at maturity. Number of visible floret positions per head were determined at maturity, and oil content of seeds measured by nuclear magnetic resonance. Growth patterns of the cypselae and its parts were established using data from daily harvests of cypselae from guard-row plants; effects of stress on cypselae growth by thrice-weekly harvests of guarded plants. Leaf water potentials (LWP) were measured in triplicate at one or two-day intervals during the stress periods using a Scholander pressure bomb. Plants

were sampled at nightfall only to restrict loss of leaf area. Nightfall (ca. 20.00 hs.) LWP differences between stressed and control plants were a more reliable indicator of the onset of stress than pre-dawn or mid-day measurements.

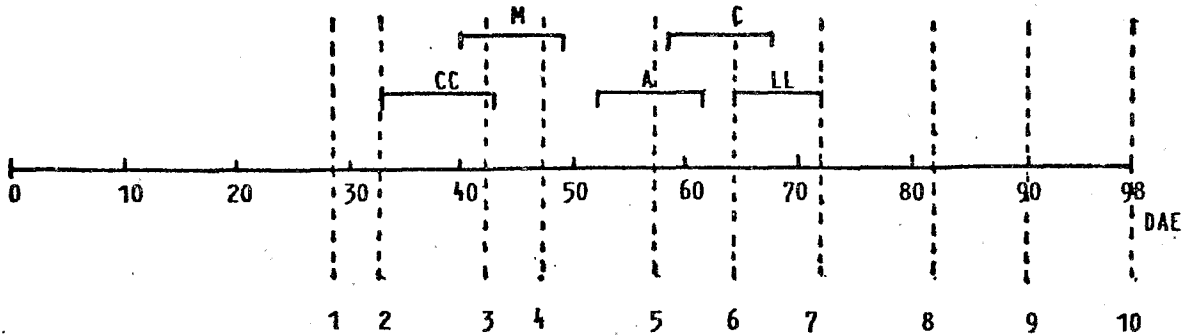


Fig. 1. Timing of exposure to stress and coding of treatments in relation to days after emergence (DAE) and phenological stages. Horizontal bars show duration of visible stress. Stages indicated are: 1 and 2, Floral stages 4 and 6 (Marc and Palmer, 1981), respectively, 2 coincides with appearance of star; 3, microsporogenesis (tetrads); 4 and 5 first and last anthesis; 6, 7 and 8, start, mid-point and end of linear phase of embryo growth in mid-radial file cypselae; 9, inflorescence bracts yellow or brown; 10, harvest. 1982-83 experiment; differences between cultivars did not exceed 2 days at any given stage.

Results and Discussion

Our objective was to expose plants to ten days of stress; shorter durations at some stages (Table 1) occurred when heavily overcast days near the end of the planned exposures forced us to resume regular watering earlier than planned. Intensity of stress, as reflected in mean LWP, increased with season, this effect was not associated with increases in leaf area, atmospheric demand (Table 1) or leaf conductance (data not shown) over the treatments A, C and LL. Plant leaf area was severely restricted by stress (Table 1); mainly through limitation of leaf expansion in CC and M, and by increased senescence in A, C and LL (data not shown).

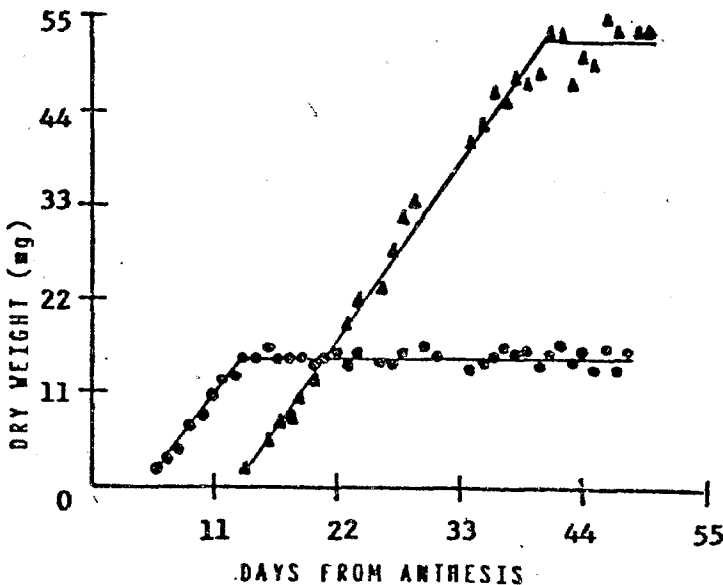


Fig. 2. Changes in embryo (triangles) and pericarp (circles) dry weight with time from floret anthesis. Second-row cypselae, B-14 guard row-plant, 1982-83.

Table 1 Plant size and atmospheric conditions, duration and effects of stress on two sunflower cultivars, 1982-83. ED: estimated evaporative demand (Priestley and Taylor 1972); DVS: duration of visible stress (days); LWP: mean nightfall leaf water potential during DVS (MPa); ATS and AFS: mean green leaf area of control and stressed plants, respectively at end of exposure to stress (square cm/plant). LWP of control plants fell between measurements made at stage CC and stage LL, extreme values and LSD ($P=0.05$) (in brackets) being 8-14: -0.58 and -1.20 MPa (0.08); R-16: -0.52 and -0.85 MPa (0.06).

Stress treatment	Cultivars	ED	DVS	LWP	AFT	AFS
CC	B-14	4.39	9	-1.11	4123	1783
	R-16	5.13	7	-0.80	2534	1017
M	B-14	3.92	9	-0.92	4908	3322
	R-16	3.56	7	-0.77	3093	1643
A	B-14	4.68	10	-1.48	5093	4046
	R-16	4.68	10	-1.13	3439	1958
C	B-14	4.80	10	-2.00	4727	2878
	R-16	4.70	9	-1.37	2914	2339
LL	B-14	4.94	9	-2.02	4370	2237
	R-16	4.94	8	-1.43	2448	1347
LSD		-	-	0.27	635	465

Cypsela number was reduced by all exposures to stress (Table 2), as was cypsela weight in all treatments except C and LL in R-16. Cypsela weight in this cultivar drops by a factor of 2 from the border to the centre of a radial file in unstressed plants (data not shown), and calculations show that the above results reflect decreased cypsela set in the central portion of the head rather than stable cypsela weight at all positions under stress. Kernel oil content decreased only when the plants were stressed at anthesis or later (Table 2). The net effect of these changes in yield components was a fall in oil yield per plant in all treatments and cultivars. There was no clearly defined period of greater sensitivity to stress, although treatment M had the highest oil yield among stressed treatments in both cultivars and years. The effects shown are consistent with the observations of Robelin (1967) and Yegappan et al. (1982).

Our findings extend those of the abovementioned authors in relation to the causes of the changes in cypsela number, weight and oil content in response to stress. Cypsela set (cypsela/floret position) was reduced by early and late, but not intermediate, exposures to stress (Table 2). This suggests there may be at least two different pathways through which stress affects cypsela set. Floret number per head was reduced, as expected, only by early exposures to stress (Table 2).

Embryo dry weight increase in guard-row plants did not begin until some time after anthesis of the respective floret, and then increased linearly with time until close to maximum embryo weight (Fig. 2). This pattern of growth was repeated in both cultivars and with cypselae from border, mid-radial file and centre positions. Pericarp growth ceased close to the time of initiation of embryo linear growth, although exact timing varied slightly with cultivar. We examined embryo growth in cypselae harvested from both border and mid-radial file position in both cultivars and all treatments, and exemplify results obtained in Table 3. Initiation of linear growth was more rapid in guarded plants (cf. Fig. 2), but did not respond to stress. Greatest effects of stress on embryo growth were on rate of filling, although a slight reduction of duration was a consistent response to late stress, and there was a consistent (and significant) lengthening in response to early stress. The data in Table 3 show that the changes in oil content with late stress (Table 2) cannot have originated in changes of pericarp: embryo ratios. More detailed analysis of these ratios at six positions on

Table 2 Yield and its components in cultivars R-16 (above) and B-14 (below) exposed to stress at one of each of five phenological stages or unstressed throughout (T) in 1982-83. Units of cypsela weight, oil content of cypsela and plant oil yield are: mg/cypsela, % and g/plant respectively. LSD is for P=0.05.

Treatment	Florets/head	Cypselae/floret	Cypselae/head	Cypsela weight	Oil content	Oil yield
R-16						
T	1560	0.57	882	34.1	40.0	12.1
CC	1246	0.34	421	25.0	41.4	4.1
M	1274	0.48	582	29.0	43.1	7.2
A	1313	0.46	575	27.0	38.5	6.1
C	1435	0.39	544	39.0	37.0	7.6
LL	1548	0.33	500	33.0	31.2	5.1
LSD	267.7	0.11	119	3.8	1.7	1.5
B-14						
T	1734	0.61	1059	46.2	50.5	25.7
CC	1479	0.47	697	28.0	53.6	10.2
M	1636	0.53	831	37.8	53.8	16.8
A	1675	0.41	685	37.0	48.6	12.2
C	1684	0.77	778	34.0	45.8	12.5
LL	1789	0.52	902	31.0	36.8	10.3
LSD	283.0	0.10	122	8.3	3.3	3.4

the radial file from edge to centre of head in material harvested in 1981-82 is consistent with this conclusion (data not shown). Thus there was a direct effect of stress on the partition of carbon between oil and other embryo components. Because pericarp growth ceases before embryo growth, changes in oil content in response to even later exposures to stress than those we used are possible.

Table 3 Embryo growth characteristics, final embryo weight (mg/embryo) and pericarp as a proportion (%) of total cypsela weight of external cypselae of plants subjected to stress in one of each of five phenological stages or irrigated throughout (T); cv. B-14, 1982-83. Units are: initiation (days after anthesis of respective floret), rate (mg/day), duration (days). LSD is for P=0.05.

Treatment	Embryo linear growth			Final embryo weight	Pericarp proportion
	Initiation	Rate	Duration		
T	9.6	2.3	19.5	44.0	19.0
CC	8.7	1.1	25.2	25.7	18.0
M	9.1	1.6	22.8	37.1	19.0
A	9.5	1.6	18.1	29.1	19.0
C	9.3	1.8	17.4	31.4	21.0
LL	9.7	1.7	17.4	29.4	22.0
LSD	-	0.3	4.2	7.3	-

A strong association between yield per plant and leaf area has been found for plants exposed to differing water availability patterns up to or slightly beyond anthesis (e.g. Rawson and Turner, 1983). This association holds for our treatments T, CC, and M, but the observed values for the

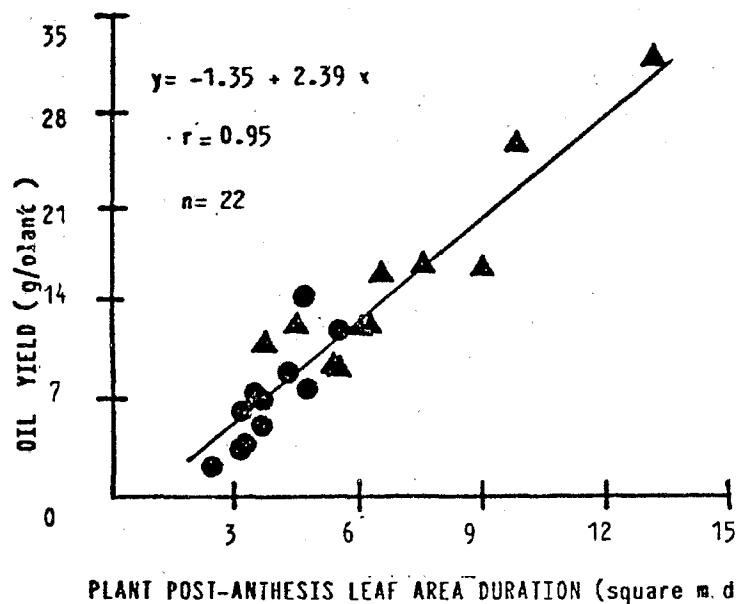


Fig. 3. Oil yield/plant post-anthesis leaf area duration relationship. Values for B-14 (circles) and R-16 (triangles), 1981-82 and 1982-83.

remaining treatments are about 50% of the ones expected from the regression fitted to the first three. A much more robust association is that between oil yield per plant and post-anthesis leaf area duration (Fig.3). It should be noted this association is not merely a reflection of the size of the photosynthetic apparatus. Large changes in post-anthesis dry weight partitioning resulted from exposure to stress at different stages, as exemplified in Fig.4. These changes suggest that intensive use of pre-anthesis assimilates for grain filling occurs only if plants are exposed to stress at anthesis or later. The oil yield/leaf area duration relationship therefore appears to



Fig.4. Changes in dry weight of organs and the whole plant between anthesis and maturity for three selected treatments of B-14 in 1982-83: I (a), CC (b) and LL (c). Parts are coded as follows: R, fine roots; T, stem and thick roots; H, leaves; C, inflorescence; P, whole plant. Asterisks denote significant ($P=0.05$) differences in weight between anthesis and maturity.

be able to integrate size of photosynthetic apparatus, change in use of pre-anthesis assimilates, and changes in ratio of oil and non-oil components of the embryo.

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