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PARTITIONING OF ASSIMILATE IN SUNFLOWER (HELIANTHUS ANNUUS) IN RESPONSE TO MOISTURE STRESS.

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Abstract

Sunflower (Helianthus annuus) cultivar Suncross 52 was grown in large containers in the glasshouse and subjected to moisture stress at either anthesis or rapid seed fill. Plants were labelled with $^{14}CO_2$ at either an upper, lower or midcanopy position and the distribution of assimilate determined for each plant 30 hours after labelling.

Moisture stress had little effect on the distribution of assimilate at both times of labelling. However, during rapid seed fill significantly more ($P<0.05$) assimilate was exported from the leaves of the stressed plants. Most of this extra assimilate accumulated in the plant parts above the labelled leaf. The upper leaf position translocated to the upper stem and capitulum. In contrast the lower leaf translocated to the lower stem and roots. The midleaf position partitioned assimilate to both upper and lower plant parts at anthesis however, during seedfill assimilate was preferentially translocated to the upper plant parts. Other leaves were insignificant sinks at both times of labelling. The results are further discussed with respect to the specific activity of the plant components and adaptation of sunflower to moisture limited conditions.

Introduction

Within the semi-arid cropping zone of Australia sunflower crops are often subjected to moisture stress from the late vegetative phase of development and more particularly in the period from anthesis to maturity. This stress usually causes reductions in yield (Dubbelde et al. 1982) with the extent of the reduction being related to the timing, severity and duration of the stress. Yield reduction in sunflower caused by moisture stress may result from reduced photosynthetic rates (English, 1976; Connor and Cawood, 1978 and Rawson, 1979) and/or changes in the pattern of distribution of photosynthate to the various plant parts (Connor and Cawood, 1978). Reductions in photosynthetic rates of different leaves in moisture stressed sunflower has been quantified by English (1976) and Rawson (1979). No figures are available on the partitioning of assimilate by different leaves of the mature sunflower and their contribution to yield. Furthermore the effect of moisture stress on the partitioning of assimilate by different leaves has not been examined.

The work reported in this paper was undertaken to evaluate the effects of moisture stress on the short term partitioning of assimilate by leaves at different positions on the sunflower plant. This distribution was determined at either anthesis or peak seed fill.

Materials and Methods

Individual sunflower plants (Helianthus annuus, cultivar Suncross 52) were grown in 15cm. x 90cm. soil columns within the glasshouse under conditions of non-limiting nutrient and water supply. Photoperiod was artificially extended to 14 hours using mercury vapour lamps and temperatures maintained between 5 and 25°C. Insect attack was prevented by regular applications of malathion.

At first anthesis 24 individual plants were selected and divided into two equal groups namely the control and moisture stress treatments. Soil moisture for control plants was maintained near field capacity by regular watering. For stressed plants water was withheld for 48 hours prior to labelling with $^{14}CO_2$. This caused plants to be severely wilted at dawn on the day of labelling. To facilitate $^{14}CO_2$ uptake 0.5 litres of water was added to the stress plants 2hours before the commencement of the labelling procedure. This was insufficient water to allow plants to regain turgor.

Individual plants of each treatment were labelled with $^{14}CO_2$ at one of three leaf positions namely; 12, 18 or 24 leaves from the base of the plant. Each treatment was replicated four times. 30 hours after labelling plants were destructively harvested and divided into the following components; labelled leaf, leaves above and leaves below the labelled leaf, stem above and stem below the labelled leaf, capitulum and roots. Plant components were dried, weighed and ground for digestion and scintillation counting. This procedure was repeated during rapid seed fill (anthesis plus 300 growing degree days) with the capitulum being further subdivided at harvest into it's structural and seed components for separate analysis.

Labelling Procedure: Plants were labelled by sealing the attached leaf in an illuminated (1000 μEm^{-2}) perspex chamber through which $^{14}CO_2$ labelled air was circulated at 6 litres per minute. The leaf chamber was part of a closed system which consisted of silica-gel drying columns to absorb excess moisture and a 0.1M HCl bath into which two separate injections of 0.46MBq $Na_2{}^{14}CO_3$(740MBq/mmol) were made to release $^{14}CO_2$. The $^{14}CO_2$ content of the airstream was measured with a calibrated Geiger Meuller tube connected to a chart recorder. When the airstream was almost depleted of label it was diverted through a 0.25M NaOH solution to absorb the residual $^{14}CO_2$.

Scintillation Counting: Duplicate 300mg samples of each plant component were placed in scintillation vials to which 1.0ml of NCS tissue solubolizer was added. The vials were gently shaken and allowed to incubate for 12 hours at 50°C. After cooling the digest was bleached using 1ml of benzoyl peroxide (1g benzoyl peroxide in 5mls toluene) per sample. 10mls of scintillation fluid (6g PPO and 0.75g POPOP per litre of toluene) was added to each sample and they were counted in a quench corrected scintillation counter. Total activity per plant component was determined and expressed as a percentage of total plant activity. In addition the specific activity of each component was calculated. Results were analysed using standard analysis of variance techniques.

TABLE 1: SHORT TERM DISTRIBUTION OF ^{14}C LABELLED ASSIMILATE BY SUNFLOWER AT ANTHESIS.

	Labelled Leaf Number	Percentage of Total Assimilate		Specific Activity counts g^{-1}		Percentage of Total Dry Matter	
		Control	Stressed	Control	Stressed	Control	Stressed
Labelled Leaf	24	50.6	56.0	1235207	1660624	1.6	1.4
	18	45.3	42.3	741174	693079	1.9	2.0
	12	49.6	49.8	787305	1475405	1.3	1.1
		NS		NS			
Leaves Above The Labelled Leaf	24	0.28	0.15	1524	982	7.4	5.3
	18	0.43	0.30	722	570	16.3	16.6
	12	0.78	0.88	584	420	24.3	27.0
		*0.39		*728			
Leaves Below The Labelled Leaf	24	0.13	0.10	115	122	24.5	25.2
	18	0.10	0.10	197	145	13.6	15.7
	12	0.13	0.10	405	206	6.6	5.6
		NS		NS			
Stem Above The Labelled Leaf	24	13.1	11.3	62843	77190	7.9	6.1
	18	10.0	14.6	17820	30187	15.7	14.4
	12	4.3	6.1	3506	4029	24.1	26.1
		*4.2		*36350			
Stem Below The Labelled Leaf	24	14.5	7.5	18874	8540	38.8	36.6
	18	33.1	21.5	31994	28228	29.9	31.8
	12	31.0	26.4	34368	25543	21.4	19.7
		*9.1	***2.5	**7.5			
Capitulum	24	21.3	24.9	110684	37665	8.0	9.5
	18	7.5	18.9	25330	98144	8.4	7.8
	12	3.6	1.9	6936	2861	10.8	7.8
		*8.8		*46028			
Roots	24	0.2	0.1	444	144	12.8	15.7
	18	3.7	2.4	7791	7691	14.2	11.7
	12	10.7	14.9	18722	26370	11.6	12.6
		*2.5		NS			

NS-not significant; *5% lsd leaf position; **5% lsd moisture stress; ***5% lsd interaction

TABLE 2: SHORT TERM DISTRIBUTION OF ^{14}C LABELLED ASSIMILATE BY SUNFLOWER AT PEAK SEED FILL.

	Labelled Leaf Number	Percentage of Total Assimilate		Specific Activity counts g^{-1}		Percentage of Total Dry Matter	
		Control	Stressed	Control	Stressed	Control	Stressed
Labelled Leaf	24	43.4	37.6	800056	778026	1.6	1.6
	18	52.3	38.8	1000629	869553	1.3	1.4
	12	64.8	43.1	1216164	1079297	0.9	0.8
		*10.3	**8.4	NS			
Leaves Above The Labelled Leaf	24	0.08	0.13	496	197	5.7	6.7
	18	0.18	0.20	335	402	14.1	14.0
	12	0.58	0.50	398	444	23.5	20.2
		*0.21		NS			
Leaves Below The Labelled Leaf	24	0.13	0.08	100	128	18.7	17.1
	18	0.05	0.03	188	135	8.7	8.9
	12	0.08	0.03	500	232	2.5	2.4
		NS		*104			
Stem Above The Labelled Leaf	24	3.6	5.7	20913	34884	5.3	5.5
	18	5.7	8.7	14203	27501	10.2	10.4
	12	2.0	10.9	1853	11969	17.3	19.6
		***3.7		*10854	**8862		
Stem Below The Labelled Leaf	24	3.6	8.1	3658	8220	30.7	32.4
	18	7.1	9.1	7597	10486	24.0	26.8
	12	14.4	14.6	17614	18375	13.4	15.6
		*6.1		*7943			
Capitulum-Seed	24	21.0	28.2	42815	62173	15.1	15.8
	18	17.2	16.7	22875	31675	19.3	17.2
	12	0.9	8.7	825	10024	17.7	19.7
		*7.8		*21897	**17878		
Seed	24	27.7	18.0	107221	66108	13.5	13.1
	18	15.9	24.4	43578	92376	12.9	12.1
	12	0.8	11.6	1405	25414	15.1	11.2
		*10.5		*37454			
Roots	24	0.6	2.2	1307	467	9.3	7.8
	18	1.7	2.1	3336	4675	9.5	9.1
	12	16.4	10.8	18456	16885	9.6	10.7
		*6.4		*7188			

Results and Discussion

Results for ^{14}C distribution and specific activity at anthesis and peak seed fill are presented in Tables 1 and 2. At anthesis neither leaf position or moisture treatment affected the percentage of total plant ^{14}C retained by the labelled leaf. In contrast at peak seed fill the two lower leaf positions and the control treatment retained significantly more ($P<0.05$) ^{14}C than the upper leaf and stressed treatments respectively. The increased export by the stressed leaves during seedfill probably results from the increased relative sink strength of the capitulum and seed under conditions of limited assimilate supply.

During seedfill approximately twice the percentage of assimilate was translocated to the infloresence as at anthesis. This assimilate was partitioned evenly between the structural tissue of the capitulum and the seed. The relative contributions of the individual leaf positions were similar to that at anthesis except for enhanced flow to the infloresence from the lower leaf position under moisture stress conditions and the mid-leaf position of the unstressed treatment. At both times of labelling the upper leaf position was the major source of assimilate to the infloresence however during seedfill the midcanopy position increased supply to the developing infloresence. The increased total translocation to the infloresence at peak seedfill is consistent with the patterns observed in winter cereals by Rawson and Hofstra(1969).

More assimilate remained in the stem at anthesis than during seed fill. This is consistent with the results of Connor and Cawood (1978) although a greater proportion was retained in the current study. From the specific activity of the stem above the labelled leaf it is evident that percentage distribution does not reveal the extent of differences between leaf positions when the plant component under comparison is of disproportionate size between treatments. Specific activity reveals similar differences for the stem sections below the labelled leaves. The quantity of label in the various stem fractions is consistent with source-sink concepts which associate the direction of flow to the proximity of a source(leaves) to major sinks(infloresence and roots).

All treatments resulted in insignificant assimilate accumulating in the nonlabelled leaves. This is consistent with all leaves having reached stages of maturity for both times of labelling which make them nett exporters rather than importers of assimilate (Wardlaw,1968).

The lower leaf position was the major source of root assimilate at both times. Minimal contributions were made by the two upper leaf positions. Total assimilate requirement by the roots was similar for both times of labelling and was not affected by moisture stress. The lower leaf position used in this study was the lowest active leaf as most leaves below this had senesced. The importance of the lower leaves to root growth during the later stages of development is more clearly defined than the sources of assimilate for seed development.

The failure of moisture stress to modify short term assimilate partitioning as observed in the current study may have resulted from the rapid manner in which moisture stress was induced. Indeed Jones and Turner(1980) observed that osmotic adjustment in sunflower only develops in response to several days of moisture stress. In addition the current results are in conflict with those of Connor and Cawood(1978) who found impairment of assimilate partitioning to the seed when plants were subjected to moisture stress. In their study as in Jones and Turner's(1978) study stress was allowed to develop at a slower rate giving plants time to adapt their physiological processes. Therefore the current results should be applied with caution.

If however the results of this study do withstand more rigorous testing then they provide considerable insight into the ability of the sunflower to produce substantial yields under conditions of inadequate moisture supply during the later growth phases. Decreases in the yield and harvest index of moisture stressed crops (Turner and Rawson,1982) would result from reductions in the quantity of assimilate as opposed to it's distribution pattern. Such an adaptative mechanism would greatly facilitate the process of accurately modelling the sunflower crop to include the growth modifying effects of moisture stress.

Conclusion

The ability of sunflower to maintain significant photosynthetic activity and increase water use efficiency when moisture stressed (Rawson,1979) and the apparent inflexibility of assimilate partitioning and possible enhancement of pathways to the capitulum as observed in this study are indicative of the sunflowers ability to produce substantial seed yields under the conditions of severe moisture stress often observed in semi arid cropping areas.

Acknowledgements

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