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EFFECTS OF SULFUR DEFICIENCY AS MODIFIED BY NITROGEN SUPPLY ON THE GROWTH, YIELD COMPONENTS AND SEED QUALITY OF SUNFLOWER

P.J. Hocking, P.J. Randall and A. Pinkerton
CSIRO, Division of Plant Industry, G.P.O. Box 1600, Canberra, A.C.T. 2601, Australia.

SUMMARY

Many soils suitable for growing sunflowers are low in sulfur (S) and nitrogen (N). We investigated how S deficiency and N supply interacted on the growth and development of yield components of sunflower. The S supplies of some plants were changed at the end of floret initiation and at first anthesis, to simulate the onset or relief of S deficiency at these important growth stages, and to ascertain when yield components were determined by S supply. S deficiency did not decrease the number of leaves per plant, but N deficiency did; however, both S and N deficiencies reduced leaf area. Increasing the S supply from deficient to adequate at the end of floret initiation resulted in a large increase in the area of those leaves still capable of expansion. Both S and N deficiencies had detrimental effects on yield by reducing the number of seeds per plant and, to a lesser extent, by decreasing single seed weight. The effects of changing the S supply at the end of floret initiation and at anthesis indicated that floret number and hence seed number were largely determined by the S supply before the end of floret initiation. Single seed weight responded positively to the relief of S deficiency after floret initiation, but only if the N supply was adequate. The concentration of oil in seeds was not affected by S supply. The essential amino acids, cysteine and methionine, each decreased by 30% in seeds from S-deficient but N-sufficient plants, whereas arginine increased by 35%. Consequently, meal from such seeds would have reduced nutritional value as stock feed.

INTRODUCTION

The areas suitable for sunflower production in Australia and elsewhere have a wide range of soil types, some of which are marginal for or deficient in S. A sunflower crop of 2t/ha removes about 8 kg S/ha in the seeds (Kanwar and Mudahar, 1983). Removal of S at this rate has been compensated in Australia by the extensive use of single superphosphate (containing 11%S) to correct widespread P deficiency. However, the recent increased use of high analysis P fertilizers, which lack this adventitious S, has resulted in the removal of S by sunflower crops often exceeding additions in fertilizer. Consequently, the incidence of S deficiency in sunflower crops is likely to increase if the trend towards greater use of high analysis P fertilizers continues.

We report here on the effects of S deficiency in sunflower using controlled S supplies at 3 levels of N application. We measured the effects of S deficiency on key vegetative characters such as leaf area, and on the yield components, namely seed number per plant, single seed weight and seed oil concentration (%). In particular, we used changes in S supply at different growth stages to determine the yield penalty incurred if the crop ran into S deficiency, and the yield recovery resulting from the correction of S deficiency. These changes in S supply were also used to ascertain when each yield component was determined by S supply, and to assess when S deficiency has its most detrimental effect on a particular yield component. Aspects of seed quality were investigated, as S deficiency decreases the proportions of essential S-containing amino acids in seeds of other crops (Randall and Wrigley, 1986), and thus could reduce the value of sunflower meal as stockfeed.

MATERIALS AND METHODS

Plants of a hybrid sunflower, cv. Kernel, were grown in sand culture in a glasshouse at Canberra, Australia. Seedlings were thinned to 3 uniform plants per 10-litre pot, or to 5 plants for the most deficient treatments. The experiment was a factorial design with 5 levels of S and 3 levels of N. S was added to the basal nutrient solution (Steer and Hocking, 1983) to give 1, 5, 10, 25 and 75 mg S/l, and N to supply 7, 84 and 168 mg N/l. Plants received 500 ml of solution daily. The S supplies to some plants were decreased or increased at the end of floret initiation and at 3-row anthesis to simulate the onset or relief of S deficiency at these stages. Floret initiation was regarded as complete when the flower bud reached the R_1 or "Star" stage (Schneiter and Miller, 1981). All plants were grown to maturity.

Leaf area was estimated at anthesis by measuring the length and greatest width of laminae of attached leaves, and applying the formula of Rawson et al. (1980). The number of florets initiated per plant was estimated using the empirical expression of Palmer and Steer (1985). Mature heads were threshed, and the number of filled seeds counted. Total N in plant material was determined by colorimetry on Kjeldahl digests, and total S by X-ray fluorescence spectrometry. The oil content of seeds was measured by wide-band nuclear magnetic resonance. Amino acid analyses of de-fatted kernels were done as described by Steer et al. (1984).

RESULTS

Severe S deficiency delayed the completion of floret initiation by 9 days, and 3-row anthesis by 6 days, but did not delay seed maturity (Table 1). N deficiency also delayed these growth stages but the effect, unlike that of S deficiency, persisted through to maturity.

TABLE 1. Effects of S and N supplies (mg/l) on the timing of phenological development.

S supply	N supply								
	7	84	168	7	84	168	7	84	168
	Days to end of floret initiation			Days to 3-row anthesis			Days to seed maturity		
1	45.2d	44.8cd	46.0d	71.3e	65.3c	65.8c	115.0c	111.5b	109.7ab
5	42.8c	36.3a	35.2a	67.0c	59.3b	59.2b	115.5c	108.0ab	103.3a
10	44.2cd	36.2a	36.5a	69.5d	58.5ab	58.0ab	115.8c	104.3a	106.0a
25	44.4cd	37.8ab	34.5a	69.8d	59.7b	56.7a	115.2c	106.5a	104.3a
75	44.3cd	36.8a	37.2ab	71.2e	59.3b	59.8b	116.6c	104.5a	108.6ab

For each phenological stage, values followed by the same letter do not differ at $P < 0.05$.

Sulfur deficiency did not reduce leaf number, but N deficiency did (Table 2); both deficiencies caused a large reduction in the total leaf area. Relief of S deficiency at the end of floret initiation resulted in a 2.5-fold increase in total leaf area, most of which occurred in the upper leaves which were still capable of expanding.

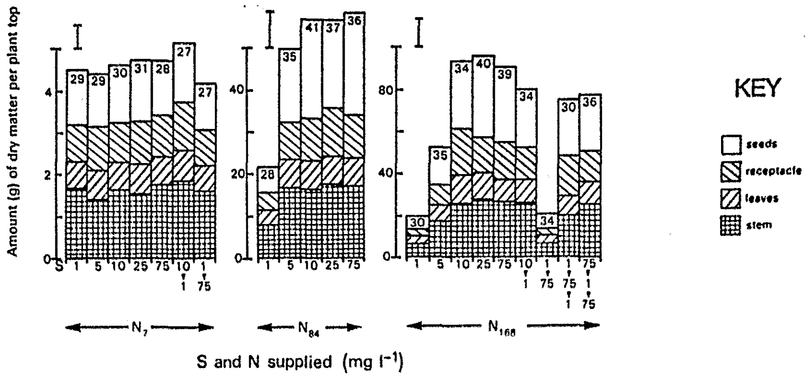
TABLE 2. Effects of S and N supplies on leaf number and area.

S supply	N supply					
	7	84	168	7	84	168
	No. leaves at 3-row anthesis			Leaf area at 3-row anthesis (cm^2)		
1	16.8a	21.3b	22.5bc	181a	1260b	1154b
5	16.2a	20.5b	24.3c	198a	1967c	2446e
10	16.0a	21.5b	24.0c	209a	2241d	3849h
25	16.5a	22.7bc	21.8b	205a	2181d	3837h
75	16.8a	21.8b	24.0c	183a	2218d	3597g
Changed S supply at end of floret initiation and at anthesis:						
S_1-S_{75}-S_1			21.8b			2902f
S_{75}-S_1-S_{75}			22.5b			3157f

Values followed by the same letter do not differ at $P<0.05$.

Dry matter production was reduced by both S and N deficiencies (Fig. 1). Relief of S deficiency at the end of floret initiation resulted in a large increase in dry matter, whereas a similar change made at anthesis had no effect, indicating that sunflower is unable to respond to improved S supply at the latter stage. The dry matter harvest index was lowest for S-deficient plants (29%), compared with 37% for plants which received an adequate S supply.

FIGURE 1. Distribution of dry matter as affected by S and N supplies. Within a N treatment, the bar represents the LSD ($P < 0.05$) for plant tops. Changes in S supply at star stage and back to original S supply shown as $S_1 \rightarrow S_{75} \rightarrow S_1$ and $S_{75} \rightarrow S_1 \rightarrow S_{75}$; changes at anthesis only are shown as $S_{10} \rightarrow S_1$ and $S_1 \rightarrow S_{75}$. Values in histograms are seed yields as a % of whole top dry matter.



Constant S deficiency reduced the diameter of the receptacle and the number of florets initiated per head, but only when the N supply was adequate (Table 3). The seed yield under these conditions was only 20% of that for S-sufficient plants as a result of a 60% reduction in both seed number per plant and single seed weight (Table 4). N supply also had a large effect on these yield components. Seed oil concentration was not affected by the range of S supplies used here, but it was depressed by high N supply. However, the highest oil yields were obtained from plants which received the highest supply of N and a S supply of 10 mg/l or greater.

TABLE 3. Effects of S and N supplies on receptacle diameter and floret number.

S supply	N supply					
	7	84	168	7	84	168
	Receptacle diam. (mm) at maturity			No. florets per capitulum		
1	28a	57b	58b	127a	425b	420b
5	29a	104c	100c	136a	725c	832c
10	28a	102c	131d	127a	761d	942g
25	30a	101c	135d	125a	794de	953g
75	31a	95c	129d	139a	751d	866f

Values followed by the same letter do not differ at $P<0.05$.

TABLE 4. Effects of S and N supplies (mg/l) on yield components and oil yield.

S supply	N supply														
	7	84	168	7	84	168	7	84	168	7	84	168	7	84	168
	Single seed dry weight (mg)			Oil % seed dry weight			No. of seeds/plant			Seed yield/plant (g)			Oil yield/plant (g)		
1	32.8a	44.2c	31.4a	47.0e	40.4b	38.6b	39a	134b	188c	1.28a	5.92b	5.90b	0.60a	2.39b	2.28b
5	32.2a	60.6e	50.3d	46.3de	42.1c	37.7ab	39a	288d	361e	1.26a	17.45c	18.16c	0.58a	7.35c	6.85c
10	38.2b	72.0g	69.5fg	47.0e	42.5c	40.5b	36a	323d	463f	1.38a	23.26cd	32.18de	0.65a	9.88d	13.03e
25	36.4ab	66.2f	76.5gh	45.8d	41.4bc	40.0b	40a	315d	496f	1.46a	20.85c	37.94e	0.67a	8.63d	15.18e
75	36.1ab	62.5e	78.5h	44.9cd	43.6c	40.0b	36a	306d	454f	1.30a	19.13c	35.64e	0.58a	8.34cd	14.26e
Changes in S supply:															
(a) at anthesis															
S_{10}-S_1	33.3a		71.1g	45.6d		39.9b	41a		381e	1.63a		27.09d	0.62a		10.81d
S_1-S_{75}	35.4a		34.3a	47.3e		40.3b	32a		199c	1.13a		6.83b	0.54a		2.75b
(b) at end of floret initiation and at anthesis															
S_1-S_{75}-S_1			91.8i			35.8a			222c			20.38c			7.30c
S_{75}.S_1-S_{75}			67.2f			37.5ab			398e			26.75d			10.03d

For each character, values followed by the same letter do not differ at $P<0.05$.

Changing the S supply of N-deficient plants from adequate to deficient and vice versa had no effect on any yield component, irrespective of when the changes were made (Table 4). For N-sufficient plants, the onset of S deficiency at anthesis resulted in a 17% decrease in oil yield. This was due to reduced seed number per plant as a consequence of the abortion of some developing seeds. Single seed weight and seed oil concentration were unaffected by the onset of S deficiency at anthesis, and the relief of S deficiency at this stage had no effect on any yield component. If the onset of S deficiency occurred earlier, at the end of floret initiation, then there was a 30% reduction in oil yield as a result of decreased single seed weight and seed number per plant. Relief of S deficiency at the end of floret initiation resulted in a large increase in single seed weight, but a decrease in seed oil concentration. There was a slight though not significant increase in seed number.

Analysis of variance of the data for N-sufficient plants which received constant and changed S supplies showed that floret number, and hence seed number, were mainly determined by the S supply before the end of floret initiation, whereas single seed weight was determined by the S supply between the end of floret initiation and anthesis. Since seed number per plant is the dominant yield component, oil yield per plant is mainly determined by the S supply before the star stage.

Nitrogen to sulfur concentration ratios in seeds decreased with increasing S supply. The ratios were particularly high (*ca* 25) for the most severely S-deficient plants. A critical seed N/S ratio corresponding to 90% of maximum seed yield was calculated from relative (%) seed yields and N/S ratios. The critical N/S ratio for the N_{168} treatments in which the plants were N-sufficient was 15.6; however, this value should be regarded as tentative pending further work.

S deficiency affected the amino acid composition of seeds only when the N supply was non-limiting (Table 5). The main effect of S deficiency was to decrease the essential S-containing amino acids, cysteine and methionine, by about 30% and increase the content of arginine by 35%. The chemical score (P.A.G., 1976) for cysteine + methionine was reduced from 114 to 78 between S_{75} and S_1 at N_{168}. However, the lysine score changed only from 50 to 47 over the same

TABLE 5. Amino acid composition of defatted seed meal extracts after performic acid oxidation*. Single change in S supplies made at anthesis; double change made at end of floret initiation and at anthesis.

Amino acid	Constant S supply						Changed S supply			
	S_1N_7	$S_{75}N_7$	S_1N_{168}	S_5N_{168}	$S_{10}N_{168}$	$S_{75}N_{168}$	S_1 to S_{75} N_7	S_1 to S_{75} N_{168}	S_{10} to S_1 N_{168}	S_1 to S_{75} to S_1 N_{168}
Ala	7.0	6.9	7.0	6.8	6.7	6.7	6.8	6.6	6.6	6.3
Arg	7.1	7.4	10.1	9.5	7.7	7.9	7.2	7.8	10.9	8.1
Asp	9.0	9.1	9.7	9.4	9.2	9.2	8.9	9.2	9.4	9.2
½Cys	1.9	2.1	1.4	1.4	1.9	2.0	2.0	1.9	1.3	1.9
Glu	18.7	18.6	16.5	19.2	19.9	19.0	18.9	20.6	19.1	21.9
Gly	10.5	10.1	10.8	10.9	10.0	10.0	10.5	9.8	10.5	9.5
His	2.2	2.1	2.2	2.2	2.2	2.2	2.2	2.1	2.1	2.0
Ile	4.5	4.7	4.8	4.5	4.7	4.8	4.5	4.7	4.5	4.6
Leu	6.6	6.6	6.5	6.3	6.5	6.5	6.5	6.3	6.0	6.2
Lys	3.3	3.1	2.6	2.6	3.0	2.8	3.4	2.8	2.8	2.4
Met	2.4	2.4	1.4	1.4	1.9	2.1	2.5	1.8	1.3	1.7
Phe	4.2	4.3	4.5	4.2	4.4	4.5	4.1	4.3	4.1	4.4
Pro	5.1	5.3	5.4	4.9	5.3	5.2	5.2	5.2	4.8	5.2
Ser	5.6	5.6	5.6	5.6	5.6	5.5	5.7	5.5	5.5	5.4
Thr	4.3	4.2	3.8	3.8	4.1	3.9	4.3	3.9	2.7	3.6
Tyr**	1.5	1.5	1.4	1.3	1.4	1.5	1.5	1.4	1.3	1.4
Val	6.2	6.2	6.5	6.1	6.3	6.3	6.0	6.2	6.1	6.2

Results expressed as percentage distribution of amino acid residues recovered. Values are means of duplicate analyses.
S and N supplies as mg/l.
*Performic acid oxidation done to fully recover ½ Cys and Met.
**Values for Tyr are underestimated by 23% due to performic acid treatment.

treatments, so even in S-deficient plants, lysine was the most limiting essential amino acid.

DISCUSSION

It is clear that S deficiency has detrimental effects similar to N deficiency (Steer and Hocking, 1983; Steer <u>et al</u>. 1984) on agronomically important characters of sunflower including leaf area, floret number and seed size. However S deficiency, unlike N deficiency, has little effect on leaf number, suggesting that the activity of the vegetative meristem is determined to a much greater extent by the N rather than the S status of the plant.

About 20% of the total S in mature sunflower plants is taken up before the completion of floret initiation, 45% between then and anthesis and 35% after anthesis (Hocking and Steer, 1983). Although the requirement of sunflower for S is fairly modest between germination and the end of floret initiation, our results emphasize the importance of providing an adequate S supply to young plants up to the end of floret initiation to obtain maximum numbers of florets (or potential seeds) and a large leaf area to provide photosynthates to developing florets and seeds. It is also important that the S supply is adequate during the period from the end of floret initiation to anthesis, as this helps maintain floret development and establishes the potential for large individual seeds. After anthesis, the yield components of sunflower seem relatively unresponsive to the relief of S deficiency. However, severe S deficiency during seed filling can result in the abortion of some developing seeds, and it can be detrimental to seed quality because of the synthesis of sulfur-poor proteins, thus reducing the nutritional value of the meal as stockfeed.

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