COMPARATIVE EFFECTS OF INDUCED WATER STRESS ON NUTRIENT UPTAKE AND WATER-SOLUBLE CARBOHYDRATES ACCUMULATION IN SUGAR BEET AND WHEAT.

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ABSTRACT

Two experiments were conducted to investigate the comparative effects of water stress induced at different growth stages on nitrogen (N), phosphorous (P), potassium (K) and sodium (Na) uptake and water-soluble carbohydrate (WSC) accumulation in two contrasting crop species. The first trial investigated the effect of water stress induced at four growth stages in one variety each of wheat (Triticum aestivum (L), var Wembley) and sugar beet (Beta vulgaris (L) var Gala), while in the second trial water stress was induced at two growth stages of both crop species in the second trial. Water stress at any of the growth stages significantly reduced N, P, K and Na uptake in wheat, while it had no appreciable effects on nutrients uptake in sugar beet. However, water stress at any of the growth stages significantly increased water-soluble carbohydrate accumulation in wheat leaves, while the parameter did not show consistent response to water stress in sugar beet. Early stress (very early and early) decreased WSC in sugar beet, while late stress (late and very late) resulted in increased WSC in the species. This study revealed significant relationships between reduced nutrient uptake and decreased grain yield in wheat, while in sugar beet, there was no evidence to suggest that any response to water stress was related to reduce nutrients uptake. These results suggest that reduced nutrient uptake due to water stress can play significant role in yield reduction in wheat but not in sugar beet.

Key words:_Water stress, nutrients uptake, water-soluble carbohydrates accumulation, *Beta vulgaris, Triticum aestivum*

INTRODUCTION

The development of water deficits in soil leads to a wide range of responses by plants. However, many of the earlier responses were later recognized to be secondary responses arising as a result of primary processes being directly affected rather than them being primary responses to water deficit *per se* (Turner and Begg, 1981). For instance, the adverse effects of drought on crop yield are sometimes attributed to reduced nutrient uptake, especially, the macro elements. Many workers have shown that nutrients uptake is decreased by water stress induced by soil moisture deficit (Dunham and Nye, 1974; Gerakis *et al.,* 1975), osmotic stress by polyethylene glycol (PEG) or NaCl (Erlandson, 1975). The decrease has been reported to be due to reduced transpiration (O'Toole and Balda, 1982; Yambao and O'Toole, 1984) and impaired active transport and membrane permeability (Hsiao, 1973) resulting in reduced root absorbing power. Marais and Wiersma (1975) and Viets (1972) also reported that a decline in soil moisture is also associated with a decrease in the diffusion of nutrients from soil matrix to the absorbing root surface.

Reduction of N and P uptake induced by water deficit had been well demonstrated (Greenway and Klepper, 1969; Gates, 1974). Greenway et *al.* (1969) reported that the absorption of ^{32}P by root cells of maize and soybean was severely inhibited by water potential below –1.2 to –1.5 Mpa. This decrease in P uptake was however, shown to be due to increased leakage from cells, whereas ion uptake *per se* was not affected (Greenway *et al.,* 1968). Dunham and Nye (1976) reported that in onion, P uptake was much more sensitive to moisture stress than was K, Mg, or Ca uptake, hence, the increased Ca: K and Ca: P ratios in water stressed wheat and yellow peas. Nambiar (1970) showed that Zn uptake by oat roots was less sensitive to water stress, 40% as much as being absorbed from dry as from dry soils. Furthermore, it has been shown that the effect of water stress is not only on ions in roots, but also in leaves. For example, Chamel and Bougie (1974) reported that the uptake and translocation of ^{42}K decreased significantly even when deposited on corn leaves when osmotic potential of the culture solution was lowered to 0.82 Mpa by PEG. It was thus concluded that the rates of translocation vary directly with water content of the plant.

Water-soluble carbohydrates (WSC) are the main substrates for starch synthesis in cereal grain. Many workers have reported increases in concentration of non-structural carbohydrates in response to water stress in many crop species (Deng *et al.*, 1990; Fredrick *et al.*, 1990). A higher leaf WSC concentration in dry land grown than in irrigated spring wheat plants has been reported (Frank *et al.*, 1989). Similarly, increase in WSC concentration in stressed pre-anthesis ears of spring wheat had earlier been observed (Dougherty *et al.,* 1975). An accumulation of WSC in leaves resulted from cessation of translocation out of the leaves to the root in sugar beet or to the ear in wheat (Fredrick *et al.,*1990).

Plant species are known to differ widely in their responses to induced or natural water stress. These differences in response are also known to be influenced by both the age of the plant at the onset of the stress and the duration of the stress itself. The present study was therefore conducted to evaluate the nutrient uptake status and WSC accumulation responses of spring wheat and sugar beet to water stress induced at different growth stages.

MATERIALS AND METHODS

Two experiments were conducted in a glasshouse at the Faculty of Agricultural and Forest Sciences, University of Wales College Farm, Aber, Gwynedd, U.K, in 1991 and 1992 A spring wheat, cultivar Wembley and a sugar beet, cultivar Gala (a monogerm) were used in the study. The plants were grown in lysimeter tanks 1m x 1m x 1m, filled with sandy soil having a pH of 6.7 in water. The study was designed and laid out in a randomized complete block with four replications. Even though both species were randomized together, the wheat and sugar beet were treated separately due to differences in growth pattern and the developmental stages at which water stress was applied.

Wheat seeds treated with a dual purpose seed dressing were planted at a rate of 300 seeds per m^2 while the beet seeds which were pelleted and treated as normal commercial seeds were planted at a rate of 16 seeds per m^2. Fertilizer was applied to wheat at standard rates equivalent to 100 kg N ha^{-1}, 100 kg K_2O ha^{-1} and 50 kg P_2O_5 ha^{-1}, while sugar beet plots received fertilizer at rates equivalent to 100 kg N ha^{-1}, 200 kg K_2O ha^{-1} and 50 kg P_2O_5 ha^{-1}, The fertilizer was applied to each plot in two equal amounts at planting and at 6 and 12 weeks after sowing (WAS) for wheat and sugar beet respectively. Weed control inside the tanks was achieved by hand rogueing at two-weekly intervals.

In the first trial, there were five water stress treatments including a well-watered control in each of the two test crop species. The water stress treatments in wheat involved withholding watering during the four physio-morphological growth stages of tillering to stem elongation (T-SE), stem elongation to booting (SE- B), booting to anthesis (B-ANT) and anthesis to maturity (A-MAT) as described by Abayomi and Wright (1999). In sugar beet, there are no distinct phenological growth stages (Milford, 1973) and therefore the choice of period for stress application was largely arbitrary by dividing the period between sowing and maturity into four equal periods during each of which soil water stress was induced and designated as very early stress (VES), early stress (ES), late stress (LS) and very late stress (VLS). In the second trial, longer stress periods were adopted, hence there were three water stress treatments including a well-watered control. The water stress treatments in wheat therefore included cessation of watering at tillering to stem elongation (T-SE) and at stem elongation to anthesis (SE-ANT). As in the first trial, the choice of water stress periods was arbitrary by cessation of watering during each half of the period between sowing and harvesting designated as early stress (ES) and late stress (LS) respectively.

At the end of each stress period and before re-watering in both trials, leaf samples were taken to determine the nutrients uptake and WSC accumulation. The samples from each plant species were oven dried at 80°C for 72 hours, ground and stored in sealed envelopes for chemical analyses. The samples were analyzed for total nitrogen using the Kjeldahl method (AOAC, 1955), potassium and sodium by flame photometry (Isaac and Kerber, 1971), phosphorus, spectrophotometrically as the yellow phospho-vanado-molybdate complex (Cavell, 1955) and water soluble-carbohydrate spectrophotometrically as the blue-green complex formed when carbohydrates are heated with anthrone in sulphuric acid (Deriaz, 1961). The concentration of the elements and WSC were obtained in percentages in the two trials, while the total uptake per plant was calculated in the second trial by multiplying the percent concentration with the total dry matter per plant.

All data for both wheat and sugar beet were subjected to analyses of variance (ANOVA) separately, using complete randomized block design model. Tests were made at 5 percent probability level and significantly different means were separated calculating the least significant difference (LSD).

RESULTS

Experiment 1

In wheat, water stress at any growth stage significantly decreased N concentration (%) with the exception of a stress at booting to anthesis (B-ANT) which had no significant effect (Fig 1a). However, in sugar beet, N concentration was increased by water stress at any growth stage, with significant effect at VES (Fig 1a). Water stress at any growth stages significantly decreased K concentration in wheat with the exception of a stress at anthesis to maturity (A-MAT) which showed no significant effect on K uptake (Fig 1b). However, K concentration was not significantly affected by water stress at any growth stage in sugar beet (Fig 1b).

Phosphorus concentration was decreased by water stress at tillering (T-SE) and at booting (B-ANT) growth stages in wheat with significant effect at T-SE. However, water stress at stem elongation (SE-B) and anthesis (A-MAT) growth stages had no significant effect on P concentration (Fig 1c). Similarly, VES and ES treatments decreased P concentration in sugar beet with significant effect at VES, while LS and VLS had no significant effects on P (Fig 1c). Water stress at any growth stage had no significant effects on Na concentrations in both wheat and sugar beet (Fig 1d). Water soluble carbohydrates concentration in wheat was increased by water stress induced at any growth stage with significant effects at T-SE and SE-B (Fig 1e). In sugar beet, however, VES and ES treatments resulted in decreased WSC with significant differences at VES, while LS and VLS treatments significantly increased WSC concentration (Fig 1e).

Experiment 2

Water stress during T-SE significantly decreased N concentration in wheat, while N uptake was increased by a stress at SE-ANT (Fig 2a). In sugar beet, early stress (ES) significantly increased N uptake while a late stress (LS) significantly decreased N concentration (Fig 2a). Total N content per plant was significantly decreased by water stress at any growth stage in wheat (Table 1). Similarly, ES increased N content in sugar beet, LS had no significant effect (Table 2). Potassium concentration in wheat plant was significantly decreased by water stress at the two growth stages (Fig 2b). Consequently, the total K uptake per plant was significantly decreased by water stress at the two periods (Table 1). However, there was no significant effect of water stress at any period on K concentration (Fig 2b), and hence no significant impact of water stress at any period on total K uptake in the species (Table 2).

Water stress at both growth stages significantly decreased both P and Na concentrations in wheat (Fig 2c and 2d), thereby resulting in significant decreases in the total uptake of the elements at both growth stages (Table 1). However, ES decreased P concentration in sugar beet, while LS resulted in significant increase in P concentration (Fig 2c). Both the ES and LS treatments had no significant effects on Na concentration in the species (Fig 2d), even though the total Na uptake was decreased by water stress at the two periods (Table 2).

Water stress applied during T-SE and SE-ANT resulted in significant increase in WSC concentration n wheat (Fig 2e), thereby resulting in significantly higher total WSC in plants stressed at T-S, but a lower content in plants stressed at SE-ANT(Table 1). Both ES and LS decreaased .

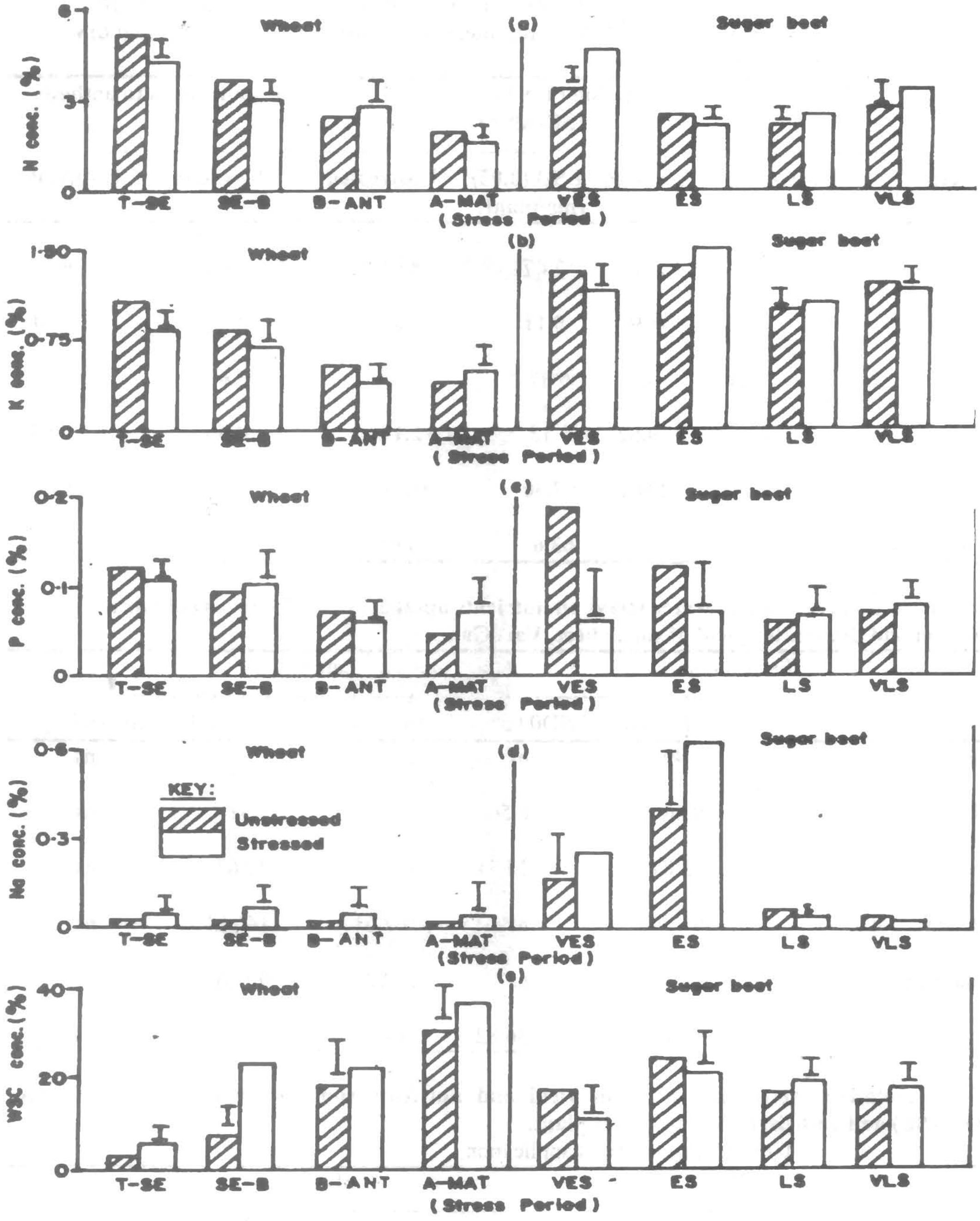

Fig. 1: Effect of water stress at different growth periods on (a) N, (b) P, (c) K, (d) Na and (e) WSC concentration in wheat and sugar beet, plants in Experiment 1. For wheat T-SE = tillering to stem elongation, SE-B = stem elongation to booting, B-ANT = booting to anthesis, and A-MAT = anthesis to maturity, growth stages for sugar beet, VES = very eary stress ES = early stress, LS = late stress and VLS = very late stress, I LSD (0.05)

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Table 1. Both ES and LS decreased WSC concentration in sugar beet with a Table 1: Effects ofwater stress at T-SE and SE-ANT on nutrients uptake, water soluble carbohydrates and dry matter of a spring wheat variety, Wembley.

	Tillering to stem elongation (T-SE) (SE-ANT)			Stem elongation to anthesis		
Parameters	**Unstressed**	**Stressed**	**LSD (0.05) (mg/plant)**	**Unstressed**	**Stressed**	**LSD(0.05)**
N	61.9	27.9	7.47	86.8	29.2	9.96
P	0.93	0.36	0.11	1.67	0.31	0.24
K	50.3	6.5	6.39	22.5	3.6	3.57
Na	. 92	0.52	0.13	2.17	0.36	0.58
WSC	55.1	294.2	57.30	916.12	69.4	154.00
Dry matter (g m^{-2})	420	270	63.6	865	189	90.4

Table 2: Effects of early and late water stress on nutrients uptake, after soluble carbohydrate accumulation and dry matter yield of sugar beet, Var. Gala.

	Early stress			Late stress		
Parameters	Unstressed	Stressed	LSD0.05	Unstressed	Stressed	LSD0.05
N (g/plant)	1.52	0.99	ns	2.38	2.3	ns
P (mg/plant)	1.28	0.64	0.56	1.63	1.51	ns
K (mg/plant)	30.66	13.81	13.31	47.30	42.67	ns
Na (mg/plant)	101.91	57.59	ns	167.61	146.81	ns
WSC (mg/plant)	47.11	26.30	ns	87.82	90.16	ns
DM (g m^{-2})	85.46	45.24	36.82	144.57	137.13	ns

Table 3: Correlation coefficients of grain yield and nutrients concentrations in shoot at stem elongation (SE) and antheisi (ANT) in wheat plant.

	Growth stage at stress application			
	T – SE		SE – ANT	
Element	SE	ANT	SE	ANT
N	0.697*	0.906*	0.663	0.520
P	-0.339	-0.127	-0.986**	0.520
K	0.889*	0.928**	0.986**	0.605
Na	0.906*	-0.598	-	0.685*

***, ** denote r significant at 5 and 1 percent probability levels respectively.**

WSC concentration with significant effect by ES (Fig 2e). Nevertheless, both stress treatments resulted in significantly lower total WSC per plant. (Table 2). Table 3 shows that grain yield in wheat plants stressed at T-SE was positively correlated with N, P and K in plant at stem elongation and N and K at anthesis. Similarly, there were strong relationships between percent loss in grain yield and percent reduction in nutrients concentrations in shoot due to water stress (Fig 3) in the species.

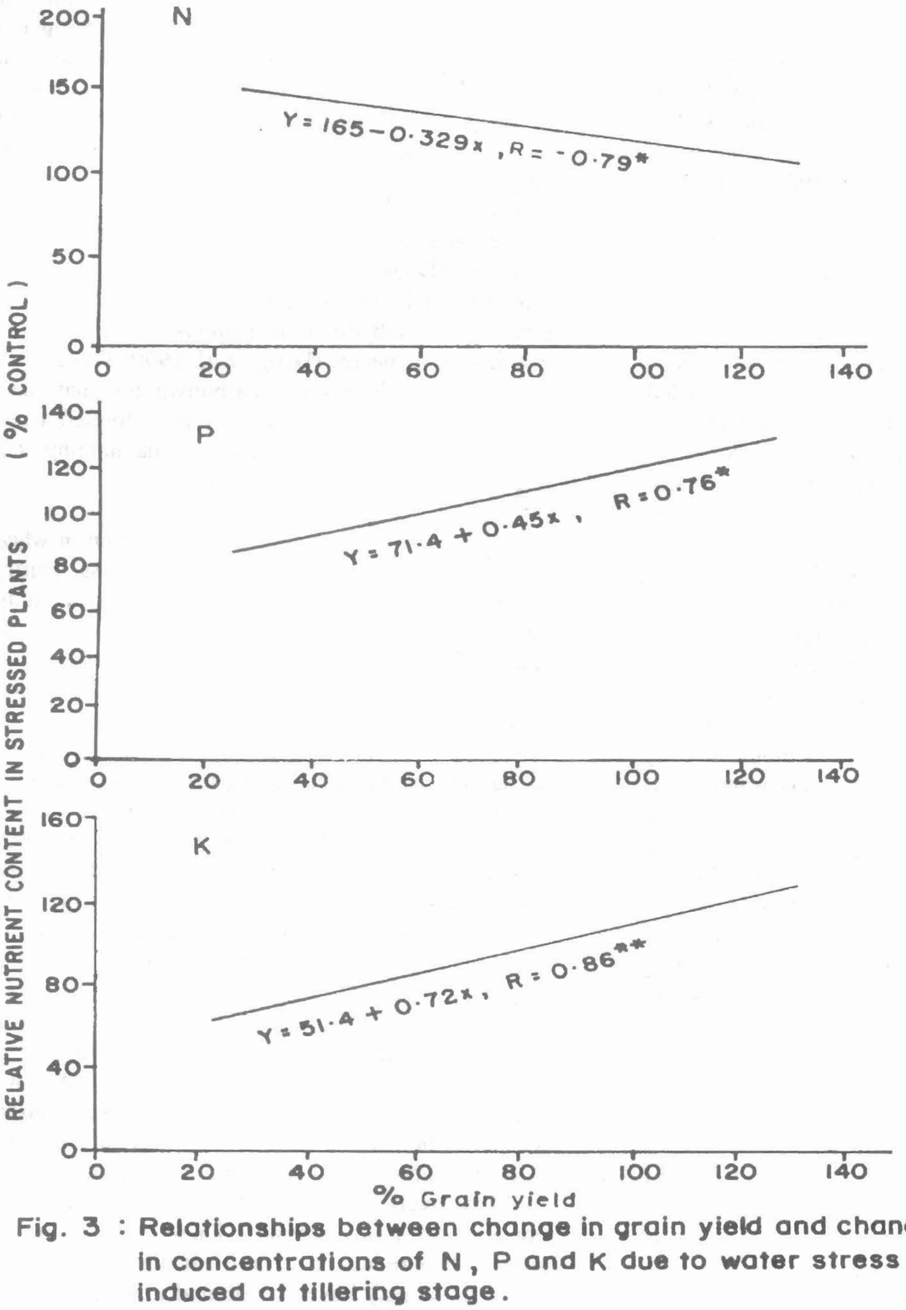

Fig. 3 : Relationships between change in grain yield and changes in concentrations of N, P and K due to water stress induced at tillering stage.

DISCUSSION

Nutrient uptake

Water stress significantly reduced N uptake at all growth stages, excepting B-ANT in wheat (Fig 1a). However, in sugar beet, it was only the ES that had significant effect on N uptake. The trend obtained for wheat is in line with the findings of other workers who have reported decreases in N uptake in soybean and pigeon pea (Devries *et al.,* 1989) and maize (Wolf *et al.,* 1988; Frederick *et al.,* 1990). Similarly, the data for sugar beet are in conformity with the results of Pande and Singh (1969), Day *et al.* (1978) and Lawlor *et al.* (1981) who reported that water stress has little or no effects on N concentration in plant tissue. Brown *et al.* (1987) have also reported that the effects of drought on sugar yield in sugar beet crop were not related to N uptake. Similarly, Draycott (1972) and Last *et al.* (1983) have concluded that the amount of N fertilizer needed for maximum yield of sugar beet is not affected by irrigation. Specific differential responses of N uptake under water stress have been reported for rice, maize and soybean (Tanguilig *et al.*, 1987).

Potassium uptake in wheat was also significantly decreased by water stress at any growth stage before anthesis after which there were no significant effects (Fig 1b). However, the effect of water stress on K uptake were not significant for sugar beet at any period. Similar differential effects of water stress on K uptake of crop species has been demonstrated by Tanguilig *et al.* (1987), who found that water stress significantly decreased K uptake in rice but not in maize and soybean. Other workers have reported that K absorption in barley decreased with drought (Day *et al.* 1978; Lawlor *et al.* 1981)Results of this study showed that P uptake was significantly decreased by water stress at tillering and booting stages in wheat and VES and ES in sugar beet, but has little effects at all other growth stages (Fig 1c). Significant decreases in P uptake due to water stress have been reported for other crops (Day *et al.,*1978; Lawlor *et al.,* 1981;Tanguilig *et al.*, 1987). There were no significant effects of water stress on Na uptake, although the ion concentration tended to be increased by water stress in both crop species (Fig 1d). A similar lack of appreciable effects of water stress on Na uptake had been reported by Day *et al.* (1978).

Water Soluble Carbohydrate (WSC)

Water stress at any growth stage increased water soluble carbohydrate in wheat, while in sugar beet it did not show such consistent trend (Fig 1e). Early stresses (VES and ES) decreased WSC, while late stress (LS and VLS) increased WSC. According to Frederick *et al*, (1990), an accumulation of sugar in the leaves resulted from cessation of translocation out of leaves to the root (in sugar beet) or to the ear (in wheat). A higher leaf WSC concentration in dry land-grown than in irrigated spring wheat plants had been reported (Frank *et al.*, 1989). Similarly, increased in WSC concentration in water-stressed pre-anthesis ears of spring wheat had also been observed (Dougherty *et al.*, 1975). Other workers also reported increases in concentration of non-structural carbohydrates in response to water stress in other crop species (Deng *et al.* 1990; Frederick *et al.*, 1990). Moreover, carbohydrates may have accumulated in the leaves of water- stressed wheat plants to serve as an osmoticum in maintaining leaf turgor (Michelena and Boyer, 1982).

The effects of water on WSC accumulation in wheat were greater with pre-anthesis water stress. During the early reproductive development in this study, carbohydrate accumulated probably due to lack of sink demand as hypothesized by Jungens *et al.* (1978). Wardlaw (1967) suggested that water stress may have decreased the permeability of cells to sugar, and the higher sugar concentration in the leaf tissue may have resulted in the progressive decline in the net photosynthesis as reported by many workers (Gummuluru *et al.*, 1989a; 1989b; Abayomi, 1992). The results of this study therefore suggest that current photo-assimilate may be temporarily stored in source leaves and stems of crop plants such as wheat, and /or in the sink root of sugar beet during periods of plant water deficit.

Conclusively, the results of this study showed that grain yield in wheat plants stressed at T-SE was positively correlated with N, P and K concentrations at stem elongation, and N and K at anthesis. Similarly, grain yields in plants stressed at SE-ANT were positively associated with shoot N, P, K and Na concentrations at antesis. These results further suggest that reduction in nutrient absorption due to water stress may have contributed in part to loss of grain yield due to water stress. However, in sugar beet, there was no evidence to suggest that any response to water stress was related to reduce nutrients uptake.

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