INFLUENCE OF HIGH TEMPERATURE STRESS ON CONTENT AND TRANSLOCATION OF CARBOHYDRATES IN WHEAT(*TRITICUM AESTIVUM* L.) DURING GRAIN FILLING

by

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INTRODUCTION

Carbohydrates are integrally involved in responses of plants to high temperature stress. They are primary products of the heat-sensitive photosynthetic process (Berry and Bjorkman, 1980), major substrates of elevated respiration rates from high temperatures (Spiertz, 1977; Wardlaw et al., 1980), and constitute most of the economic yield of heat-sensitive crops (Al-Khatib and Paulsen, 1984).

Many studies have implicated carbohydrates in high temperature injury in plants. Levitt (1980) suggested that temperatures above the compensation point deplete carbohydrates so that cells starve. Carbohydrates may also dissipate in some organs when they accumulate in leaves from blocking of sieve plates by heat induced callose (Dinar et al., 1983; McNairn, 1972). In other cases, inhibition of growth processes by high temperatures can cause general accumulation of carbohydrates (Aldous and Kaufmann, 1979; Duff and Beard, 1974; Youngner and Nudge, 1976).

The role of carbohydrates in high temperature effects is uncertain. Santarius (1973) showed that high concentrations of soluble carbohydrates protect photosynthetic membranes from heat inactivation. Glucose and sucrose also delay chlorophyll loss in floating leaf discs in darkness (Tetley and Thimann, 1974; Thimann et al., 1977), but accelerate it under high light intensity as the temperature increases (Khudairi, 1970). Cooling the attachment node of flag leaves to decapitated culms, on the other hand, hastens chlorophyll loss and accumulation of carbohydrates (Lazan et al.,1983).

Cessation of shoot growth at supraoptimal temperatures is attributed to heat-labile root processes associated with loss of root soluble carbohydrates (Aldous and Kaufmann, 1979). Other recent results indicate that effects of both high root and high shoot temperatures are mediated through roots and expressed as acceleration of shoot senescence (Kuroyanagi and Paulsen, 1985b).

The numerous indications of involvement of carbohydrates in high temperature injury and the equivocal nature of their role prompted investigations reported here. Objectives were to determine changes in carbohydrate composition during whole-plant senescence at elevated temperatures and their relationship to changes in other constituents reported previously (Al-Khatib and Paulsen, 1984; Kuroyanagi and Paulsen, 1985a, 1985b).

MATERIALS AND METHODS

Plants were cultured as described previously (Al-Katib and Paulsen, 1984) except that spring wheat (Triticum aestivum L. cv. 'Chris') was used without vernalization. They were supplied with continuously aerated nutrient solution (Hoagland and Arnon, 1950) and grown under controlled conditions of 25°C day/15°C night, 16-hr photoperiod with 320 umol $m^{-2}s^{-1}$ photon flux density, and relative humidity of 0.4 until 5d after anthers were extruded by 50% of the spikes. At 50% anthesis, plants were assigned to temperature regimes of 25°C/15°C, 30°C/20°C, or 35°C/25°C in a completely randomized design with three replications. Other conditions were maintained as before for growing the plants to physiological maturity.

Samples for carbohydrate assays, dry matter accumulation, chlorophyll content, and invertase activity were taken 0, 7, 14,

21, and 28 days after temperature treatments were initiated. Additional samples of plants grown at the lower temperature, which were delayed in maturity, were obtained after 61 days. Three plants from each treatment of all replications were used each date. Plants were separated into viable and senesced leaf blades on the basis of visual appearance, sheaths, stems, roots, and spikes. Area of viable leaves was measured with an electronic meter. A subsample of each plant was retained for further analyses and the balance of the plant material was dried at 70°C for 72h and weighed.

Subsamples for carbohydrate and chlorophyll analyses were immersed in 50 ml of 90% (v/v) ethanol immediately after they were taken. The suspensions were homogenized for two 15-s periods, shaked for one h, and filtered (Kuhbauch and Soberalske, 1977). The residue was washed with 90% ethanol until it lost color and the filtrate was diluted to 100-ml volume. Chlorophyll in the filtrate exhibited the same absorbance characteristics as in 96% and 100% ethanol (Knudson et al., 1977) and was measured directly.

An aliquot of the ethanol extract was evaporated to near dryness, taken up in hot water, cooled and diluted to 100-ml volume. The solution was filtered and ethanol-soluble carbohydrates were measured on the filtrate by a phenol-sulfuric acid method (Nalewaja and Smith, 1963) using fructose as a standard.

The residue from the ethanol extraction was freeze-dried, shaked in 100 ml of water for one h, and filtered to obtain

water-soluble carbohydrates (Kuhbauch and Soberalske, 1977). The phenol-sulfuric acid method (Nalewaja and Smith, 1963) and fructose standards were used for the assays.

Invertase enzyme activity was measured in leaves of plants grown under the different temperature regimes by the method of Roberts (1953). Leaf blade samples (0.3 g) were homogenized in 10 ml of 0.2 M acetate buffer (pH 4.4) for two 15-s periods. Homogenates were filtered through Miracloth and centrifuged at 20,000 xg for 15 min. A 0.2-ml aliquot of the supernatant was incubated with 0.8 ml of reaction medium [0.2 M acetate (pH 4.4) and 0.2 M sucrose] at 25°C for 30 min. The reaction was stopped with 1 ml of copper reagent and reducing sugars were assayed by the method of Nelson (1944) using the mixture of equimolar glucose-fructose as standards.

Detached leaf blades from 1-week-old seedlings were used for studying the relationship between carbohydrates and other constituents during dark induced senescence. Leaf blades were floated on distilled water or 10^{-5} M kinetin solution at 25°C/15°C day/night temperature regime in darkness. Chlorophyll, ethanol- and water-soluble carbohydrates, and invertase enzyme activity were assayed as described above.

Statistical analysis of data was by conventional analysis of variance procedures. LSDs were expressed at the $P = 0.05$ level and CVs were calculated for precision of data.

RESULTS

Viable leaf blade area remained high under the low temperature regime and declined slowly under the intermediate regime during four weeks of treatment (Table 1). Under the high temperature regime, however, leaf area declined significantly each week and all leaves had senesced by the fourth week. Chlorophyll concentration was also high in the viable leaves of plants grown at the low temperature and declined slowly as plants matured. Loss of chlorophyll was slightly faster under the 30°C/20°C regime, particularly after 21 d, but was greatly accelerated under the 35°C/25°C regime at all sampling dates.

Leaf invertase activity varied slightly, but showed no general trend as plants matured at the low temperature (Table 1). Activity declined slightly at the intermediate temperature and fell rapidly at the high temperature during the same period.

Ethanol-soluble carbohydrates were usually 5-fold or more important quantitatively than water-soluble carbohydrates in all plant parts (Table 2). They also responded more to temperature treatments during aging. Little change in ethanol-soluble carbohydrates in leaf blades occured at the two lower temperatures, but large amounts accumulated quickly after imposition of the high temperature treatment. The accumulated carbohydrates dissipated gradually after the first week, however, and were at a low level at the final sampling date. Water-soluble carbohydrates, in contrast, changed little.

Both ethanol-soluble and water-soluble carbohydrates in the sheaths and stems followed trends opposite those in the blades (Table 2). Both fractions stayed at high levels in sheaths at the

Table 1. Area, chlorophyll concentration, and invertase enzyme activity in leaf blades of 'Chris' wheat grown under three temperature regimes during grain development.

Treatment duration	Day/night temperature	Leaf area	Chlorophyll	Invertase activity
Days	°C	$cm^2\ plant^{-1}$	$mg\ g^{-1}$ DW	$\mu mol\ g^{-1}\ hr^{-1}$
0	25/15	229.03	4.59	250.40
7	25/15	241.37	5.00	275.76
7	30/20	233.42	4.75	216.50
7	35/25	174.70	3.50	158.37
14	25/15	213.40	4.03	249.33
14	30/20	198.55	3.85	173.33
14	35/25	121.17	2.03	111.17
21	25/15	219.93	4.02	174.77
21	30/20	178.27	3.09	158.50
21	35/25	80.70	0.42	61.17
28	25/15	174.43	3.53	217.20
28	30/20	147.03	2.25	179.45
28	35/25	0.00	0	52.30
LSD (0.05)		49.02	0.79	73.90
C.V. (%)		14.4	12.6	21.2

Table 2. Ethanol- and water-soluble carbohydrate concentrations in vegetative parts of 'Chris' wheat grown under three temperature regimes during grain development.

Treatment duration	Day/night temperature	Plant parts							
		Blades		Sheaths		Stems		Roots	
		ESS*	WSS**	ESS	WSS	ESS	WSS	ESS	WSS
Days	°C	$mg \cdot g^{-1}$ DW							
0	25/15	94.68	12.50	91.63	9.77	85.53	9.25	59.06	14.63
7	25/15	82.10	18.00	103.23	15.77	153.23	43.17	60.37	17.80
7	30/20	95.60	17.23	118.03	20.77	147.05	36.37	78.97	16.43
7	35/25	227.77	19.10	82.07	10.37	77.40	9.47	66.20	11.30
14	25/15	103.60	18.10	106.07	22.63	104.97	20.40	59.27	15.87
14	30/20	113.80	17.76	112.57	20.67	107.17	19.57	77.93	14.93
14	35/25	147.37	12.23	98.97	9.20	54.50	8.43	53.50	10.03
21	25/15	109.80	13.90	111.10	19.83	62.73	15.90	75.75	12.35
21	30/20	114.17	19.77	112.90	23.37	70.10	10.63	78.25	13.25
21	35/25	134.33	19.20	129.07	12.67	72.80	9.50	66.37	14.16
28	25/15	115.37	17.50	94.33	15.23	55.43	8.73	63.90	12.27
28	30/20	116.63	16.50	108.53	16.60	60.03	7.48	43.00	14.37
28	35/25	91.33	19.80	76.27	11.16	41.87	8.17	69.57	14.53
61	25/15	79.97	21.80	60.30	13.35	26.00	9.73	34.60	16.13
61	30/20	28.20	22.97	52.10	14.87	21.83	6.47	51.80	19.20
LSD(0.05)		25.40	4.50	17.18	6.93	13.64	14.24	13.02	4.91
C.V. (%)		8.1	10.0	6.3	16.1	6.3	33.2	7.6	14.8

* ESS = Ethanol soluble carbohydrates

** WSS = Water soluble carbohydrates

low temperature until the fourth week. At high temperature, however, levels of both fractions were usually low. Disappearance of the two fractions from the stems coincided closely with senescence. After increasing during the first week, soluble carbohydrates decreased to low levels at the last sampling under the lower temperature regimes. The two fractions remained low under the high temperature regime as plants senesced rapidly. In contrast, no discernible trend or differences occurred in roots.

Dry matter accumulation in all parts responded to temperature (Table 3). Grain growth was accelerated early by high temperature, but also ceased early. Duration of grain filling was greatly prolonged by the low temperature regimes so that highest yields occured with the lowest temperatures. Weights of leaf blades, sheaths, stems, and roots remained high and, in some cases, increased during maturation at low temperatures. Leaf blades and stems were affected more adversely than other vegetative parts by high temperatures.

Dark-induced senescence caused rapid loss of chlorophyll and ethanol- and water-soluble carbohydrates from detached leaf blades (Table 4). Reducing sugars increased the first day, probably as a consequence of hydrolysis of ethanol-soluble sucrose by the highly active invertase enzyme present the first several days. Kinetin slowed the loss of chlorophyll and ethanol-soluble carbohydrates, had no effect on water-soluble carbohydrates, and decreased the level of reducing sugars. It also slightly increased invertase enzyme activity the third day.

Table 3. Dry matter accumulation in grain and vegetative parts of 'Chris' wheat grown under three temperature regimes during grain development.

Days duration	Day/night temperature	Plant parts				
		Grain	Blades	Sheaths	Stems	Roots
Days	°C	- - - - - - - - - - g·plant^{-1} - - - - - - - - - -				
0	25/15	0.06	0.73	0.61	1.27	0.40
7	25/15	0.38	1.02	0.76	1.82	0.61
7	30/20	0.50	1.02	0.76	1.75	0.71
7	35/25	0.59	1.04	0.73	1.42	0.48
14	25/15	0.92	1.04	0.75	1.78	0.41
14	30/20	1.06	0.99	0.77	1.69	0.50
14	35/25	1.15	0.81	0.68	1.37	0.35
21	25/15	2.23	1.18	0.86	2.31	0.56
21	30/20	2.29	1.06	0.82	1.91	0.53
21	35/25	1.13	0.86	0.69	1.19	0.31
28	25/15	3.25	1.22	1.12	2.31	0.58
28	30/20	2.95	1.19	1.03	2.04	0.65
28	35/25	1.36	0.79	0.60	1.10	0.38
61	25/15	3.82	1.19	1.10	2.30	0.79
61	30/20	3.32	1.15	1.00	2.20	0.82
LSD (0.05)		0.51	0.30	0.24	0.62	0.25
C.V. (%)		16.2	13.9	14.1	17.1	24.0

Table 4. Chlorophyll, ethanol-soluble and water-soluble carbohydrate, and reducing sugar concentrations and invertase enzyme activity in detached 'Chris' leaf blades incubated in darkness in the absence and presence of kinetin.

Days in darkness	Chlorophyll		ESS*		WSS**		RDS***		Invertase	
	CK	Kinetin	CK	Kinetin	CK	Kinetin	CK	Kinetin	CK	Kinetin
Days	- - - - - - - - - - - - - - - - $mg \cdot g^{-1}$DW - - - - - - - - - - - - - - - -								$\mu mole \cdot g^{-1} \cdot hr^{-1}$	
0	12.14		166.80		22.06		94.74		338.50	
1	11.55	12.10	151.01	155.54	19.11	19.49	115.93	102.11	452.59	412.38
2	8.32	10.31	118.10	128.04	15.23	16.22	99.77	89.63	564.70	620.20
3	5.01	8.08	95.05	101.63	15.16	15.56	80.42	76.66	331.00	403.77
4	3.50	7.06	72.89	88.23	14.25	13.04	61.86	74.01	--	--
5	1.56	5.89	55.94	71.56	11.76	13.26	47.96	60.45	--	--
LSD (0.05)	1.36		7.89		2.87		5.86		63.46	
C.V. (%)	11.2		4.5		11.4		4.4		7.8	

* ESS = Ethanol Soluble Sugar

** WSS = Water Soluble Sugar

*** RDS = Reducing Sugar

DISCUSSION

Results confirm the sensitivity of carbohydrates in plants to high temperature stress (Aldous and and Kaufmann, 1979; Dinar et al.,1983; Lazan et al., 1983; McNairn, 1972; Spiertz, 1977; Wardlaw et al., 1980). They also indicate, however, that involvement of carbohydrates is considerably more complex than starvation at the one extreme (Levitt, 1980) and general accumulation at the other extreme (Duff and Beard,1974; Youngner and Nudge, 1976). The plant part, developmental stage, and the level of stress appear to be particularly important.

Fructose, glucose, and sucrose are probably the most important ethanol-soluble carbohydrates, whereas fructans constitute most of the water soluble fraction (Smith, 1968). The leaf polysaccharide that may be induced by wounding (Giridhar and Thimann, 1985) does not appear to be involved in high temperature injury. This polysaccharide, which is also a proteinase inhibitor-inducing factor (PIIF), is present in many species, including wheat (McFarland and Ryan, 1974). It's involvement in high temperature injury is unlikely considering the rapid induction of high protease enzyme activity that also occurs (Al-Khatib and Paulsen, 1984).

Ethanol-soluble carbohydrates in leaf blades in the present study were critical to changes in other plant parts. Early rapid accumulation at 35°C/25°C was similar to that in other species (Dinar et al., 1983; McNairn, 1972), although heat-induced callose, to our knowledge, has not been reported in wheat. After the initial accumulation at the high temperature regime, carbohydrates were lost from leaf blades. Spiertz (1977) and Wardlaw et

al. (1980) attributed disappearance of carbohydrates at high temperatures to low photosynthesis rates and high respiration and translocation rates.

Changes in dry matter suggested that photosynthate normally allocated to the stem constituted much of the carbohydrate for early rapid growth at high temperatures. Prolonged grain growth at the lower temperatures, under which vegetative weights remained high, in contrast, probably came from current photosynthesis (Al-Khatib and Paulsen, 1984). Marked differences at the temperature extremes demonstrated the great superiority of long grain filling rate for obtaining high grain yields (Austin et al., 1976; Spiertz, 1974, 1977; Vos, 1981; Wardlaw et al., 1980).

No direct involvement of carbohydrates in roots was indicated in the present study. Other studies have suggested, however, that loss of carbohydrates from high temperatures increases lability of roots to injury (Aldous and Kaufmann, 1979). Roots of wheat are highly sensitive to injury and appear to mediate responses of both shoots and roots to high temperatures (Kuroyanagi and Paulsen, 1985b). The latter studies implicate cytokinins, not carbohydrates, in these effects.

Induction of senescence of detached leaves in the absence and presence of kinetin is relevant to the rapid senescence (Al-Khatib and Paulsen, 1984) and suspected role of cytokinins (Kuroyanagi and Paulsen, 1985b) in high temperature injury. Rapid disappearance of all carbohydrate fractions after the first day concurrent with loss of chlorophyll indicate a close relationship among the processes. The process suffers from being a closed

system (Lazan et al.,1983), however, and lacks the correlative influences that occur during whole-plant senescence(Nooden, 1980).

Responses of carbohydrates to high temperature stress are important in both physiological and economic terms. It must be concluded, however, that carbohydrates are probably involved indirectly and are not the primary loci of injury. Because the economic yield of many crops consists largely of carbohydrates, on the other hand, the effect of stress, whether direct or indirect, on carbohydrates is highly important.

REFERENCES

Aldous, D. E. and J. E. Kaufmann. 1979. Role of root temperature on shoot growth of two Kentucky Bluegrass cultivars. Agron. J. 71:545-547.

Al-Khatib, K. and G .M. Paulsen. 1984. Mode of high temperature injury to wheat during grain development. Physiol. Plant. 61:363-368.

Austin, R. B., J. A. Edrich, M. A. Ford, and R. D. Blackwell. 1976. The fate of dry matter, carbohydrates and ^{14}C lost from the leaves and stems of wheat during grain filling. Ann. Bot. 41:1309-1321.

Berry, J. and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. Ann. Rev. Plant Physiol. 31:491-543.

Dinar, M., J. Rudich, and E. Zamski. 1983. Effects of heat stress on carbon transport from tomato leaves. Ann. Bot. 51:97-103.

Duff, D. T. and J. B. Beard. 1974. Supraoptimal temperature effects upon Agrostis palustris. Part II. Influence on carbohydrate levels, photosynthetic rate, and respiration rate. Physiol. Plant. 32:18-22.

Giridhar, G. and K. V. Thimann. 1985. Interaction between senescence and wounding in oat leaves. Plant Physiol. 78:29-33.

Hoagland, D. R. and D. I. Arnon. 1950. The water culture method for growing plant without soil. California Agric. Exp. Sta. Cir. 347.

Khudairi, A. K. 1970. Chlorophyll degradation by light in leaf

discs in the presence of sugar. Physiol. Plant. 23:613-622.

Knudson, L. L., T. W. Tibbitts, and G. E. Edwards. 1977. Measurement of ozone injury by determination of leaf chlorophyll concentration. Plant Physiol. 60:606-608.

Kuhbauch, W. and R. M. Soberalske. 1977. Molecular weight and ^{14}C distribution of fructosan in timothy stem bases at three stages of development. Crop Sci. 17:239-242.

Kuroyanagi, T. and G. M. Paulsen. 1985a. Mode of high temperature injury to wheat. II. Comparisons of wheat. and rice with and without inflorescences. Physiol. Plant. (In press).

Kuroyanagi, T. and G. M. Paulsen. 1985. Mode of high temperature injury to wheat. III. Role of root and shoot temperatures. (Submited for publication).

Lazan, H. B., E. W. R. Barlow, and C. J. Brady. 1983. The significance of vascular connection in regulating senescence of detached flag leaf of wheat. J. Exp. Bot. 34:726-736.

Levitt, J. 1980. Response of plants to environmental stresses Acedemic Press New York. pp341-470.

McFarland, D. and C. A. Ryan. 1974. Proteinase inhibitor-inducing factor in plant leaves. A phylogenetic survey. Plant Physiol. 54:706-708.

McNairn, R. B. 1972. Phloem translocation and heat induced callose formation in field grown Gossypium hirsutum L. Plant Physiol. 50:366-370.

Nalewaja, J. and L. H. Smith. 1963. Standard procedure for the quantitative determination of individual sugars and total soluble carbohydrate material in plant extracts. Agron. J. 55:523-525.

Nelson N. 1944. A photometric adaptation of the Somogyi method for the determination of glucose. J. Biol. Chem. 153:375-380.

Nooden L. D. 1980. Senescence in the whole plant. In: Senescence in plants K. V. Thimann (ed.) CRC Press Boca Raton, Florida, pp219-258

Roberts D. W. A. 1953. Physiological and biochemical studies in plant metabolism VIII. The distribution of invertase in the first leaf of Khapli wheat. Can. J. Bot. 31:367-382.

Santarius, K. A. 1973. The protective effect of sugars on chloroplast membranes during temperature and water stress and its relationship to frost, dessication and heat resistance. Planta 113:105-114.

Spiertz J. H. J. 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. Neth. J. Agric. Sci. 22:207-220.

Spiertz J. H. J. 1977. The influence of temperature and light intensity on grain growth in relation to carbohydrate and nitrogen economy of wheat plant. Neth. J. Agric. Sci. 25:182-197.

Tetley, R. M. and K. V. Thimann. 1974. The metabolism of oat leaves during senescece. I. Respiration, carbohydrate metabolism, and the action of cytokinins. Plant Physiol. 54:294-303.

Thimann K. V., R. M. Tetley, and B. M. Krivak. 1977. Metabolism of oat leaves during senescence V. Senescence in light. Plant Physiol. 59:448-454.

Vos J. 1981. Effects of temperature and nitrogen supply on post-floral growth of wheat; measurements and simulations. Centre for agr. pub. and doc., Wageningen, Netherlands.

Wardlaw I. F., I. Sofield, and P. M. Cartwright 1980. Factors limiting the rate of dry matter accumulation in the grain of wheat grown at high temperature. Aust. J. Plant physiol. 7:387-400.

Youngner V. B. and F. J. Nudge. 1976. Soil temperature, air temperature, and defoliation effects on growth and non-structural carbohydrates of kentucky bluegrass. Agron. J. 68:257-260.

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High temperature stress severely alters carbohydrate metablism in wheat (Triticum aestivum L.) during grain development. The role of carbohydrates in injury and their relationship to other processes, however, is equivocal. Experiments to determine changes in carbohydrates during maturation at elevated temperatures were conducted under controlled conditions. 'Chris' spring wheat was grown under three temperature regimes after anthesis and sampled weekly for carbohydrates and other constituents. Further studies measured changes in detached leaves incubated in the absence and presence of kinetin. High temperature accelerated senescence as measured by loss of leaf area and chlorophyll, induced early accumulation of soluble carbohydrates in leaf blades, and disappearance of carbohydrates in most other vegetative parts. Early grain filling, apparently from photosynthate from stems, was rapid but brief under high temperatures. Low temperatures prolonged grain filling from current photosynthesis and increased yields. Kinetin decreased senescence and loss of ethanol-soluble carbohydrates from detached leaves. Water-insoluble carbohydrates were quantitatively less important and polysaccharides implicated in wounding were not involved. We concluded that carbohydrates are involved indirectly and are not the primary loci of high temperature injury, but that their responses are physiologically and economically important.