/Senescence of Wheat and Rice
Under Three Temperature Regimes/

by

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Introduction

Growth of wheat (Triticum aestivum L.) and other temperate cereals is directly related to leaf area duration after anthesis (Herzog 1982, Sofield et al. 1977, Spiertz 1974,1977). Senescence, the antithesis of plant leaf area, is a complex process that terminates leaf viability and metabolic activities and reduces plant growth (Noodén 1980, Thomas and Stoddart 1980).

Sink (inflorescence) removal slows senescence and delays deleterious changes associated with the process in cereals. In wheat, for instance, removing spikes retards loss of chlorophyll, RuBPCase activity, and glucose-6-phosphate dehydrogenase activity in leaves (Patterson and Brun 1980). In rice (Oryza sativa L.), removing panicles also delayds senescence and loss of chlorophyll and protein from leaves (Biswas and Choudhuri 1980). Two interpretations have been advanced for these effects: that senescence is caused by diversion of nutrients from the source (leaves) and that it is induced by a signal from the inflorescence sink (Biswas and Choudhuri 1980, Noodén 1980, Patterson and Brun 1980).

Stress from high temperatures decreases growth during maturation by accelerating senescence reactions (Spiertz 1977). The normal increase in leaf protease activity and changes in rates of other processes during senescence of wheat are greatly slowed by low temperatures and speeded by high temperatures (Al-Khatib and Paulsen 1984). The site of high temperature responses is uncertain, however, because both source and sink activities are altered. High temperatures decrease leaf photosynthesis, including electron transport, photosystem II, and RuBPCase enzyme activities (Al-Khatib and Palusen 1984, Mukohata 1971, Spiertz,

1974). In the sink, high temperatures may reduce yields directly by causing cessation of grain growth (Sofield et al. 1977, Spiertz 1974, Wardlaw et al. 1980).

Induction of senescence and the site of high temperature responses in wheat can be elucidated by comparing plants with intact inflorescences with those from which the inflorescences have been removed. Wheat and rice are excellent species for these studies because both have the C_3 photosynthesis pathway, however, wheat is of temperate origin and rice is of tropical origin (Schmitt and Edwards, 1981). Wheat has a distinct low temperature optimum for grain filling, whereas grain development of rice changes little over a wide temperature range (Chowdhury and Wardlaw 1978). Objectives of studies reported here were to determine whether senescence is induced by diversion of nutrients from the source or by signals from the sink, and to identify the site of high temperature responses of wheat relative to nonresponsiveness of rice.

Abbreviations - ABA, abscisic acid; $\overline{CGR}$, mean crop growth rate; $\overline{LAD}$, mean leaf area duration; $\overline{LAR}$, mean leaf area ratio; PVP, polyvinylpolypyrrolidone; RNA, ribonucleic acid; RNase, ribonuclease; RuBPCase, ribulose-1,5-bisphosphate carboxylase; TCA, trichloroacetic acid; Tris, tris(hydroxymethyl)aminoethane.

Materials and methods

Foundation seeds of spring wheat (Triticum aestivum L. cult. 'Chris') and rice (Oryza sativa L. cult. 'Newbonnet') were germinated in moistened vermiculite. One-week-old wheat seedlings and 2-week-old rice seedlings were transplanted into 2-L opaque polystyrene containers; each container

held six seedlings of one species. Wheat was supplied with continuously aerated nutrient solution (Hoagland and Arnon 1950). The nutrient solution for rice (Yoshida et al. 1976) was not aerated. All solutions were changed weekly for the duration of the experiments.

Plants were grown in a glasshouse with regimes of 30°C/20°C day/night and 12-1500 μmol photon $m^{-2}s^{-1}$ at solar noon. Ten days after first anther extrusion was observed, inflorescences were removed from one-half of the plants in each container. The containers were randomly assigned to three controlled environment chambers maintained at 25°C/15°C, 30°C/20°C, and 35°C/25°C day/night temperatures. Photon flux density was 320 μmol $m^{-2}s^{-1}$ during a 16-hr photoperiod and relative humidity was 0.4 kg^{-1}.

Samples were taken the day plants were placed in controlled environment chambers (day 0) and 7, 14, 21, and 28 days afterward. Each sample consisted of three plants from each temperature regime. Treatments were arranged in a randomized complete block design and were sequentially replicated three times.

Viable leaf area of one plant in each sample was measured with an electric area meter (Li-Cor, Inc., Lincoln, NE) each date. All plant parts were then dried at 70°C for 72 hr and weighed. $\overline{CGR}$, $\overline{LAD}$, and $\overline{LAR}$ were calculated by formula of Hunt (1978).

Leaf blades of two plants from each sample were cut into 1-cm-long sections for extracting and assaying RuBPCase, protease, and RNase enzyme activities and chlorophyll and protein concentrations.

RuBPCase activity was determined by following incorporation of $NaH^{14}CO_3$ into acid-stable products (Huffaker et al. 1970). One-g sectioned leaf blade samples were homogenized in 2 x 10^{-2} L of 0.2 mol

Tris sulfate (pH 8.0)$\cdot L^{-1}$. Homogenized samples were filtered through Miracloth (Calbiochem-Behring, Inc., San Diego, CA) and centrifuged 20,000 x g at 4°C for 15 min. Enzyme activity was assayed by adding 10^{-4} L of sample to 5.5 x 10^{-4} L of reaction medium [2 x 10^{-6} mol ribulose-1,5-bisphosphate, 10^{-5} mol $NaH^{14}CO_3$ (specific activity 0.497 Ci mol^{-1}), 1.1 x 10^{-5} mol $MgCl_2$, and 2.5 x 10^{-5} mol Tris sulfate (pH 8.0) $\cdot L^{-1}$]. Reactions were stopped after 5 min at 35°C with 5 x 10^{-5} L of 1.0 mol $HCl\cdot L^{-1}$. Aliquots (10^{-4} L) were dried on filter paper strips, which were placed in toluene-based scintillation fluid, and radioactivity was measured by scintillation counting. (LKB Inc)

Protease enzyme was extracted by homogenizing 1-g leaf blade samples in 10^{-2} L of medium [0.2 mol Tris sulfate (pH 8.3), 0.005 mol mercaptoethanol, and 10 g PVP$\cdot L^{-1}$]. Extracts were filtered and centrifuged as described above. Crude protease activity was assayed by adding 2 x 10^{-4}-L aliquots of sample to 8 x 10^{-4} L of reaction medium [0.125 mol sodium phosphate (pH 8.3), 0.04 mol $NaHCO_3$, and 3.75 g azocasein$\cdot L^{-1}$]. Reactions were stopped after 2 hr at 50°C by adding 10^{-3}L of 2.5 mol $TCA\cdot L^{-1}$. The precipitated protein was removed by centrifugation and the absorbance of the supernatant solution was read at 340 nm.

RNase enzyme was extracted from 1-g leaf blade samples and assayed by the method of Wyen et al. (1972). Samples were homogenized in 10^{-2}L of medium [0.05 mol sodium citrate (pH 5.0) and 0.05 mol $KCl\cdot L^{-1}$] and filtered and centrifuged as described above for RuBPCase extraction. Assay reactions were started by adding 4 x 10^{-3} L of extract to 1.6 x 10^{-3}L of medium [10^{-4} mol sodium acetate (pH 5.5) and 0.9 g yeast RNA$\cdot L^{-1}$] and were stopped after 30 min at 37°C with 5 x 10^{-4} L of 0.007 mol $La(NO_3)_3$ and 0.15 mol $TCA\cdot L^{-1}$. Absorbance of the supernatant solution

obtained after centrifugation was read at 260 nm.

Total chlorophyll was measured by the method of Arnon (1949) and total protein was measured by the modified Lowry method of Miller (1959) using extracts prepared for protease enzyme assays described above.

Results

Weights of wheat and rice were affected similarly by decapitation, but responded very differently to increased temperatures during grain development (Table 1). Removing inflorescences increased shoot weights of both species at most temperature regimes and sampling dates. Root weights, particularly of wheat, increased more at lower temperatures and at later dates after spikes were removed.

High temperatures markedly decreased weight of wheat shoots at later dates and inhibited the increase in root weights that occurred at low temperatures (Table 1). Shoot and root weights of rice were highest at the intermediate temperatures. Wheat spike weights from intact plants increased nearly 5-fold at the lowest temperatures, but remained constant at the highest temperatures, from the first to last dates. Rice panicle weights increased most at the intermediate temperatures and least at the highest temperatures. In contrast to wheat inflorescences, however, rice inflorescences grew significantly at all temperature regimes.

Growth analysis of wheat and rice reflected the effect of inflorescences and temperatures on plant weights (Table 2). $\overline{CGR}$ was higher in all instances except one when plants were decapitated. Wheat $\overline{CGR}$ was highest at the lowest temperature and declined to negative values at the highest temperatures with or without inflorescences. Rice $\overline{CGR}$

was highest at the intermediate temperatures. $\overline{LAD}$ was affected little by decapitation of either species, but it increased slightly in rice and decreased rapidly in wheat as temperatures increased and plants aged. $\overline{LAR}$ followed similar trends, with the greatest change being a marked decline in wheat $\overline{LAR}$ at the highest temperature.

Viable leaf area of wheat was increased slightly by inflorescence removal, but was decreased greatly by ageing and high temperatures (Table 3). At the last sampling date, substantial viable leaf area remained at the lowest temperature, but not at the highest temperature. Leaf area of rice responded much less than that of wheat to inflorescence removal, ageing, and temperature. Chlorophyll concentration in viable wheat leaves increased slightly after decapitation, particularly at low temperatures, but declined as leaves aged, particularly at high temperatures. Chlorophyll concentration in rice leaves was affected slightly by inflorescence removal and temperature, and declined slowly as leaves aged. RuBPCase activity in viable leaves was not affected by sink removal in either species. Activity in wheat, however, declined rapidly as leaves aged and temperatures increased. Activity in rice, on the other hand, declined slowly as leaves aged and was usually highest at highest temperatures.

Removing inflorescences increased the protein concentration in viable wheat leaves, but did not slow the decline in protein during ageing (Table 4). Protein in rice leaves was increased slightly by decapitation, but changed little during ageing. High temperatures greatly accelerated loss of protein in wheat leaves, but had little effect in rice leaves. The increase in protease activity during senescence and at high temperatures was slowed by sink removal in wheat. In

rice, removing panicle lowered protease activity only slightly and temperature had little effect. RNase activity responded similarly to protease activity to decapitation, ageing, and temperature.

Specific protease activity (activity protein^{-1}) in intact wheat increased 2.7-fold at the lowest temperature and 16-fold at the highest temperature between days 0 and 28. Specific RNase activity increased 6-fold and 20-fold, respectively, during the same period. Removing inflorescences of wheat lowered the increase in specific protease activity to 2.2-fold and 9-fold and the increase in specific RNase activity to 4.5-fold and 10-fold at the lowest and highest temperatures, respectively. Specific enzyme activities also increased slower after removal of inflorescences of rice, but were altered little, if any, by temperature.

Discussion

Changes in ageing wheat and rice plants shown here are typical features of monocarpic senescence in both species (Biswas and Choudhuri 1980, Cheng and Kao 1984, Feller and Erismann 1978, Frith and Dalling 1980, Noodén 1980, Patterson and Brun 1980). Removing inflorescence sinks and imposing high temperatures changed the rate, but not the course, of senescence processes. These results raise the possibility that neither the source nutrient depletion hypotehsis nor the sink signal hypothesis adequately elucidate the mechanism of senescence. An alternative and more plausible explanation might be found in the suggestion that source and sink activities are regulated jointly during grain filling (Herzog 1982).

Monocarpic senescence is a programmed change (Nooden 1980) that is necessary for survival of species (Thomas and Stoddard 1980). The nearly ubiquitious increase in proteolytic activity during onset of senescence (Frith and Dalling 1980), for instance, is an effective mechanism for rapidly mobilizing nutrients (Feller and Erismann 1978). High initial grain growth rates of wheat under high temperatures (Spiertz 1977) probably could not occur without the markedly elevated protease and RNase activities observed here and in other studies. These and the other responses of wheat to teperatures in the range of 25 C to 35 C during grain development are consistent with accelerated senescence (Al-Khatib and Paulsen 1984). The failure of protease in rice to respond to inflorescence removal and temperature may be related to the unimportance of proteolytic activity during reproductive deveropment (Cheng and Kao 1984) and the wide temperature range for grain filling (Chowdhury and Wardlaw 1978)

Nutrient depletion inadequately explains the similar responses of intact and decapitated plants to ageing and high temperatures. Changes in plants aged at high temperatures without inflorescences mimincked those in plants with inflorescence sinks. It was apparent that nutrients were mobilized for transport and that senescence followed even in the absence of strong sinks. Roots were not an effective alternate sinks: their weights increased when shoot senescence was slow and decreased when scenescence was rapid. The response of decapitated plants is like that of intact plants, in which grain growth ceases at high temperatures when nutrients are still available (Chowdhury and Wardlaw 1978).

The similar responses intact and decapitated plants also suggest that senescence is not triggered by signals from the inflorescences. If

effects of high temperature are interpreted as accelerating senescence (Al-Khatib and Paulsen 1984, Spiertz 1977), the developing grain probably is not the primary site of high temperature responses. The most likely signal in cereal grains, ABA, rises during early rapid growth, peaks at maximum grain weight, and then declines (Nooden 1980). ABA in wheat grains is not distributed in other plant parts, however, and is accumulated and lost as quickly in excised grains as in attached grains (McWha 1975).

The preponderance of evidence points to involvement of cytokinins in accelerated senescence at high temperatures. Cytokinins appear to jointly regulate source and sink activities of wheat during grain filling (Herzog 1982). They are synthesized primarily, if not exclusively, in roots (Nooden 1984), strongly inhibit de novo protease enzyme synthesis in leaves (Martin and Thimann 1972), retard senescence of leaves (Nooden 1980, Thomas and Stoddart 1980), and increase growth of grain (Herzog 1982). Cytokinins also reverse thermosensitivity of wheat roots to brief exposures of lethal temperatures (Skoqovist and Fries 1970). In other species, brief heating of roots decreases content of cytokinins and increases content of ABA in xylem exudate (Itai et al. 1973).

Involvement of cytokinins in high temperature senescence is consistent with their suspected role in monocarpic senescence (Nooden 1980, 1984). Presumably, high temperatures speed the normal decline in transport of cytokinins from roots to other parts during maturation. The decline in cytokinins then induces other processes associated with senescence, including loss of leaf viability and grain growth. It is not clear that cytokinins function alone in this regard, however, and their interaction with other factors cannot be excluded.

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Tab. 1. Dry weights of shoots, roots, and inflorescences of wheat and rice plants grown with and without inflorescences under three temperature regimes after anthesis.

Days after anthesis	Temperature day/night	With inflorescences						Without inflorescences			
		Shoots		Roots		Inflorescences		Shoots		Roots	
		Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice
Days	°C	g plant^{-1}									
0	30/20	6.0	6.4	0.7	1.4	0.7	0.6	---	---	---	---
7	25/15	7.3	5.6	0.7	1.2	0.8	0.6	8.0	6.3	1.0	1.3
	30/20	7.1	6.0	1.0	1.5	0.9	0.7	8.4	6.8	1.1	1.5
	35/25	7.9	7.0	0.6	1.7	0.8	0.9	7.6	8.1	0.7	1.4
14	25/15	6.8	5.8	0.8	1.7	1.8	0.7	7.7	7.4	1.4	1.6
	30/20	6.2	7.5	0.9	1.7	1.6	0.7	7.5	7.8	1.4	1.9
	35/25	5.1	8.2	0.6	1.7	0.8	0.9	6.8	8.4	0.8	1.9
21	25/15	7.3	7.3	1.1	1.8	2.5	1.0	10.4	8.3	1.5	2.1
	30/20	6.1	7.9	1.1	2.0	2.3	1.2	8.9	9.7	1.4	2.2
	35/25	3.2	8.2	0.6	1.9	0.8	1.1	5.6	10.7	0.6	2.1
28	25/15	6.6	7.6	1.4	1.9	3.4	1.5	11.5	8.5	1.8	2.1
	30/20	5.9	7.8	1.0	2.2	2.4	2.0	8.4	10.6	1.4	2.4
	35/25	3.1	6.5	0.5	2.0	0.7	1.1	6.2	9.1	0.8	2.2
LSD (0.05)		0.7	0.8	0.2	0.2	0.1	0.2	0.7	0.6	0.2	0.2

Tab. 2. $\overline{CGR}$, $\overline{LAD}$, and $\overline{LAR}$ of wheat and rice plants grown with and without inflorescences under three temperature regimes after anthesis

Temperature day/night	With inflorescences						Without inflorescences					
	$\overline{CGR}$		$\overline{LAD}$		$\overline{LAR}$		$\overline{CGR}$		$\overline{LAD}$		$\overline{LAR}$	
	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice
°C	$gm^{-2}d^{-1}$		Days		m^2kg^{-1}		$gm^{-2}d^{-1}$		Days		m^2kg^{-1}	
25/15	4.2	2.7	30	13	4.2	1.6	6.1	2.5	32	13	4.3	1.7
30/20	2.0	3.8	26	15	4.0	1.9	2.5	5.9	27	16	4.1	1.9
35/25	-3.3	1.2	18	16	3.0	2.3	-0.4	3.0	19	17	3.1	2.2
LSD (0.05)	1.4	1.1	2	1	0.4	0.3	1.4	1.1	2	1	0.4	0.3

Tab. 3. Leaf areas, chlorophyll concentrations, and RuBPCase activities of wheat and rice plants grown with and without inflorescences under three temperature regimes after anthesis

Days after anthesis	Temperature day/night	With inflorescences						Without inflorescences					
		Leaf area		Chlorophyll		RuBPCase		Leaf area		Chlorophyll		RuBPCase	
		Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice
Days	°C	$cm^2\ plant^{-1}$		$mg\ g^{-1}$		$\mu mol\ CO_2 g^{-1} s^{-1}$		$cm^2\ plant^{-1}$		$mg\ g^{-1}$		$\mu mol\ CO_2 g^{-1} s^{-1}$	
0	30/20	451	178	3.4	2.4	1.3	1.2	---	---	---	---	---	---
7	25/15	451	160	4.1	2.1	1.3	0.9	706	251	4.5	2.1	1.3	0.9
	30/20	521	249	3.7	1.3	0.8	1.0	552	268	4.3	2.4	0.8	1.0
	35/25	125	247	3.2	1.8	0.7	1.1	163	260	3.3	2.0	0.7	1.1
14	25/15	526	178	3.5	1.7	1.1	0.8	611	268	4.3	1.8	1.1	0.8
	30/20	475	210	3.3	1.9	0.7	1.0	440	235	3.9	2.0	0.7	1.0
	35/25	75	272	2.1	1.6	0.6	1.0	107	246	2.1	1.7	0.6	1.0
21	25/15	467	131	2.1	1.5	0.6	0.8	519	132	2.2	1.5	0.7	0.8
	30/20	319	194	1.9	1.8	0.4	0.8	410	220	2.3	2.0	0.4	0.8
	35/25	51	220	1.0	1.5	0.1	0.9	72	226	1.3	1.8	0.1	0.9
28	25/15	273	128	1.7	1.2	0.4	0.6	325	130	2.0	1.0	0.4	0.7
	30/20	185	180	1.3	1.3	0.3	0.7	200	180	1.6	1.5	0.3	0.7
	35/25	0	219	0	1.2	0	0.8	5	219	0	1.2	0	0.8
LSD (0.05)		46	25	0.4	0.3	0.2	0.2	46	25	0.4	0.3	0.2	0.2

Tab. 4. Protein concentrations, protease activities, and RNase activities in wheat and rice plants grown with and without inflorescences under three temperature regimes after anthesis

Days after anthesis	Temperature day/night	With inflorescences						Without inflorescences					
		Protein		Protease		RNase		Protein		Protease		RNase	
		Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice	Wheat	Rice
Days	°C	mg g^{-1}		$\Delta A\ g^{-1}hr^{-1}$		$\Delta A\ g^{-1}hr^{-1}$		mg g^{-1}		$\Delta A\ g^{-1}hr^{-1}$		$\Delta A\ g^{-1}hr^{-1}$	
0	30/20	13.0	9.0	1.2	0.8	0.8	0.5	---	---	---	---	---	---
7	25/15	13.0	9.0	1.3	0.8	1.5	0.8	13.3	8.2	1.3	0.8	1.5	0.6
	30/20	12.4	9.3	1.4	0.8	1.8	0.7	12.7	10.1	1.3	0.7	1.5	0.6
	35/25	8.4	9.3	2.1	0.8	2.8	0.9	10.4	9.6	1.9	0.8	2.6	0.5
14	25/15	10.0	8.3	1.3	0.9	1.6	0.9	8.2	8.9	1.3	0.9	1.5	0.8
	30/20	8.6	9.7	1.5	0.9	2.2	0.7	10.3	10.5	1.4	0.7	2.1	0.7
	35/25	6.8	8.6	2.9	0.9	2.9	1.0	11.7	9.4	2.5	0.8	2.8	0.7
21	25/15	9.3	8.4	1.7	1.1	2.0	0.8	9.9	9.2	1.5	1.0	1.8	0.7
	30/20	7.4	9.0	2.1	1.0	2.7	0.7	8.8	9.9	1.8	0.9	2.4	0.6
	35/25	5.1	8.3	4.0	1.0	3.4	1.0	6.3	8.9	2.8	0.9	3.1	1.0
28	25/15	8.2	8.3	2.0	1.3	2.9	0.9	8.8	8.7	1.8	1.1	2.4	0.6
	30/20	6.2	8.9	2.6	1.0	3.2	0.8	7.6	10.0	2.3	0.9	2.9	0.6
	35/25	3.2	8.3	4.6	1.2	3.8	1.3	5.3	8.7	4.3	1.0	3.3	1.0
LSD (0.05)		1.0	0.5	0.2	0.2	0.1	0.1	1.0	0.5	0.2	0.2	0.1	0.0

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Toshiyuki Kuroyanagi
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Senescence of Wheat and Rice Under Three Temperature Regimes

by

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High temperature injury to wheat (Triticum aestivum L.) during grain development is manifested as acceleration of senescence. Experiments were conducted to elucidate the mode of senescence and site of high temperature responses. Wheat and rice (Oryza sativa L.), which have C_3 photosynthesis but different temperature responses, were grown with and without inflorescences under different temperature regimes after anthesis. Removing inflorescences increased vegetative weights and slowed most senescence processes more in wheat than in rice. Increasing temperatures from 25°C/15°C to 35°C/25°C day/night after anthesis decreased growth, leaf viability, chlorophyll and protein concentrations, and RuBPCase activity and increased protease and RNase activities in wheat. Temperature treatments caused much smaller changes in rice. . Decapitation slowed the rate but did not alter the course of high temperature tesponses. Neither the nutrient depletion hypothesis nor the source signal hypothesis adequately explain the results. We concluded that source and sink activities are regulated jointly, probably by cytokinins from roots, during senescence at normal and elevated temperatures.