

Possible role of alternative respiration in temperature rise of water stressed plants

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Abstract. Role of alternative respiration, a thermogenic pathway, was evaluated in temperature rise of water stressed plants. Transpiration rate, plant temperature and respiratory dynamics were monitored in field grown irrigated and unirrigated sorghum (*Sorghum vulgare* Pers.) hybrid CSH 6 and pearl millet (*Pennisetum typhoides* (Burm. f.) Stapt and Hubbard) var. J 104 for 22 days. Transpiration rate of irrigated plants was always higher than the unirrigated plants. But the plant temperature and the alternative respiration activity of irrigated plants was always lower than unirrigated plants. The reduction in transpiration rate of unirrigated pearl millet was more as compared to unirrigated sorghum. Nonetheless, alternative respiration activity was higher in unirrigated sorghum as compared to unirrigated pearl millet. Temperature of unirrigated sorghum plants increased by 10.4°C during 22 days and it was 8.0°C higher than irrigated sorghum at day 22. Stressed pearl millet showed an increase of 3.9°C during 22 days and it was 2.9°C higher than the irrigated pearl millet at day 22. It is suggested that the heat released because of the alternative respiration activity also contributes towards temperature rise of water stressed plants.

Keywords. *Pennisetum typhoides* (Burm. f.) Stapt and Hubbard; *Sorghum vulgare* Pers.; alternative respiration; thermogenesis; water stress.

1. Introduction

Several crop plants have been shown to raise their temperature during various stresses, particularly water stress (Jackson *et al* 1981; Idso *et al* 1982, 1984). This character has been used as a remote sensing parameter (Saha *et al* 1984). In addition, temperature similar or closer to ambient has been considered as a selection criterion for drought resistance (Blum *et al* 1982). The mechanism responsible for raising temperature of water stressed plants is attributed to energy balance dependent upon transpirational cooling (Poljakoff-Mayber and Gale 1972). It is assumed in this explanation that metabolism plays no role. Interestingly, plant systems have the capability to raise their temperature above the ambient. *Arum* spadix is the best known example. It has the capability to raise its temperature several degrees (approximately 22°C) above the ambient (Diamond 1989). This has been shown to

Abbreviations used: $g (i)$, Respiration by the sodium cyanide (NaCN) treated tissue at different salicylhydroxamic acid (SHAM) concentrations; ρ slope of curve between V_T and $g (i)$ which indicates the fraction of the maximum alternative respiration operative *in vivo*; V_{alt} , alternative respiration capacity; v_{alt} , alternative respiration activity; V_T respiration by tissue at different SHAM concentrations in the absence of NaCN.

be related to alternative respiration activity (Meeuse 1975). Salicylic acid acts as a thermogen in this mechanism (Raskin *et al* 1987). It is now known that alternative respiration occurs widely in plants. However, its importance in thermogenesis has not been evaluated. We have recently reported the occurrence and possible role of alternative respiration in parallel with thermogenesis in ripening mango and banana fruits (Kumar *et al* 1990; Kumar and Sinha 1992). Here, we present results to demonstrate the possible involvement of alternative respiration in raising the temperature of water stressed plants.

2. Materials and methods

2.1 Plant material

Seeds of sorghum (*Sorghum vulgare* Pers.) hybrid CSH-6 and pearl millet (*Pennisetum typhoides* (Burm. f.) Stapf and Hubbard) var. J 104 were sown in the field with 30 cm row to row spacing and 10 cm plant to plant spacing. The fertilizer dose of N : P : K at the rate of 20 : 40 : 40 kg ha⁻¹ was applied to the field before sowing. Fields were irrigated following the usual agronomic practices and the stress was created by withholding irrigation in the treatment plots.

Various measurements/sampling was done between 9:00 AM-11:00 AM in fully developed canopy and the top leaves were used for various estimations.

2.2 Temperature measurements

Temperature of irrigated and unirrigated plants of sorghum and pearl millet was measured with the help of a thermocouple placed at the tip of a long needle. Thermocouple was placed deep inside the top leaf whorls or in the space between the leaf sheaths for one minute when the stable reading was obtained under the comparatively insulated environment.

2.3 Measurement of transpiration rate

Transpiration rate was measured using steady state porometer (Licor Inc., USA). The leaves used for transpiration rate measurement were further used for the measurement of water potential.

2.4 Water potential measurements

Water potential of the leaf was measured using a pressure chamber (Soil Moisture Equipment Corp., USA) following Scholander *et al* (1964). After the leaf was cut from the plant it was immediately enclosed in the chamber with at least 1.0 cm of the cut portion protruding out from the sealing gasket. The pressure inside the chamber was gradually increased with compressed nitrogen gas until xylem sap appeared at the cut end of the leaf. At this point, the pressure inside the chamber was recorded as water potential of the enclosed leaf.

2.5 Respiratory measurements

Respiratory measurements were carried out polarographically in leaf tissues (7×9 mm) using a Clark type oxygen electrode (Gilson Medical Electronics, 5/6 H Oxygraph). A portion of the leaf was stored for sugar estimation as described later.

Oxygraph was set to a full scale deflection with a polarized voltage of 0.8 mV and leaf tissue was suspended in an oxygen electrode cuvette (1.5 ml capacity) containing 1.5 ml of reaction medium (50 mM Hepes, 0.2 mM CaCl_2 , and 5.0 mM MgCl_2). Cuvette was covered with black cloth during the measurement.

Capacity and the contribution of the alternative respiration *in vivo* was estimated according to the titration technique of Bahr and Bonner (1973).

To measure maximum capacity of the alternative pathway (V_{alt}) leaf tissue was suspended in the reaction medium containing 0.5 mM NaCN and the oxygen uptake was recorded as described earlier. SHAM (20 mM; Azcon-Bieto *et al* 1983) was used to study the capacity of cytochrome pathway. It was added to the original suspending medium and the oxygen uptake by tissue was recorded. It gives the cytochrome pathway capacity.

With the cyanide (CN) (0.5 mM) treated tissue oxygen uptake was measured in the presence of different concentrations of SHAM (0.0, 5.0, 10.0, 15.0 and 20.0 mM; Azcon-Bieto *et al* 1983). Respiration rates thus obtained were designated as $g(i)$. The titration of alternative pathway was then repeated in the absence of CN to obtain V_T at each inhibitor (of alternative oxidase) concentration.

V_T was plotted against $g(i)$ after correcting for residual respiration. The slope of the curve (ρ) indicates the fraction of maximum alternative pathway operative in the absence of added inhibitor. Alternative respiration activity (v_{alt}) was calculated by multiplying V_{alt} , with ρ .

2.6 Sugar estimation

Sugar was estimated according to the Method of Dubois *et al* (1956). Leaf tissue (500 mg) was homogenized in 80% ethanol followed by centrifugation at 5,000 g for 10 min. Suitable amount of the clear supernatant was taken for estimation. Five ml of concentrated H_2SO_4 (specific gravity, 1.84; minimum assay, 98.0%) was added to 1.0 ml of adequately diluted ethanolic solution. After 30 min 1.0 ml of phenol (5% in water, w/v) was added to the above solution. Tube was shaken vigorously and A_{490} was recorded after 20 min of mixing. Sugar was calculated from a standard curve prepared in the same way with sucrose.

3. Results

3.1 Leaf water potential, plant temperature and transpiration rate

Leaf water potential, plant temperature and transpiration rate in irrigated and unirrigated sorghum and pearl millet were analysed over a period of 22 days. The leaf water potential of irrigated sorghum decreased from -1.4 ± 0.08 MPa at day zero to -1.6 ± 0.07 MPa at day 22. The leaf water potential in unirrigated plants remained around -1.85 MPa during the entire period of experimentation (table 1).

The plant temperature of irrigated sorghum increased from $28.4 \pm 0.2^\circ\text{C}$ to $30.6 \pm 0.2^\circ\text{C}$. In unirrigated plants it increased from $27.4 \pm 0.2^\circ\text{C}$ to $38.26 \pm 0.5^\circ\text{C}$ during 22 days (table 1).

In pearl millet where the leaf water potential ranged between -1.2 ± 0.01 MPa to -1.3 ± 0.017 MPa in irrigated plants, it dropped down drastically from -1.2 ± 0.01 MPa to -2.5 ± 0.10 MPa in unirrigated plants. Plant temperature showed only a little increase during 22 days (table 2).

Transpiration rate of irrigated plants was always higher than the unirrigated plants (tables 1, 2).

3.2 Total soluble sugars

Sugar content in the leaves of irrigated and unirrigated sorghum and pearl millet is shown in table 3. Irrigated plant leaves always had higher sugar content than unirrigated plant leaves.

Table 1. Changes in leaf water potential, plant temperature and transpiration rate in irrigated (Irri) and unirrigated (Unirr) sorghum hybrid CSH 6 over a period of 22 days. Irrigation in the treatment plot was withheld at day "zero".

Days	Leaf water potential (MPa)		Plant temperature (°C)		Transpiration rate ($\mu\text{g cm}^{-2} \text{s}^{-1}$)	
	Irri	Unirr	Irri	Unirr	Irri	Unirr
0	-1.4 ± 0.08	-1.4 ± 0.04	28.4 ± 0.2	27.4 ± 0.2	65.2 ± 2.2	64.6 ± 1.8
7	-1.4 ± 0.07	-1.8 ± 0.04	28.6 ± 0.2	31.3 ± 0.3	61.0 ± 3.6	25.3 ± 1.5
10	-1.4 ± 0.11	-1.8 ± 0.03	29.6 ± 0.8	32.2 ± 0.2	60.3 ± 2.5	33.6 ± 2.5
13	-1.4 ± 0.03	-1.9 ± 0.01	29.3 ± 0.3	32.3 ± 0.3	71.6 ± 2.5	25.7 ± 2.1
16	-1.4 ± 0.05	-1.8 ± 0.03	30.3 ± 0.3	35.3 ± 0.4	63.1 ± 2.7	30.0 ± 2.0
19	-1.4 ± 0.05	-1.9 ± 0.01	30.3 ± 0.1	38.5 ± 0.4	57.1 ± 2.8	22.0 ± 2.0
22	-1.6 ± 0.07	-1.9 ± 0.01	30.6 ± 0.2	38.6 ± 0.5	56.0 ± 1.7	20.6 ± 3.1

± represents SD for three separate determinations.

Table 2. Changes in leaf water potential, plant temperature and transpiration rate in irrigated (Irri) and unirrigated (Unirr) pearl millet var. J 104 over a period of 22 days. Irrigation in the treatment plot was withheld at day "zero".

Days	Leaf water potential (MPa)		Plant temperature (°C)		Transpiration rate ($\mu\text{g cm}^{-2} \text{s}^{-1}$)	
	Irri	Unirr	Irri	Unirr	Irri	Unirr
0	-1.2 ± 0.10	-1.2 ± 0.10	29.8 ± 0.2	29.4 ± 0.2	58.2 ± 3.2	59.1 ± 2.2
7	-1.2 ± 0.15	-1.5 ± 0.07	29.0 ± 0.4	31.2 ± 0.2	55.1 ± 2.6	24.2 ± 1.6
10	-1.3 ± 0.12	-1.7 ± 0.14	30.1 ± 0.5	32.3 ± 0.3	60.6 ± 3.0	25.6 ± 2.0
13	-1.3 ± 0.15	-1.9 ± 0.08	29.0 ± 0.5	31.4 ± 0.4	50.6 ± 2.4	28.2 ± 1.3
16	-1.3 ± 0.10	-2.1 ± 0.05	29.6 ± 0.1	32.3 ± 0.3	54.9 ± 2.7	24.6 ± 2.5
19	-1.3 ± 0.15	-2.3 ± 0.03	30.3 ± 0.2	33.5 ± 0.4	48.3 ± 3.2	21.3 ± 2.3
22	-1.3 ± 0.17	-2.5 ± 0.10	30.4 ± 0.2	33.3 ± 0.3	45.3 ± 2.1	15.3 ± 1.5

± represents SD for three separate determinations.

3.3 Respiratory dynamics

Total respiration, alternative respiration and cytochrome respiration were studied in irrigated and unirrigated sorghum and pearl millet.

The rate of respiration in irrigated sorghum leaves ranged from 64.6 ± 2.0 to 76.7 ± 4.0 nmol O_2 min^{-1} g^{-1} dry wt during the experimentation period while in unirrigated leaves it was from 71.3 ± 4.6 to 92.5 ± 4.5 nmol O_2 min^{-1} g^{-1} dry wt. Both the capacity (V_{alt}) and the actual operation (v_{alt}) of alternative respiration was higher in the leaves of unirrigated plant. (V_{alt}) in unirrigated plants was 1.2 to 1.9 times than the irrigated plants at different days. However, with increasing age even the irrigated plants showed a higher V_{alt} and v_{alt} (table 4).

Respiration rate of leaves of irrigated pearl millet ranged from 52.8 ± 4.2 to 60.1 ± 2.0 nmol O_2 min^{-1} g^{-1} dry wt while in unirrigated leaves it ranged from 58.2 ± 2.4 to 66.2 ± 5.0 nmol O_2 min^{-1} g^{-1} dry wt. v_{alt} values for irrigated plants were not very different from that of the unirrigated plants except for day 12 where v_{alt} in unirrigated plants was twice the irrigated plants (table 5).

Table 3. Changes in soluble sugars in irrigated (Irri) and unirrigated (Unirr) sorghum and pearl millet over a period of 22 days. Irrigation in the treatment plot was withheld at day "zero".

Days	Total soluble sugars (mg g^{-1} dry wt)			
	Sorghum		Pearl millet	
	Irri	Unirr	Irri	Unirr
0	113.7 ± 4.0	110.2 ± 1.8	110.7 ± 6.1	101.0 ± 2.9
7	114.0 ± 4.5	99.0 ± 2.3	108.0 ± 5.6	82.6 ± 0.5
12	119.3 ± 5.3	98.5 ± 3.1	109.1 ± 4.5	86.8 ± 3.8
17	116.8 ± 6.1	91.3 ± 2.5	106.1 ± 4.0	89.1 ± 5.5
22	113.7 ± 9.1	91.5 ± 1.0	110.7 ± 1.0	87.6 ± 6.8

± represents SD for three separate determinations.

Table 4. Changes in dark respiration and its components over a period of 22 days in sorghum hybrid CSH 6. Values in parentheses are obtained by multiplying p with Alt resp and represent the actual alternative respiration operative *in vivo* (v_{alt}). Irrigation in the treatment plot was withheld at day "zero".

Days	Respiration rate (nmol O_2 min^{-1} g^{-1} dry wt)							
	Total		Alt resp		Cyt resp		p	
	Irri	Unirr	Irri	Unirr	Irri	Unirr	Irri	Unirr
0	70.6 ± 1.3	69.3 ± 2.2	36.8 ± 2.0 (19)	34.9 ± 3.2 (18)	56.2 ± 3.3	57.2 ± 1.3	0.51	0.51
7	70.4 ± 2.2	81.2 ± 5.2	36.4 ± 2.0 (18)	52.6 ± 4.3 (35)	54.6 ± 2.3	52.6 ± 3.3	0.53	0.65
12	66.4 ± 3.4	71.3 ± 4.6	31.0 ± 1.9 (17)	44.0 ± 3.0 (30)	50.2 ± 3.3	46.8 ± 2.2	0.55	0.69
17	76.7 ± 4.0	89.3 ± 2.2	36.5 ± 2.3 (23)	40.9 ± 2.7 (29)	52.4 ± 4.1	64.9 ± 3.2	0.63	0.71
22	64.6 ± 2.0	92.5 ± 4.5	42.4 ± 3.6 (27)	61.6 ± 2.2 (40)	40.7 ± 2.2	55.2 ± 4.2	0.63	0.65

± represents SD for three separate determinations.

Alt resp, alternative respiration; Cyt resp, cytochrome respiration; Irri, irrigated; Unirr, unirrigated; p , fraction of maximum alternative respiration operative *in vivo*

Table 5 Changes in dark respiration and its components over a period of 22 days in pearl millet var. J 104. Values in parentheses are obtained by multiplying p with Alt resp and represent the actual alternative respiration operative *in vivo* (v_{alt}). Irrigation in the treatment plot was withheld at day "zero".

Days	Respiration rate (nmol O ₂ min ⁻¹ g ⁻¹ dry wt)									
	Total		Alt resp		Cyt resp		p			
	Irri	Unirr	Irri	Unirr	Irri	Unirr	Irri	Unirr		
0	57.2 ± 2.1	58.2 ± 2.4	18.2 ± 2.1 (8.2)	17.3 ± 3.3 (7.4)	53.2 ± 2.4	56.2 ± 2.3	0.45	0.44		
7	58.6 ± 3.2	59.4 ± 3.6	21.7 ± 1.2 (11)	30.1 ± 2.2 (15)	45.7 ± 3.0	53.9 ± 4.2	0.52	0.55		
12	52.8 ± 4.2	59.4 ± 4.2	23.2 ± 2.0 (7)	34.5 ± 2.0 (14)	46.4 ± 2.9	46.1 ± 3.2	0.55	0.50		
17	60.1 ± 2.0	66.2 ± 5.0	29.4 ± 2.0 (15)	34.1 ± 1.9 (18)	46.8 ± 3.0	47.9 ± 3.6	0.50	0.50		
22	59.4 ± 4.2	62.6 ± 3.0	27.6 ± 2.2 (15)	37.6 ± 2.2 (19)	46.6 ± 3.7	46.6 ± 3.2	0.34	0.42		

± represents SD for three separate determinations.

Alt resp, alternative respiration; Cyt resp, cytochrome respiration; Irri, irrigated; Unirr, unirrigated; p , fraction of maximum alternative respiration operative *in vivo*.

4. Discussion

A close association between plant temperature and plant water stress has been explained on the basis of reduction in transpirational cooling of the leaf upon stomatal closure at low leaf water potential (Blum *et al* 1982). Gates (1973) also believed that temperature of the plant is affected by solar energy transferred by radiation, convection, conduction and evaporation or condensation and metabolism has almost a negligible role to play. Nonetheless, our effort was to evaluate the role of a thermogenic reaction *i.e.*, alternative respiration in context to the temperature rise of water stressed plants.

Cyanide resistant and SHAM sensitive alternative respiration is associated with thermogenesis in the flowers of inflorescence of some species of Araceae, Annonaceae, Nymphaeaceae, Palmae, Cyclanthaceae and Aristolochiaceae (Meeuse 1975; Raskin *et al* 1987). Alternative pathway branches from the classical cytochrome pathway at the ubiquinone site, thereby bypassing two out of the total three phosphorylating sites. Therefore 65% energy of the electron remains uncoupled (Lambers 1980; Moore and Siedow 1991). The energy thus released is supposed to be involved in thermogenesis.

Therefore, alternative respiration was studied in irrigated and unirrigated sorghum (CSH-6) and pearl millet. Interestingly, unirrigated sorghum showed 1.2 to 1.9 times higher v_{alt} than the irrigated sorghum. Unirrigated pearl millet also showed an increased v_{alt} than the irrigated control. When compared in absolute terms, v_{alt} for unirrigated sorghum was twice the values for unirrigated pearl millet (tables 4, 5).

One cannot rule out the fact that reduced transpiration rate is responsible for increased temperature of the stressed plants. Moreover, our results have also shown that the transpiration rate of unirrigated plants was lower than the irrigated plants. Concomitantly, the unirrigated plant leaves had higher alternative respiration activity than the irrigated plants. Therefore, it could be argued that the heat released because of alternative respiration activity also contributes towards temperature rise of stressed plants. It is quite likely that the transient changes in temperature may not be detected as long as transpirational cooling occurs maximally, but with a reduction

in transpiration rate the heat generated due to alternative pathway may become evident.

Sugar content in sorghum as well as pearl millet decreased under water stress (table 3). The observation that respiration rate is increased in spite of reduction in sugar content evokes questions on the mechanism of the electron partitioning between cytochrome and the alternative oxidase. Is it that the redox state of the ubiquinone pool (Moore *et al* 1988) changes under water stress, which in turn differentially partitions the electrons between cytochrome and the alternative oxidase?

Temperature increase of unirrigated plants has been described earlier and seems to fit well with the hypothesis that alternative respiration could also contribute towards heat generation. A very high correlation between temperature and the alternative respiration activity ($r = 0.8301$ for unirrigated sorghum, and $r = 0.9819$ for uninigated pearl millet) was also observed in the present experiment. Moreover, unirrigated sorghum hybrid CSH 6, which had alternative respiration activity more than two-fold compared to unirrigated pearl millet var. J 104, showed more temperature rise compared to the uninigated pearl millet.

Higher alternative respiration activity was found to be associated with the cold acclimatized winter rape, low temperature grown corn seedlings and cold tolerant wheat (McCaig and Hill 1977; Rychter *et al* 1988; Stewart *et al* 1990). Suspension cells of tobacco grown at lower temperature (18°C) have also been shown to have higher alternative respiration as compared to those grown at relatively higher temperature (30°C) (Vanlerberghe and McIntosh 1992). But the authors attributed no role of this mechanism in protection through thermogenesis. Recently, Rychter *et al* (1988) attributed alternative respiration to protect the cold affected, chilling resistant plant against metabolic disorder induced by transient temperature change at the time when functional and structural adjustment of plants to chilling temperature was not accomplished. The common occurrence and induction of alternative respiration has been observed by many workers (*cf.* Patterson and Graham 1987). However, there has been hesitation to attribute its function in thermogenesis other than in certain lilies (Diamond 1989). It could be that the changes in temperature are transitory and hence difficult to monitor. Our results on ripening mangoes (Kumar *et al* 1990) and banana fruits (Kumar and Sinha 1992) have established a closer relationship between alternative respiration and temperature rise inside fruits. Our present results for the first time show that alternative respiration could possibly be involved in thermogenesis of unirrigated plants. However, functional significance of this pathway in water stressed plants remains to be studied.

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