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Physiological and biochemical impact of heat stress on the yield of tomato genotypes

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Abstract
Tomato (Solanum lycopersicon) is one of the most important and widely grown vegetables crops in both temperate and tropical regions of the world. Global warming leading to high temperature is predicted to be one of the limiting factors for cultivation of tomato and other plants in the future. In this study, plants were grown under two different temperature regimes, one at ambient (30 °C) and other at elevated temperature (38±1ºC) in open top chambers at the Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore. The physiological and biochemical responses of 20 tomato genotypes to heat stress were evaluated. The cell membrane stability was high in IIVR-L thereby preventing the damage to the lipid bilayer of biological membranes as compared to other genotypes under elevated temperature conditions. Proline content increased at a higher rate in IIVR-L that helped in maintaining the tissue water potential under high temperature while nitrate reductase activity (NRA) decreased in all the genotypes by 16-20%, as the enzyme is very sensitive to stress conditions. There was no fruit production in the genotypes like IIHR – 2388 and IIHR – 709 though flowers were produced by these genotypes (100% reduction in fruit set) that might be due to their higher sensitivity of post flowering stage to high temperature The physiological and biochemical changes clearly connotes how the best performed genotypes like IIVR-L were able to overcome the heat stress as compared to the poorly performed genotypes (IIHR-2388 and IIHR–709).

Keywords: Tomato, Heat stress, Cell Membrane Stability, Nitrate reductase activity, Proline, Antioxidant enzymes, Yield

Introduction
Tomato (*Solanum lycopersicon* L.) is one of the most significant vegetable ever used all over the world. It is one of the most universally known, widely consumable nutritious and widely grown vegetable in the world. This is a herbaceous plant and it is typically cultivated for its edible fruit. It presents itself in different shapes, sizes and colours with different Brix or sugar levels. It is a moderate nutritional crop and is considered an important source of vitamin A, vitamin C and minerals. Tomatoes have very high lycopene content, which has several health benefits. In addition, lycopene that imparts red colour to the fruit is a potent antioxidant and scavenger of free radicals, which is often associated with carcinogenesis. India is the second largest producer of tomato after China in the world. Its position in the whole world is after potato and sweet potato both in area and production. The major tomato producing state is Bihar, Karnataka, Uttar Pradesh, Orissa, Andhra Pradesh, Maharashtra, Madhya Pradesh and Assam.The total production of tomato in Tamil Nadu was about 332.50 thousand MT from 25.15 thousand hectares of land (NHB, 2014) which is very low as compared to the other tomato producing states. Moreover, the production of tomato in our country lags behind the demand.

The global average surface temperature is predicted to increase by 0.6–4.8ºC compared with the beginning of this century and Kothawale and Rupa (2002) reported a rise of 0.5°C in mean annual temperature over last century. In addition to mean increase in annual temperatures, there will also be increase in the frequency, duration, and severity of periods with exceptionally high temperatures (Haldimann and Feller, 2004) [5]. Thus, in future, plants are likely to undergo an increases in heat stress which can impact plant growth and development, decreasing crop and ecosystem productivity and biodiversity (Thomas *et al*., 2004).

Extreme temperatures have always been a serious threat to agriculture including tomato production owing to its heat and cold sensitivity. Elevated temperature stress leads to inhibition in plant growth both in vegetative and relatively delicate reproductive developments and yield of several crops (Peet and Willits, 1998; Hussain *et al*., 2006) [9, 6]. In general, each 1ºC increment in the average temperature during the growth season may reduce the crop yield up to 17% (Lobell and Asner, 2003) [8]. The optimum temperature range for growing tomato is

20-26/15-20°C day/night. The prevalence of high ambient temperatures in a significant proportion of the tomato growing areas of the world is one of the most crucial problems in tomato production. Heat stress results in fruit set reduction and declined tomato yields (Peet *et al*., 1997) [10]. To devise some adaptable strategies to extend the tomato production spans and improve the yield volumes in rising temperatures is imperative. However genotypes possessing desirable traits need to be identified for further exploitation. Therefore, it is necessary to study the detailed physiological analysis of adaptation of tomato crop to high temperature stress. With this background, twenty tomato genotypes were evaluated for heat tolerance to understand the genetic variation of 20 tomato genotypes to elevated temperature based on their physiological and biochemical approaches.

Materials and Methods

The present investigation was carried out to study the genetic variation for heat tolerance related traits in tomato through physiological and biochemical approaches. This study also paves way to understanding the molecular basis of heat tolerance in tomato. The investigation consists of controlled environment studies using pot culture trials.

The pot culture experiment were initiated with 20 genotypes at the Department of Crop Physiology (11º N latitude, 77º E longitude; 426.7 MSL), TamilNadu Agricultural University, Coimbatore to screen the heat tolerance and the experimental period was 27th November 2015 to 4th April 2016. Recommended dose of fertilizers and common package of practices were followed in a timely fashion. Each genotype was replicated thrice in a completely randomized block design. The seeds were treated with Carbendazim @ 0.5g kg^{-1} of seeds for protection against seed borne diseases. The seeds were sown uniformly in the well prepared portrays maintaining a thin film of water. Twenty days after sowing, uniform seedlings were transplanted to pots with recommended soil proportion.Two sets of pots one for elevated temperature and the other for ambient temperature were maintained for each genotype. The pots were shifted to ambient and elevated temperature chambers after 10 DAT (days after transplanting). Recommended management and plant protection measures were followed.

The two open top temperature controlled chambers with the dimensions of 3 m x 3 m were fabricated for this study. This chamber was made using poly carbonate sheets recommended for crop growth experiments. The air temperature of the chamber was maintained automatically with controller using PT100 thermostat sensor. The generation of heat was manipulated by heater fixed outside the chamber. Once the required temperature (38ºC) is reached, the controller will automatically shut off the heater and blower. The standard deviation of temperature was +/-0.5 ºC. One chamber was maintained at an ambient temperature of 30ºC± 1ºC (T1) and the other chamber was maintained at an elevated temperature of 38 ± 1ºC (T2) for a duration of 6 hours from 10 am to 4 pm. Twenty tomato genotypes were sown in portrays and transplanted in pots after twenty days of sowing. They were transferred to the open top chambers after 10 DAT and irrigation was given at 50 percent available soil moisture (ASM).

The observations were recorded at different plant growth stages viz., 30 DAT, 60 DAT and 90 DAT by selecting samples randomly from each replication. The methods followed to record the observations are explained based on the standard procedures.Cell Membrane Stability was measured by an electrolytic leakage technique (Premchandra *et al*., 1990) during different stages. Leaf cell membrane stability (CMS) was estimated using following equation

$$\text{CMS (\%)} = 1 - \frac{\text{Conductivity at 45°C}}{\text{Conductivity at 100°C}} \times 100$$

Nitrate reductase (NR) activity is estimated by following the method of Nicholas *et al*. (1976) and the enzyme activity was expressed as µmol NO_2 g^{-1} h^{-1}. The estimation of proline content was adopted from Bates *et al*. (1973) [3] with slight modifications.

The number of flowers per cluster and the number of clusters per plant was counted to calculate total number of flowers per plant. The total number of fruits in each plant was counted to get fruit number per plant. The fruit set percent was derived from the total number of flowers produced per plant and the total number of fruits per plant and was expressed in per cent.

$$\text{Fruit set percent} = \frac{\text{Total number of fruits}}{\text{Total number of flowers}} \times 100$$

Results and Discussion

Heat stress has a strong influence on the physiological and biochemical parameters in plants. Investigation on these parameters like cell membrane stability, nitrate reductase activity (NRA), antioxidant enzymes and their effect has thrown light on the tolerance capacity of plants under elevated temperature stress. This study clearly explained how the best performed genotypes were able to overcome the heat stress as compared to other poorly performed genotypes.

Cell membrane stability which is a measure of electrolyte diffusion, resulting from heat induced cell membrane leakage, has been used to screen and evaluate different wheat genotypes for thermal tolerance and other plants including cotton (Ashraf *et al*., 1994) [2], cowpea and barley (Wahid and Shabbir, 2005). High temperature may accelerate kinetic energy of membrane molecules, thereby loosening the chemical bonds of membrane molecules with ultimate increase in membrane fluidity and even to the denaturation of proteins or collapse of deformed cell (Savchenko *et al*., 2002; Chen *et al*., 2002) [14]. Generally membrane integrity is evidenced as heat sensitive event, as heat stress can negatively affect structural organization of membrane proteins increasing membrane permeability and electrolyte leakage. The present study indicates the genotypic variation for cell membrane stability (CMS) was observed under high temperature stress (Table 1) The maximum CMSI values recorded for the genotype IIVR – L was 50.88 %, 51.00 % and 51.08 % under ambient and 50.66 %, 50.73 %, 50.77 % under elevated temperature condition for 30 DAT, 60 DAT and 90 DAT respectively

Table 1: Effect of elevated temperature on cell membrane stability in tomato genotypes under different stages of plant growth

S. No.	Genotypes	30 DAT			60 DAT			90 DAT		
		AT	ET	Mean	AT	ET	Mean	AT	ET	Mean
1.	LE – 114	45.98	44.88	45.43	46.10	44.95	45.53	46.18	44.99	45.59
2.	EC – 608456	48.32	47.92	48.12	48.44	47.99	48.22	48.52	48.03	48.28
3.	EC – 170047	49.31	48.22	48.77	49.43	48.29	48.86	49.51	48.33	48.92
4.	EC – 170089	46.89	45.99	46.44	47.01	46.06	46.54	47.09	46.10	46.60
5.	EC – 168290	47.55	46.94	47.25	47.67	47.01	47.34	47.75	47.05	47.40
6.	LE – 118	50.32	49.99	50.16	50.44	50.06	50.25	50.52	50.10	50.31
7.	LE – 1	49.69	48.58	49.14	49.81	48.65	49.23	49.89	48.69	49.29
8.	LE – 3	49.53	48.37	48.95	49.65	48.44	49.05	49.73	48.48	49.11
9.	IIHR – 709	43.24	42.11	42.68	43.36	42.18	42.77	43.44	42.22	42.83
10.	EC – 177360	46.99	46.35	46.67	47.11	46.42	46.77	47.19	46.46	46.83
11.	EC – 608395	50.77	50.58	50.68	50.89	50.65	50.77	50.97	50.69	50.83
12.	EC – 169966	50.63	50.46	50.55	50.75	50.53	50.64	50.83	50.57	50.70
13.	IIHR – 2388	42.54	41.44	41.99	42.66	41.51	42.09	42.74	41.55	42.15
14.	EC – 175957	46.43	45.34	45.89	46.55	45.41	45.98	46.63	45.45	46.04
15.	EC – 177325	47.97	47.45	47.71	48.09	47.52	47.81	48.17	47.56	47.87
16.	EC – 168283	46.73	45.68	46.21	46.85	45.75	46.30	46.93	45.79	46.36
17.	IIVR – L	50.88	50.66	50.77	51.00	50.73	50.87	51.08	50.77	50.93
18.	EC – 177824	44.43	43.22	43.83	44.55	43.29	43.92	44.63	43.33	43.98
19.	EC – 177371	45.68	44.37	45.03	45.80	44.44	45.12	45.88	44.48	45.18
20.	LE – 20	49.88	48.69	49.29	50.00	48.76	49.38	50.08	48.80	49.44
Mean		47.69	46.86	47.28	47.81	46.93	47.37	47.89	46.97	47.43
		G	T	GxT	G	T	GxT	G	T	GxT
SEd		0.72	0.23	1.03	0.76	0.24	1.08	0.69	0.21	0.97
CD (P=0.05)		1.44	0.45	2.05	1.52	0.48	2.15	1.37	0.43	1.94

AT: Ambient Temperature
ET: Elevated Temperature (38±1ºC)
G: Genotype
GxT: Interaction of genotype and Temperature

and it was on par with EC – 608395 and EC – 169966 for all the three different stages. This higher CMS in IIVR-L might prevented the damage to the lipid bilayer of biological membranes (Savchenko *et al*., 2002) [14] as compared to other genotypes under elevated temperature conditions. Thus, CMS of leaf tissue can be used as a physiological indicator of heat stress to evaluate genetic variability.

Proline has long been known to accumulate in plants experiencing water limitation and this has driven studies of proline as a beneficial solute allowing plants to increase cellular osmolarity during water limitation which is otherwise called as osmotic adjustment under stress. Proline in the present study increased at a higher rate in IIVR-L compared to other genotypes under high temperature. Higher values of proline content was observed in the genotypes IIVR – L (182.48 mg g^{-1}, 197.51 mg g^{-1}) and IIHR – 2388 (100.65 mg g^{-1}, 122.53 mg g^{-1}) recorded lower value at 30 DAT under ambient and elevated temperature condition respectively (Table 2). A higher value of nitrate reductase activity was recorded in the genotype IIVR –L and was on par with EC – 608395 and EC – 169966 for all the three stages. The nitrate reductase activity for the genotype IIVR – L was 174.85, 184.10 and 164.89 mg NO_2 g^{-1} hr^{-1} under ambient temperature and 145.46, 154.80 and 139.32, 164.89 mg NO_2 g^{-1} hr^{-1} at 30 DAT, 60DAT and 90 DAT respectively (Table 3). The nitrate reductase activity showed a reduction of 15 – 20 % under elevated temperature condition for all the genotypes when compared to the ambient temperature condition. Hence, the study explicitly shows that higher proline in IIVR-L under elevated temperature was able to maintain the tissue water potential that resulted in a better nitrate reductase activity causing a better N metabolism.

Table 2: Effect of elevated temperature on proline content (mg g^{-1}) in tomato genotypes under different stages of plant growth

S. No.	Genotypes	30 DAT			60 DAT			90 DAT		
		AT	ET	Mean	AT	ET	Mean	AT	ET	Mean
1.	LE – 114	117.23	137.45	127.34	144.46	171.81	158.14	169.01	203.04	186.03
2.	EC – 608456	136.31	161.65	148.98	163.54	196.01	179.78	188.09	227.24	207.67
3.	EC – 170047	138.54	163.82	151.18	165.77	198.18	181.98	190.32	229.41	209.87
4.	EC – 170089	125.37	143.28	134.33	152.60	177.64	165.12	177.15	208.87	193.01
5.	EC – 168290	128.22	151.36	139.79	155.45	185.72	170.59	180.00	216.95	198.48
6.	LE – 118	150.47	178.21	164.34	177.70	212.57	195.14	202.25	243.80	223.03
7.	LE – 1	144.21	165.35	154.78	171.44	199.71	185.58	195.99	230.94	213.47
8.	LE – 3	142.22	164.22	153.22	169.45	198.58	184.02	194.00	229.81	211.91
9.	IIHR – 709	112.67	127.62	120.15	139.90	161.98	150.94	164.45	193.21	178.83
10.	EC – 177360	127.25	148.58	137.92	154.48	182.94	168.71	179.03	214.17	196.60
11.	EC – 608395	179.54	193.43	186.49	206.77	227.79	217.28	231.32	259.02	245.17
12.	EC – 169966	174.78	190.21	182.50	202.01	224.57	213.29	226.56	255.80	241.18
13.	IIHR – 2388	100.65	122.53	111.59	127.88	156.89	142.39	152.43	188.12	170.28
14.	EC – 175957	120.33	140.42	130.38	147.56	174.78	161.17	172.11	206.01	189.06

15.	EC – 177325	134.32	155.21	144.77	161.55	189.57	175.56	186.10	220.80	203.45
16.	EC – 168283	122.27	142.42	132.35	149.50	176.78	163.14	174.05	208.01	191.03
17.	IIVR – L	182.48	197.51	190.00	209.71	231.87	220.79	234.26	263.10	248.68
18.	EC – 177824	113.24	129.37	121.31	140.47	163.73	152.10	165.02	194.96	179.99
19.	EC – 177371	114.29	134.51	124.40	141.52	168.87	155.20	166.07	200.10	183.09
20.	LE – 20	149.63	174.22	161.93	176.86	208.58	192.72	201.41	239.81	220.61
Mean		135.70	156.07	145.88	162.93	190.43	176.68	187.48	221.66	204.57
		G	T	GxT	G	T	GxT	G	T	GxT
SEd		1.69	0.53	2.39	2.53	0.80	3.58	3.12	0.98	4.41
CD (P=0.05)		3.37	1.06	4.76	5.04	1.59	7.13^{NS}	6.21	1.96	8.79^{NS}

AT: Ambient Temperature
ET: Elevated Temperature (38±1ºC)
G: Genotype
GxT: Interaction of genotype and Temperature

Table 3: Effect of elevated temperature on nitrate reductase (µg NO_2 g^{-1} hr^{-1}) in tomato genotypes under different stages of plant growth

S. No.	Genotypes	30 DAT			60 DAT			90 DAT		
		AT	ET	Mean	AT	ET	Mean	AT	ET	Mean
1.	LE – 114	147.85	117.69	132.77	157.10	127.03	142.07	137.89	111.55	124.72
2.	EC – 608456	159.31	127.62	143.47	168.56	136.96	152.76	149.35	121.48	135.42
3.	EC – 170047	162.45	128.15	145.30	171.70	137.49	154.60	152.49	122.01	137.25
4.	EC – 170089	152.35	121.31	136.83	161.60	130.65	146.13	142.39	115.17	128.78
5.	EC – 168290	156.33	125.00	140.67	165.58	134.34	149.96	146.37	118.86	132.62
6.	LE – 118	168.46	135.46	151.96	177.71	144.80	161.26	158.50	129.32	143.91
7.	LE – 1	165.54	133.62	149.58	174.79	142.96	158.88	155.58	127.48	141.53
8.	LE – 3	164.77	132.38	148.58	174.02	141.72	157.87	154.81	126.24	140.53
9.	IIHR – 709	140.69	114.51	127.60	149.94	123.85	136.90	130.73	108.37	119.55
10.	EC – 177360	155.69	123.54	139.62	164.94	132.88	148.91	145.73	117.40	131.57
11.	EC – 608395	173.69	141.23	157.46	182.94	150.57	166.76	163.73	135.09	149.41
12.	EC – 169966	171.15	138.54	154.85	180.40	147.88	164.14	161.19	132.40	146.80
13.	IIHR – 2388	139.92	113.40	126.66	149.17	122.74	135.96	129.96	107.26	118.61
14.	EC – 175957	149.85	119.38	134.62	159.10	128.72	143.91	139.89	113.24	126.57
15.	EC – 177325	158.69	126.15	142.42	167.94	135.49	151.72	148.73	120.01	134.37
16.	EC – 168283	150.77	120.15	135.46	160.02	129.49	144.76	140.81	114.01	127.41
17.	IIVR – L	174.85	145.46	160.16	184.10	154.80	169.45	164.89	139.32	152.11
18.	EC – 177824	142.15	115.92	129.04	151.40	125.26	138.33	132.19	109.78	120.99
19.	EC – 177371	145.92	116.38	131.15	155.17	125.72	140.45	135.96	110.24	123.10
20.	LE – 20	166.54	134.38	150.46	175.79	143.72	159.76	156.58	128.24	142.41
Mean		157.35	126.51	141.93	166.60	135.85	151.23	147.39	120.37	133.88
		G	T	GxT	G	T	GxT	G	T	GxT
SEd		2.23	3.15	3.15	2.16	0.68	3.06	1.95	0.61	2.76
CD (P=0.05)		4.44	1.40	6.28	4.31	1.36	6.10	3.89	1.23	5.50

AT: Ambient Temperature
ET: Elevated Temperature (38±1ºC)
G: Genotype
GxT: Interaction of genotype and Temperature

High temperature during reproductive development have been reported to limit the flower bud initiation with significant increment in flower drop (Sato *et al*., 2002; Abdelmajeed *et al*., 2003) [13] and significant decrease in fruit set (Berry and Rafique, 1988) [4] leading to a sharp decline in tomato fruit yield. Results of the present investigation are in agreement with these reports in some of the genotypes like IIHR – 2388 and IIHR – 709 where there was no fruit production, though flowers were produced by these genotypes (100% reduction in fruit set) when exposed to elevated temperature (Table 4&5). Poor fruit set in these genotypes might be due to their higher sensitivity of post flowering stage to high temperature (Sato *et al*., 2000; Peet *et al*., 1998) [9]. The percentage reduction of fruits per plant under elevated temperature over ambient temperature was least in IIVR – L (29.3) followed by LE – 1 (31.5). Therefore the fruit set percent in IIVR – L was 97.27 % and 69.91% and it was 96.55 % and 49.88 % in LE- 3 and 95.00 % and 67.75% in LE – 1 under ambient and elevated temperature condition respectively (Table 9). Hence, fruit yield was higher in IIVR-L and the yield was zero for IIHR-709 and IIHR-2388 at elevated temperature condition. This explicitly states that the genotypes like IIVR-L, LE-1 and LE-3 has the capacity to overcome heat stress even in the post flowering stages.

Table 5: Effect of elevated temperature on fruit set percent (%) in different tomato genotypes

S. No.	Genotypes	Fruit set percentage		Mean
		AT	ET	
1.	LE – 114	95.24	52.29	73.77
2.	EC – 608456	86.96	35.09	61.03
3.	EC – 170047	94.44	35.98	65.21
4.	EC – 170089	92.50	43.78	68.14
5.	EC – 168290	85.94	35.21	60.58
6.	LE – 118	85.40	16.56	50.98
7.	LE – 1	95.00	67.75	81.38
8.	LE – 3	96.55	49.88	73.22
9.	IIHR – 709	94.00	0.00	47.00
10.	EC – 177360	92.86	40.80	66.83
11.	EC – 608395	98.80	24.88	61.84
12.	EC – 169966	82.65	31.86	57.26
13.	IIHR – 2388	29.63	0.00	14.82
14.	EC – 175957	91.38	58.87	75.13
15.	EC – 177325	92.52	25.89	59.21
16.	EC – 168283	96.88	30.05	63.47
17.	IIVR – L	97.27	69.91	83.59
18.	EC – 177824	91.36	24.39	57.88
19.	EC – 177371	84.38	27.21	55.80
20.	LE – 20	40.91	17.41	29.16
Mean		86.23	34.39	60.31
		G	T	GxT
SEd		0.99	0.31	1.40
CD (P=0.05)		1.97	0.62	2.79

AT: Ambient Temperature
ET: Elevated Temperature (38±1ºC)
G: Genotype
GxT: Interaction of genotype and Temperature

Table 5: Effect of elevated temperature on fruits per plant in different tomato genotypes

S. No.	Genotypes	Fruits per plant		Mean
		AT	ET	
1.	LE – 114	20.0	10.7	15.35
2.	EC – 608456	20.0	5.3	12.65
3.	EC – 170047	17.0	6.3	11.65
4.	EC – 170089	18.5	8.1	13.30
5.	EC – 168290	13.8	5.0	9.40
6.	LE – 118	29.9	5.0	17.45
7.	LE – 1	30.4	20.8	25.60
8.	LE – 3	56.0	20.0	38.00
9.	IIHR – 709	11.8	0.0	5.90
10.	EC – 177360	13.0	5.1	9.05
11.	EC – 608395	24.7	5.0	14.85
12.	EC – 169966	20.1	6.5	13.30
13.	IIHR – 2388	8.0	0.0	4.00
14.	EC – 175957	13.3	7.3	10.30
15.	EC – 177325	15.1	2.7	8.90
16.	EC – 168283	15.5	3.7	9.60
17.	IIVR – L	64.1	45.3	54.70
18.	EC – 177824	16.4	4.0	10.20
19.	EC – 177371	27.0	6.7	16.85
20.	LE – 20	9.0	3.5	6.25
Mean		22.2	8.5	15.37
		G	T	GxT
SEd		0.2	0.1	0.3
CD (P=0.05)		0.5	0.1	0.7

AT: Ambient Temperature
ET: Elevated Temperature (38±1ºC)
G: Genotype
GxT: Interaction of genotype and Temperature

The results that we have discussed in the present study, elucidate that the genotype IIVR-L was able to withstand the elevated temperature by increasing their cell membrane stability, proline accumulation which in turn maintained more flower and fruit production compared to other genotypes. The genotype LE-1 followed IIVR-L in its performance under heat stress. On the other hand, IIHR – 2388 and IIHR – 709 connotes its poor performance by being very sensitive to high temperature at the post flowering stage with no production of fruits. For these genotypes, the physiological stress indicator like cell membrane stability, proline accumulation and nitrate reductase activity were also low at all the stages which signifies its sensitivity to heat stress. The genotypes like EC – 608395 and EC – 175957 showed a better response to heat stress though the yield was less than IIVR-L. Hence, we can conclude from this study that IIVR-L showed its superior performance over other selected genotypes to heat stress.

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