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Research Article

ENZYMATIC AND NON ENZYMATIC ANTIOXIDATIVE DEFENSE SYSTEM OF CASSAVA GENOTYPES DURING POSTHARVEST DETERIORATION

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Abstract- Postharvest Physiological Deterioration (PPD) is the major problem in cassava that renders the roots unmarketable, thereby reducing the economic value of the crop. The increased production of toxic oxygen derivatives is considered to be a universal feature during post harvest period. It is clear that the capacity and activity of anti oxidative defense system are important in destroying active oxygen species that are produced in excess of those normally required for metabolism. The present study was undertaken to assess the effect of PPD and hydrogen cyanide (HCN) on antioxidant scavenging system of four cassava genotypes. Tubers from four different cassava genotypes were evaluated at 1, 3, 5, 7, 9, 11, 13 and 15 days after harvest for PPD. PPD was observed along with HCN content accumulation and also analyzed enzymatic and non enzymatic antioxidants changes with postharvest physiological deterioration (PPD). The results revealed that, cassava genotypes CI-850 accumulated less HCN content and delayed PPD with increased non enzymatic antioxidants of carotenoids, flavonoids and phenolics. Also over production of peroxidase and catalase was found even at five days after harvest. This genotype can be used as novel donor for development of PPD tolerant cassava genotypes.

Keywords- Postharvest physiological deterioration, hydrogen cyanide, carotenoids, flavonoids, phenolics, peroxidase and catalase

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Introduction

Cassava (*Manihot esculenta* Crantz) is one of the six most important crops in the world. It serves as stable food for over 800 million people worldwide [1] providing about 500 calories daily for more than 70 million people [2]. Cassava has a high efficiency in carbohydrate production, as well as being tolerant to drought and thrives well on even poor soils making it an attractive crop especially to small scale farmers. It gives carbohydrate production per hectare about 40 per cent higher than rice and 25 per cent more than maize. The roots are used for animal feed, industrial starch production and income generation for many small-scale farmers [3]. The roots and leaves are available all year round [4], thus cassava is an important food security crop, especially in drought-prone areas [2]. Cassava roots, unlike any other root crop, have a remarkably short shelf life due to physiological deterioration. The extent of deterioration depends upon the degree of mechanical damage of the roots as well as the genotype and environmental conditions.

PPD is an oxidative reaction that starts immediately after harvesting when the root is detached from the mother plant [5]. PPD has been explained as a physiological process due not to microorganisms, but having a molecular basis as an oxidative burst which commences 15 min after roots being injured [6], followed by altered gene expression. During post harvest period, development of oxidative stress is the major cause for free radicals production and also activate or inactivate different enzymes [7] which in turn involved in crucial part in cellular activities [8] and metabolites production [9]. An antioxidant is a molecule that inhibits the oxidation of other molecules. During PPD alter a chemical reaction that can produce free radicals, leading to chain reactions that may damage cells.

Similarly, antioxidant mechanisms also take place to ameliorate ROS production during this particular stress condition. Some antioxidant like, enzymetic (Catalase and peroxidase) and non enzymetic (carotenoids, flavonoids and phenolics) activities are increased during PPD, its helping to delay PPD [10]. Since, Hydrogen peroxide (H_2O_2 has a long shelf-life and highly mobile from cell to cell leads PPD during storage period [11].

It resembles typical changes associated with the plant's response to wounding. Cassava roots deteriorate 24-48 hours after harvest and subsequently the roots change its colour. Visible signs of PPD are vascular streaking with blue or black discoloration rendering the roots unpalatable and unmarketable [12; 13]. PPD is a physiological in nature and not caused by microbes. It is estimated that, world postharvest losses in cassava is 15–30 per cent [14, 15] depending on the variety, climatic conditions and distance between the farmer and the consumer. PPD also results in market price reduction on three to four day old roots and high pricing on fresh roots. Eventually this encourages consumers to choose alternative supplies of carbohydrates, increasing dependency on other imported food. In order to increase cassava production to meet rising demand, research towards delaying PPD is important as it would minimize the risk of root losses. Cassava roots in storage undergo physiological changes that affect the root quality [16]. Therefore, it would be important to increase our understanding of the physiological and biochemical traits associated with PPD, especially during the early stages. Based

on this background, here we report the changes on anti oxidative defense system with PPD intensity and HCN accumulation during post harvest period of different cassava genotypes.

Materials and Methods

The field experiment was conducted in Cassava YTP-1, CI-850, H740/92 and H226 at Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore**.** Ten months old cassava plants were harvested. Cassava tubers detached from plants and stored in ambient conditions.

PPD scoring

Intensity of PPD and associated metabolic disturbances was monitored daily by using image analyzer. The experiments of PPD were carried out in which a 25, 50 and 75 per cent transverse section of randomized sampling of three sliced roots from each plant variety was scored (from 1–10 % of PPD to 10–100 % of PPD) over the 11-day experimental period. The information was imaged through an image analyzer (WinDOS 3.2) and the results were expressed as percentage.

Determination of total hydrogen cyanide

Total hydrogen cyanide (HCN) content of tuber was estimated by the method of Indian Standard, IS: 4706 - 1978 Part II [17] and expressed as ppm. Whatman No.1 filter paper was cut into strips of 10-12 cm long and 0.5 cm wide and saturated them with alkaline picrate solution (dissolve 25 g sodium carbonate and 5g picric acid in one litre of water). One gram of the tuber sample was homogenated in 25 ml of water with 3-4 drops of chloroform. Homogenate was taken in 500 ml conical flask and saturated filter paper was placed in the hanging position with the help of cork stopper inside the conical flask. Mixture was incubated at room temperature (20°C) for 20-24 hours. The sodium picrate present in the filter paper was reduced to reddish compound in proportion to the amount of hydrocyanic acid evolved from the tuber sample. Eluted the colour by placing the paper in clean test tube containing 10 ml distilled water and the absorbance was measured at 510 nm and HCN expressed in ppm.

Determination of non enzymatic and enzymatic antioxidant of fresh cassava tubers

Fresh samples and those 1, 3, 5, 7, 9, 11, 13 and 15 days after harvest were collected and used for antioxidants analysis.

Non enzymatic antioxidants

Determination of total flavonoids

The total flavonoid content of plant extracts was determined by using the aluminium chloride colorimetric method [18] and revised [19]. One ml of extract solution was mixed with 0.5 ml 95 per cent ethanol (v/v), 0.1 ml 1 M potassium acetate, 0.1 ml aluminium chloride solution (10% AlCl3) and 0.8 ml distilled water to a total volume of 2.5 ml. The mixture was well mixed and incubated at room temperature for 30 minutes versus reagent blank containing water instead of the sample. Then the absorbance was measured at 453 and 503 nm. Results were expressed in µg g^{-1} of fresh weight.

Determination of total carotenoids

The total carotenoid content of plant extracts was determined by using the method [20]. A 5g of sample was taken in pestle and mortar and macerated with acetone till the residue become colour less. The acetone extract was collected and transferred to a separating funnel containing 20 ml of petroleum ether. The extract was thoroughly mixed and 20 ml of 5 per cent sodium sulphate was added and shaken gently till a separation of two phases was seen. The lower phase was re extracted with another 20 ml of petroleum ether. The solution was taken in a 200 ml beaker and added 10g Na_2SO_4 and kept aside for 30 minutes. The petroleum ether extract was decanted into a 100 ml volumetric flask and the volume was made up by using petroleum ether. Then the absorbance was measured at 453 and 503 nm. Total carotenoids was expressed in µg g^{-1} of fresh weight.

Determination of total phenol content

Total phenol content of tuber sample was estimated by the method [21]. Weigh 500 mg tuber sample and cut into small bits. Transfer the tuber bits to a test tube and added 5ml of 80 per cent ethanol. The test tube kept in hot water bath for 10 minutes and cooled the contents. The tuber sample was macerated with another 5 ml of 80 per cent ethanol and centrifuged the contents at 5000 rpm for 10 minutes. Supernatant was collected and made up the volume to 25 ml with distilled water. One ml of supernatant was taken and 2 ml of 20 per cent sodium carbonate and 1 ml of folin reagent was added. Then, kept as such 10 minutes for colour development and measured the OD at 660 nm. Standard also prepared by using catechol of 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 ppm. Total phenolics activity was expressed as mg g^{-1} of fresh weight.

Enzymatic antioxidants

Catalase (CAT) activity

Catalase activity was estimated according to the method [22]. One g of the tuber sample was macerated with 10ml of phosphate buffer using pre chilled pestle and mortar. The content was centrifuged at 2000 rpm for 10 min. 1ml of the supernatant was taken in 5 different beakers. Added 5 ml of 1.55 sodium perborate and 1.5 ml of phosphate. Later 10 ml of 1N sulpuric acid was added at the time interval of 1 min, 2 min, 3 min, 4 min and in the fifth beaker, 10 ml of sulphuric acid was added before the addition of enzyme extract and treated as blank for comparison. The contents were titrated against 0.05N $KMnO_4$ consumed was noted (1ml of $KmnO_4$ is equal to 0.85 µg of H_2O_2) and enzyme activity was expressed in µg of H_2O_2 g^{-1} min^{-1}.

Peroxidase (POX) activity

Peroxidase activity was determined according to the procedure given [23]. 500 mg of sample was taken and macerated with 5 ml of phosphate buffer using the pre chilled pestle and mortar. The contents were centrifuged at 5000 rpm for 15 min and the supernatant was collected. 0.1 ml of the supernatant was taken and added with 3ml of pyrogallol. The contents were transferred to a cuvette and read as blank in a spectrophotometer at 430 nm, then 0.5 ml of H_2O_2 was added and the absorbance were taken immediately at the interval of 30 seconds up to two minutes. The difference between O.D. values for one minute was calculated by using average of the differences was worked out and the peroxidase activity was calculated and expressed as changes in the OD at 430 nm $min^{-1}g^{-1}$.

Result and Discussion

During post harvest period, irrespective of the genotypes, the intensity of PPD and accumulation of HCN increases significantly from first to 15 days after harvest. Large variations in HCN content along with PPD per cent were found among genotypes during 15 days of storage period [Fig.-1]. Among the genotypes, CI-850 was found to be the most tolerant while H226 is the most susceptible to PPD with less (13.06 ppm) and high (131.41ppm) accumulation of average HCN respectively over 15 days of storage period. Similarly, PPD per cent in H226 was gradually increased significantly in day by day (8.92 to 93.81 per cent) along with over production of HCN with the exception of CI-850, YTP-1 and H740/92. As shown in [Fig-1], PPD per cent along with cyanide content increased in all studied samples at gradually day by day up to 15 days. But high degree of increase was observed in H226. Similar reports were reported and they explained about the role of ROS in cassava PPD is further complicated by the cyanogenic nature of the storage roots [24]. It has been suggested that the formation of cyanogenic compounds on wounding is responsible for the oxidative burst; the cyanogenic compounds released could inhibit complex IV of the mitochondrial electron transport chain (METC) and thereby increase production of ROS in mechanically wounded cells [24]. However, this theory still relies upon the destructive nature of ROS to explain how the biochemical and molecular symptoms of PPD are able to spread throughout the root from the wound site. This might be the reason for recording more HCN content which in turn causes high intensity of PPD in H226 and less in other varieties of present study. The oxidative burst is due to cyanide production, which is rapidly induced when cassava is mechanically damaged. This variation may be explained taking into consideration the catabolism of progressive accumulation of linamarin and subsequent degradation by enzyme linamarase to

form HCN [25] in cassava tubers might be the reason for obtaining increasing trend of HCN from first to seven day after harvest. It is possible that cyanogenic compounds released on wounding interfere with the mitochondrial electron transport chain and increase ROS production or inhibit antioxidant enzyme activity and thereby contribute to PPD [26]. A similar result in hydrogen cyanide at high level was found in H226 at two days after harvest in this study also. This investigation revealed that clear differences in HCN concentration between susceptible and tolerant genotypes which causes difference in intensity of PPD.

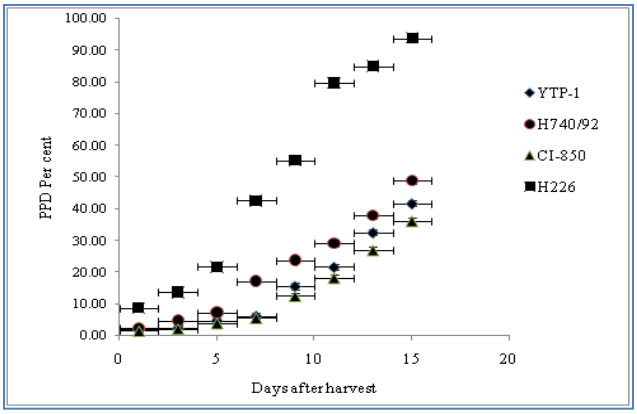

Fig-1 PPD per cent during postharvest physiological deterioration of four cassava genotypes

Table-1 *Changes in hydrogen cyanide (ppm) during postharvest physiological deterioration of four cassava genotypes studied*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	6.68a	9.66a	7.29a	5.89a	7.38
3	8.16b	12.81b	9.41b	7.16b	9.39
5	10.71c	28.26c	11.93c	8.91c	14.95
7	13.88dd	48.33d	16.48d	10.87d	22.39
9	18.19e	89.12e	25.12e	12.96e	36.35
11	24.41f	158.37f	37.26f	15.89f	58.98
13	29.75g	289.35g	46.65g	19.32g	96.27
15	36.63h	415.41h	61.42h	23.51h	134.24
Mean	18.55	131.41	26.95	13.06	47.49
SEd	0.158	0.232	0.234	0.110	
CD (P=0.05)	0.326	0.479	0.480	0.228	

Secondary metabolites (carotenoids, phenolics and flavonoids) are found in many species of the plant kingdom and are well recognized as potential antioxidants. Physiological deterioration has been related to changes in enzyme activities, which generate phenols [27]. The carotenoid assist to delayed or reduced postharvest deterioration in cassava roots [29]. The biochemical changes in carotenoids detected during the storage of fresh cassava tubers up to 15 days are summarized in [Table-2]. Spectrophotometric analysis of cassava root extracts demonstrated that, in fresh samples, on one hand the largest amount of carotenoids was detected in CI-850 (10.97 µg g^{-1}) followed by YTP-1 (9.32 µg g^{-1}) and H740/92 (7.34 µg g^{-1}) on day one. After that, drastic reduction was observed in H226 and gradual decrease was found in CI-850 from day one to 15. On other hand, flavonoids are accumulated gradually from day one to nine days of storage period in CI-850 (from 642.56 to 1581.92 µg g^{-1}) followed by YTP-1 (from 489.36 to 1261 µg g^{-1}) and H740/92 (from 276.54 to 891.29 µg g^{-1}). But in H226, no increase on flavonoid content was found after 3 days of storage period at the same time, drastic reduction was observed from day 3 (312.76 µg g^{-1}) to 15 (62.63 µg g^{-1}) [Table-3]. Carotenoids is able to quench $^1O_2$ directly or alternatively it may quench excited triplet state chlorophyll in photosystem II, the major source of $^1O_2$ [30]. Carotenoids are the major contributor of antioxidant molecules that can react with virtually any radical species to form more stable products [31]. In plant systems they have been implicated in the quenching of singlet oxygen ($^1O_2$) produced during photosynthesis and preventing lipid peroxidation chain reactions [32, 33]. Carotenoids have been shown to be associated with PPD in cassava as the level of carotenoids tends to decline as PPD progresses [34]. In addition, carotenoid content always has positive correlation with resistance to PPD. The oxidative stress model for PPD has also been supported by the discovery of high beta carotene varieties of cassava that have a longer shelf life than low beta-carotene lines [29, 28]. This earlier findings support the present investigation. Increased in flavonoid during the first 1-7 days postharvest, after 7–9 days there was some accumulation and after 9 days there was a rapid decline. Few reports stated that, reported increases in flavonoid contents during PPD delays deterioration [35, 36]. Our results are in accordance with those previously reported. In this investigation, increasing trend on accumulation of total phenolics was found in PPD tolerant CI-850 from day one (0.576 µg g^{-1}) to seven (2.199 µg g^{-1}) [Table-4]. After that, gradual decrease was observed up to the end of the storage period. The same trend was observed in YTP 1 and also in H740/92. But total phenolics content suddenly reduced on 3 day after harvest in H226 and after that, drastic reduction was found. A major visual symptom of PPD is vascular streaking, resulting from occlusions in the vascular parenchyma by oxidized phenolics [37, 38]. The present investigation also corroborated the earlier findings. Over production of enzymatic antioxidants catalase (CAT) and peroxidase (POX) during storage period play key roles in the removal of ROS [39, 40]. In the present study, CAT activity was expressed in terms of remaining unbroken H_2O_2 available in the sample. So, CAT and H_2O_2 are negatively associated with each other. Irrespective of the genotypes, remaining unbroken H_2O_2 was increased from day one to 15. Gradual increase was found in CI- 850 from day one (21.67 µg of H_2O_2 min^{-1} g^{-1}) to fifteen (259.12 µg of H_2O_2 min^{-1} g^{-1}) followed by YTP-1 and H740/92 [Table-5]. At the same time, sharp increase was observed in H226. From this we conclude the catalase activity was drastically reduced in H226 but gradual in other genotypes during storage period. But POX activity was increased up to 5 days of storage after that gradually reduced in CI-850, YTP-1 and H740/92 and drastic reduction was found in H226 [Table-6]. H226, the most susceptible cultivar to PPD, showed drastic reduction in CAT in from day 1 to 15. Interestingly, the most tolerant genotype (CI-850) to PPD showed a high level of CAT in all the day of storage period. The total POX activity of storage root tissue also experiences a transient increase after stress treatment in cassava. A yeast elicitor was able to trigger a peak four-fold induction of POX activity forty-eight hours after inoculation of a cassava cell suspension with POX activity remaining low before and after this peak. Wounding of storage roots meanwhile resulted in a transient increase in POX twenty-four hours after harvesting [41, 42]. This might be the reason for increasing POX activity in CI-850, YTP-1 and H740/92 up to day 5 and reduced the intensity of PPD. Previous reports clearly given an idea and also reported that, CAT expression increased in cassava roots after harvesting [6]. This increase was higher in a cultivar with low PPD susceptibility than a susceptible cultivar, suggesting a positive correlation between CAT activity of storage roots and resistance to PPD in cassava. The increases in hydrogen peroxide concentration were related to the augmentation of CAT activity and other scavenging enzymes [11] corroborating the findings herein described. Findings similar to these have been reproduced elsewhere [43] indicating that CAT over-expression in storage roots could increases resistance to ROS mediated PPD in cassava. The present results corroborated with the findings of previous studies.

Table-2 *Changes in carotenoid content (µg g^{-1}) during postharvest physiological deterioration of four cassava genotypes*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	9.32b	0.96a	7.34a	10.97a	7.15
3	9.99a	0.60b	6.51b	10.34b	6.86
5	8.53c	0.42c	4.79c	9.02c	5.69
7	6.79d	0.28d	3.18d	8.11d	4.59
9	4.66e	0.06e	1.91e	6.25e	3.22
11	2.92f	0.04f	1.05f	4.89f	2.22
13	1.19g	0.02fg	0.91f	3.22g	1.34
15	0.64h	0.01g	0.12g	1.05h	0.46
Mean	5.51	0.30	3.23	6.73g	3.94
SEd	0.179	0.011	0.106	0.210	
CD (P=0.05)	0.368	0.023	0.219	0.434	

Table-3 *Changes in flavonoids (µg g^{-1}) during postharvest physiological deterioration of four cassava genotypes studied*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	489.36f	228.65c	276.54f	642.56g	409.28
3	563.22e	312.76a	315.66e	723.73f	478.84
5	798.73d	290.41b	534.59c	1009.44d	658.29
7	972.18b	225.59c	669.11b	1218.07c	771.24
9	1261.25a	150.32d	891.29a	1581.92a	971.20
11	875.77c	110.43e	498.55d	1252.81b	684.39
13	558.22e	92.61f	217.32g	827.42e	423.89
15	219.64g	62.63g	93.88h	488.12h	216.07
Mean	717.30	184.18	437.12	968.01	576.65
SEd	7.396	1.914	4.762	9.734	
CD (P=0.05)	15.264	3.949	9.829	20.090	

Table-4 *Changes in total phenolics (mg g^{-1}) during postharvest physiological deterioration of four cassava genotypes studied*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	0.493g	0.145g	0.337f	0.576g	0.388
3	0.874e	0.331d	0.665d	0.928e	0.700
5	1.110c	0.778a	0.919c	1.188d	0.999
7	1.949a	0.692b	1.539a	2.199a	1.595
9	1.376b	0.561c	1.194b	1.576b	1.177
11	0.992d	0.290e	0.521e	1.232c	0.759
13	0.673f	0.195f	0.338f	0.711f	0.479
15	0.219h	0.097h	0.110g	0.347h	0.193
Mean	0.961	0.386	0.703	1.095	0.786
SEd	0.0097	0.0047	0.0078	0.0110	
CD (P=0.05)	0.0201	0.0098	0.0162	0.0227	

Table-5 *Changes in catalase (µg of H_2O_2 g^{-1} min^{-1}) during postharvest physiological deterioration of four cassava genotypes studied*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	0.73d	0.59c	0.62d	0.76e	0.68
3	1.00b	0.77b	0.85b	1.23b	0.95
5	1.14a	0.84a	0.97a	1.60a	1.14
7	0.99b	0.71b	0.75c	1.10c	0.89
9	0.95c	0.59c	0.62d	0.93d	0.77
11	0.49e	0.32d	0.39e	0.54f	0.43
13	0.29f	0.17e	0.20f	0.38g	0.26
15	0.19g	0.08f	0.11g	0.29h	0.17
Mean	0.72	0.50	0.56	0.85	0.66
SEd	0.0076	0.0055	0.0062	0.0096	
CD (P=0.05)	0.0157	0.0114	0.0127	0.0198	

Table-6 *Changes in peroxidase (changes in the OD at 430 nm min $^{-1}$g^{-1}) during postharvest physiological deterioration of four cassava genotypes studied*

Days after harvest	YTP-1	H226	H740/92	CI-850	Mean
1	33.65a	54.78a	42.35a	21.67a	38.11
3	39.20b	78.27b	50.12b	26.22b	48.45
5	61.08c	119.44c	76.94c	45.38c	75.71
7	99.60d	179.89d	129.66d	81.64d	122.70
9	138.76e	245.50e	187.09e	118.26e	172.40
11	179.92f	309.67f	250.20f	158.22f	224.50
13	229.31g	399.49g	310.48g	205.43g	286.18
15	290.02h	489.51h	379.90h	259.12h	354.64
Mean	133.94	234.57	178.34	114.49	165.34
SEd	1.153	2.021	1.567	1.007	
CD (P=0.05)	2.379	4.170	3.234	2.065	

Plants possess a limited number of strategies to avoid oxidative stress. It is not surprising then that plants have evolved complex pathways for tolerating oxidative stress. This tolerance relies on a balance between ROS production and removal and involves coordinated interplay between large suites of genes. ROS removal systems rely on antioxidant molecules that can efficiently scavenge ROS. The relative contributions of different antioxidant molecules to scavenging ROS during post harvest period play a major role in this process [44]. This study revealed that, low accumulation of HCN content along with over production of non enzymatic and enzymatic antioxidants might be the main reason to cause low level of PPD in CI-850. Over production of HCN, along with less expression of antioxidants causes oxidative burst which in turn produced high intensity of PPD in H226

Conclusion

The study clearly concluded that an appropriate physiological balance of all the components of the anti oxidative defense is necessary in order to obtain increases in PPD tolerance. Current observations suggested that in crossing the level of PPD tolerance by reinforcing the plant defense system with new genes is an attainable goal. In future, increasing the enzymatic and non enzymatic antioxidant system by manipulation of the regulatory process controlling their expression may provide additional means of improvement.

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Author Contributions

This is the part of Ph.D student's thesis work (first author S. Sowmyapriya) and all the authors participates in the work in a substantive way and contributed equally.

Abbreviations

%	:	Per cent
° C	:	Degree Celsius
CAT	:	Catalase
CD	:	Critical Difference
et al	:	Co-workers
Fig	:	Figure
g	:	Gram
HCN	:	Hydrogen cyanide
H_2O_2	:	Hydrogen peroxide
hr	:	Hour
IS	:	Indian Standard
l	:	Liter
METC	:	Mitochondrial Electron Transport Chain
ml	:	Milliliter
mg	:	Milligram
min.	:	Minutes
nm	:	Nanometer
OD	:	Optical density
POX	:	Peroxidase
PPD	:	Postharvest Physiological Deterioration
ppm	:	Parts per million
ROS	:	Reactive oxygen species
µg	:	Microgram
v/v	:	volume / volume

Conflict of Interest: None declared

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