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Original article

Differential response of banana cultivars (*Musa* spp.) to temperature-induced changes in fruit quality

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Summary

Introduction – **Banana (*Musa* spp.) is one of the most widely consumed fruits in the world. Fairly good genetic diversity exists in banana for various fruit quality parameters. However, the changing climate, especially the rising temperature, is affecting the quality of fruit.** *Materials and methods* – **In this study, fruits of banana cultivars such as 'Grand Naine' (GN), 'Robusta', 'Shrimanti', 'TellaChekkerakeli' (TC), and 'Nendran', grown in different agro-climatic conditions of India (Andhra Pradesh, Gujarat, Maharashtra and Kerala), and also in different seasons within a region, were assessed for fruit biochemical and antioxidant parameters and correlated with the temperature.** *Results and discussion* – **The results revealed that the total phenols, total flavonoids, titratable acidity, vitamin C, total antioxidant capacity (FRAP and DPPH) were significantly and positively correlated to temperature in all cultivars, whereas total carotenoids and total sugars were significantly and negatively correlated to temperature. *β*-carotene and cryptoxanthin were found to be the major carotenoid pigments and were maximum in cv. Nendran and minimum in cvs. GN and TC. Cultivars GN and Shrimanti were relatively less affected by the temperature when compared to cultivars Nendran and TC.** *Conclusion* – **Bunches harvested in February and October exhibited better quality than those harvested in June, due to relatively lower temperatures during the fruit growth period.**

Keywords
banana, carotenoids, phenols, sugars, temperature, total antioxidant capacity

Significance of this study

What is already known on this subject?

- There is wide germplasm diversity for fruit quality in banana crop. Factors contributing for fruit quality are already known. Temperature and rainfall required for getting a good crop is also available. However, the rise in temperature on fruit quality parameters and the optimum growth temperature for better fruit quality is not yet reported for banana cultivars grown in India.

What are the new findings?

- One of the ways to reduce the temperature effects on fruit quality is to identify the cultivars which are less affected by the rising temperatures and to alter the harvest time to get good quality fruits with better biochemical and antioxidant parameters in different cultivars of banana. Effect of temperature on fruit quality parameters in different cultivars is reported in this study. The study has also identified the varying response among cultivars to temperature with respect to fruit quality.

What is the expected impact on horticulture?

- Bunches harvested in February and October exhibited better quality than those harvested in June. This will help in planning the planting time to coincide with the low temperatures during the fruit growth period which varies with region and cultivar.

Introduction

Banana (*Musa* spp.) is one of the most widely distributed fruit crops in the tropic and the subtropic regions of the world (Aurore *et al.*, 2009). India is the largest producer of banana (Kudachikar *et al.*, 2011) with an annual production of 30.808 million tonnes (Horticulture Statistics at a Glance, 2017–18). Recent studies indicated the health benefits of banana in retardation of aging and prevention of cancer and cardiovascular diseases, blood pressure, peptic ulcers, colitis, *etc.* (Pereira and Maraschin, 2015). Some of the major banana cultivars like 'GN', 'Robusta', 'Shrimanti', 'TC', 'Nendran', *etc.*, are consumed as energy yielding food as well as dessert (Hailu *et al.*, 2014). Fruit quality is a combination of external parameters like color, shape, size and internal parameters of texture, flavour and nutritional qualities (Kumar *et al.*, 2011). Fruit flavour and nutritive value is primarily determined by sugars, acidity, carotenoids and vitamins, and also by antioxidants such as phenols and flavonoids. The most abundant

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antioxidants in banana are phenolics, carotenoids and ascorbic acid (Singh *et al*., 2016). Fructose, glucose and sucrose are the major sugars in ripe banana pulp (Mathew and Negi, 2017).

Trans-α-carotene and trans-β-carotene are reported to be the major carotenoid compounds in banana (Fu *et al*., 2019). Cultivars Red banana and Nendran have been reported to be rich sources of carotenoids among banana cultivars in India (Dhandapani *et al*., 2017). Yellow/red banana cultivar Asupina is the high β-carotene (1,412 µg 100 g^{-1} fresh weight) containing cultivar in Australia (Englberger *et al*., 2006). Higher carotene content in the pulp of 'Nendran' is attributed to the expression of two phytoene synthase genes whereas in other cultivars only one phytoene synthase gene was expressed (Dhandapani *et al*., 2017). Phytoene synthase expression in banana 'Nendran' was found to be responsive to abiotic stresses (Kaur *et al*., 2017). High temperature during growth as well as ripening significantly affects the fruit quality of ripe fruit and its marketable life. In addition to the environmental factors, fruit quality in terms of antioxidant capacity is also influenced by cultivar and cultivation practices (Kondo *et al*., 2004; Babu *et al*., 2012). Higher antioxidant activity due to elevated temperature was mainly contributed by the higher total phenolics in strawberries (Wang and Zheng, 2001). Environmental conditions also influence the total carotenoid production but the significant influence is by the genotypes (Setiawan *et al*., 2001). Among the carotenoid pigments lycopene is severely affected by the higher temperature (Shivashankara *et al*., 2015). TSS and acidity were the other quality parameters affected by temperature in tomato fruits (Khanal, 2012). High temperature during fruit growth is reported to reduce the starch and vitamin C content significantly in kiwifruits (Richardson *et al*., 2004). Apart from day temperature, night temperature was also found to influence the fruit quality in apples (Pan and Shu, 2007). In addition to the growing conditions, fruit quality is also affected by the storage temperatures. Cold storage increased the browning and decreased the fruit quality severely (Abuhamra and Linatoc, 2016). Low temperature storage of banana reduced the sugar synthesis due to alterations in the starch structure and reduced amylase activity (Peroni-Okita *et al*., 2013). High temperature during the fruit growth period reduced total soluble solids, sugar content and composition of sugar but increased the mineral content in banana fruits (Bugaud *et al*., 2009).

One of the ways to reduce temperature effects on fruit quality is to identify the cultivars which are less affected by the raising temperatures and to alter the harvest time. Therefore, to understand the cultivar differences in banana fruit quality, various fruit biochemical and antioxidant parameters were assessed and the influence of growth temperature on various biochemical and antioxidant quality parameters were investigated in the present study. The study was also aimed at identifying the suitable time of harvest to get good quality fruits with better biochemical and antioxidant parameters in different cultivars of banana.

Materials and methods

Chemicals

All chemicals used in the study are of analytical grade and procured from Sigma Chemical Co., USA, Himedia, India and Merck, India.

Figure 1. India map depicting different banana sample centers.

Table 1. Mean maximum temperature (°C) from shoot emergence stage to harvest period and Mean room temperature (°C) from harvest to ripe period.

Regions	Varieties	Month of harvest											
		2013 Jun.		2013 Oct.		2014 Feb.		2014 Jun.		2014 Oct.		2015 Feb.	
		Shoot emergence to harvest period	Harvest to ripe period	Shoot emergence to harvest period	Harvest to ripe period	Shoot emergence to harvest period	Harvest to ripe period	Shoot emergence to harvest period	Harvest to ripe period	Shoot emergence to harvest period	Harvest to ripe period	Shoot emergence to harvest period	Harvest to ripe period
		Max. temp. (°C)	Room temp. (°C)	Max. temp. (°C)	Room temp. (°C)	Max. temp. (°C)	Room temp. (°C)	Max. temp. (°C)	Room temp. (°C)	Max. temp. (°C)	Room temp. (°C)	Max. temp. (°C)	Room temp. (°C)
Gujarat	Grand Naine	35.6	28.5	30.6	29.3	32.5	28.2	36.3	29.7	31.4	28.1	32.3	29.3
	Robusta	35.6	28.5	30.5	29.0	32.6	28.2	36.2	30.3	31.5	28.1	32.6	29.3
Maharashtra	Grand Naine	37.6	28.4	31.7	28.7	31.5	29.6	37.7	29.5	34.5	28.0	31.7	29.7
	Shrimanti	37.6	28.5	31.7	28.7	31.5	29.4	37.7	29.5	34.5	27.9	31.7	29.5
Andhra Pradesh	Grand Naine	35.8	27.9	30.6	28.3	29.1	26.9	33.9	28.7	31.6	28.1	30.2	29.7
	TellaChekkerakeli	–	–	30.6	28.0	30.2	26.7	34.7	27.3	32.5	27.5	32.5	29.5
Kerala	Grand Naine			33.3	28.0	34.5	27.2	33.8	30.5	30.5	29.5	32.6	29.4
	Nendran	–		33.3	28.0	34.5	27.2	33.8	30.5	30.5	29.5	32.6	30.0

Plant material

Five banana cultivars were chosen for the study, namely 'GN', 'Robusta', 'Shrimanti', 'TC' and 'Nendran', grown at different locations in the following states of India: Andhra Pradesh, Gujarat, Maharashtra, and Kerala. Whereas 'GN' is grown in all the four states mentioned above (Figure 1), the other cultivars are more specific: 'Robusta' to Gujarat, 'TC' to Andhra Pradesh, 'Shrimanti' to Maharashtra, and 'Nendran' to Kerala. To ensure that the banana fruits are exposed to varying temperatures during fruit growth period, the planting dates were staggered accordingly across the year. Planting dates are in the same month for all regions. Three planting dates were followed in all the regions to have different temperatures during the fruit growth period. This is one of the approaches to study the effect of temperature on fruit growth and quality in crops like banana since it is very difficult to grow them in controlled conditions. Growth temperatures of different regions are given in the form of a table. Fully mature fruits were harvested every four months from October 2013 to February 2015. Fruits were harvested at green stage and ripened at room temperature in the laboratory. After completely ripened, fruits were taken for all biochemical analysis. It took 18 to 22 days for fruits to ripen at room temperature. Field temperatures were recorded from the shooting stage to the harvest period (Table 1). The sampling stage for analysis of all biochemical parameters were selected at fully matured stage (visual appearance of smoothening of ridges). The harvested fruit bunches were ripened at room temperature, which was recorded daily (Table 1), and analysed for the following fruit biochemical and antioxidant parameters in triplicates: titratable acidity, vitamin C, total phenols, total flavonoids, Ferric Reducing Antioxidant Potential (FRAP), 2,2-diphenyl-1-picrylhydrazyl (DPPH), total carotenoids, and total sugars. The methods of analysis are given below.

Titratable acidity

Titratable acidity of homogenized pulp (5 g) of banana fruits was determined as per Shivashankara *et al.* (2018) and expressed as percent of citric acid equivalents.

Vitamin C (ascorbic acid)

Vitamin C content was determined by the 2,6-dichlorophenol indophenol (DCPIP) method as explained by Ranjitha *et al.* (2015) using 4% oxalic acid. Vitamin C content present in the solution was estimated by titrating a known quantity of the extract against DCPIP. Vitamin C content was calculated as mg of ascorbic acid equivalents per 100 g fresh weight using a standard curve of L-ascorbic acid with 20–100 µg mL^{-1} concentration.

Total phenols

Total phenols were estimated using the Folin-Ciocalteu reagent (FCR) as described by Shivashankara *et al.* (2018). Fruit extract with 80% methanol was used for phenol estimation and the colour developed was read at 700 nm using a spectrophotometer (T80+ UV/VIS Spectrophotometer, PG Instruments, Alma Park, Leicestershire, UK). The results were expressed as mg of gallic acid equivalent per kg dry weight. Standard curve was developed using gallic acid at a concentration range of 20–100 µg mL^{-1}.

Total flavonoids

Total flavonoids were estimated by the method described by Shivashankara *et al.* (2018). Flavonoids present in the extract of fruit pulp (5 g) in 80% methanol were estimated

using 5% sodium nitrite ($NaNO_2$) and 10% aluminium chloride ($AlCl_3$). The absorbance of the pink mixture was read at 510 nm and expressed as mg of catechin equivalent per kg dry weight. Standard curve was prepared using catechin at a concentration range of 20–100 µg mL^{-1}.

FRAP assay

FRAP, a measure of antioxidant capacity, was measured using, with some modifications, the method explained by Shivashankara *et al*. (2010). The extract (0.2 mL) in 80% methanol (v/v) was mixed with 1.8 mL of FRAP reagent and the intensity of colour was read at 593 nm. The antioxidant capacity was expressed as mg of ascorbic acid equivalent antioxidant capacity (AEAC) per kg dry weight. Ascorbic acid solution was used for developing the standard curve in the range of 20–100 µg mL^{-1} concentration.

DPPH activity

DPPH, a measure of radical-scavenging ability, was measured by the method of DPPH radical assay (Shivashankara *et al.*, 2010). Five g of sample homogenised in methanol (80%) and made up to 50 mL. The reduction in colour due to scavenging of DPPH radicals by the antioxidants present in the methanol extract was estimated by reading the absorbance at 517 nm, and the radical-scavenging ability was expressed as the weight of the sample required for scavenging DPPH radicals by 50%.

Total carotenoids

Total carotenoid content was analysed with the spectrophotometric method (Ranganath *et al*., 2018). Carotenoids were extracted in acetone, partitioned to hexane, and the absorbance was read at 470 nm and expressed in mg per kg dry weight as *β*-carotene equivalents. The standard curve was prepared using *β*-carotene at a concentration range of 50–250 µg mL^{-1}.

Total sugars

Total sugars were extracted in 80% ethanol, made up to 50 mL and the assay was followed by Shivashankara *et al*. (2015). The extract was mixed with 1.0 mL of alkaline copper tartrate and 1.0 mL of arsenomolybdic acid reagent; the absorbance was read at 620 nm and expressed as gram of glucose equivalent per kg dry weight using the standard curve. The standard curve was prepared using glucose with the concentration range of 20–100 µg mL^{-1}.

Sugar profile by liquid chromatography – mass spectrometry (LC-MS/MS)

Sugars profiles of the five cultivars were determined using liquid chromatography-mass spectrometry (LC-MS/MS) by the method of Geetha *et al*. (2016) with slight modifications. 1.0 g of banana pulp was extracted with 80% ethanol, evaporated to dryness, dissolved in the mobile phase, filtered through 0.2 µm nylon filter paper, and injected into an ultra-performance liquid chromatography (UPLC) (Waters, Milford, Massachusetts, USA).

LC-MS/MS conditions

The mobile phase comprised solvent A, acetonitrile:water (80:20, v/v), and solvent B, acetonitrile:water (30:70) with 0.1% ammonium hydroxide. A gradient program was used for running the mobile phases at the rate of 0.1 mL min^{-1} with the total run lasting for 15 min. The analytical column was a 2.1 × 100 mm UPLC BEH-amide column (Waters, Milford, Massachusetts, USA) with 1.7 µm particles, protected by a 1.7 µm VanGuard BEH-amide guard column (Waters). The column temperature was maintained at 25 °C. Elution was monitored using a TQD-MS/MS system (triple quadrupole mass spectrometer, Waters, USA) optimized for sugar analysis and a multiple reactions monitoring (MRM) detection mode. The details of precursor ions, collision-induced product ions, optimized cone voltage, and collision energies for each of the sugars under ESI^{-ve} mode are given in Table 2.

Carotenoid profile by UPLC

Carotenoids profile was identified using UPLC, following the method reported by Ranganath *et al*. (2018). The Acquity-UPLC system from Waters consisted of a quaternary pump, an auto sampler injector, and a PDA (photodiode array) detector equipped with an Acquity-UPLC BEH-C18 column (1.7 µm, 2.1 × 50 mm) and a BEH-C18 (1.7 µm, 2.1 × 5 mm) guard column. The instrument was controlled and the data were processed by a software package, name-

Table 2. Multiple reactions monitoring (MRM) of sugars standards.

Sugars	Formula mass	Parent ion (m/z) $(M-H)^-$	Daughter ions	Cone voltage (V)	Collision energy (eV)	Ionisation mode
Fructose	180	178.97	89.09	18	16	ES-
Sucrose	342	341.03	89.08	32	22	ES-
Galactose	180	178.97	89.09	18	16	ES-
Glucose	180	178.97	59.08	18	16	ES-
Maltose	342	341.03	161.05	12	8	ES-
Fucose	164	162.97	89.06	18	6	ES-
Rhamnose	164	162.97	103.06	18	6	ES-
Xylose	150	148.90	89.09	18	8	ES-
Arabinose	150	148.90	89.08	18	8	ES-
Mannose	180	178.97	119.03	20	8	ES-
Sorbitol	182	180.97	89.05	26	14	ES-
Inositol	180	178.97	161.11	28	8	ES-
Lactose	342	341.03	161.05	12	8	ES-
Ribose	150	148.90	89.09	18	8	ES-
Trehalose	342	341.03	89.08	32	22	ES-

ly Mass Lynx 2010. The mobile phase comprised solvent A, namely acetonitrile:methanol:ethyl acetate (53:7:40, v/v) and solvent B, namely methanol. For isocratic elution, the ratio of A:B was 95:5 and a flow rate of 0.2 mL min^{-1} was maintained for 6 min, with photodiode array detector (PDA) scanning from 200 nm to 650 nm. Individual carotenoids were identified on the basis of their spectral characteristics, retention times, and relative elution order compared to those of the standards.

Statistical analysis

Pearson correlation coefficients (r) between the individual variables and temperature were calculated using Microsoft Excel (Microsoft Office 2010, Redmond, Washington, USA). Error bars were used to understand the extent of variability within the group.

Results and discussion

Total carotenoids and temperature

Total carotenoids are one of the major constituents of fruit biochemical parameters and antioxidant activity since it is synthesised during ripening of fruits. Therefore, the content of total carotenoids is an indicator of proper ripening and quality of fruits. In our study cultivars differed significantly for total carotenoids (Figure 2a) and the cultivar Nendran recorded highest total carotenoid which was more than the reported value for cultivar Red banana (Arora *et al*., 2008). Lower carotenoids were observed in cultivars Robusta and GN. With respect to their relationship with temperature it was observed that total carotenoids were significantly and negatively correlated to temperature in all the cultivars: 'GN' (r = -0.817), 'Robusta' (r = -0.806), 'Shrimanti' (r = -0.877), 'TC' (r = -0.955), and 'Nendran' (r = -0.787). Increase in temperature during the fruit growth period decreased the total carotenoids in all the cultivars with stronger negative correlation in 'TC'. However, regression analysis between total carotenoids and temperature indicated that greater reduction in carotenoids per degree rise in temperature was observed in 'Nendran' ($y = -0.664x + 27.99$; $R^2 = 0.653$) and 'TC' ($y = -0.298x + 12.62$; $R^2 = 0.949$). Lesser reduction was observed in 'Shrimanti' ($y = -0.199x + 8.605$; $R^2 = 0.775$), followed by 'GN' ($y = -0.197x + 8.165$; $R^2 = 0.673$) and 'Robusta' ($y = -0.113x + 5.077$; $R^2 = 0.677$). Results indicate that 'Nendran' is more susceptible in terms of carotenoids to high temperature when compared to 'GN' and 'Robusta', which were low in total carotenoids. Optimum (29.1 °C) temperature is required for maximum total carotenoid content development, and above 30 °C the carotenoid content in all the cultivars is reduced. Higher temperatures are known to affect the synthesis of carotenoids, especially lycopene, in tomato (Shivashankara *et al*., 2015). Meredith and Young (1971), working with 'Red blush' grapefruit and 'Ruby' blood sweet orange, indicated that low day/night temperatures (16/5 °C) are required for carotenoid formation, but higher day/night temperatures (35/30 °C) were necessary for lycopene formation whereas more than 35 °C also inhibited lycopene formation. This may be due to inhibition of carotenoid biosynthesis enzymes at higher temperatures. In addition to temperature, carotenoid content is also influenced by the cultivar, stage of maturity, and locality (Ekesa *et al*., 2012). In terms of total carotenoids, the best month for harvest was February in states of Maharash-

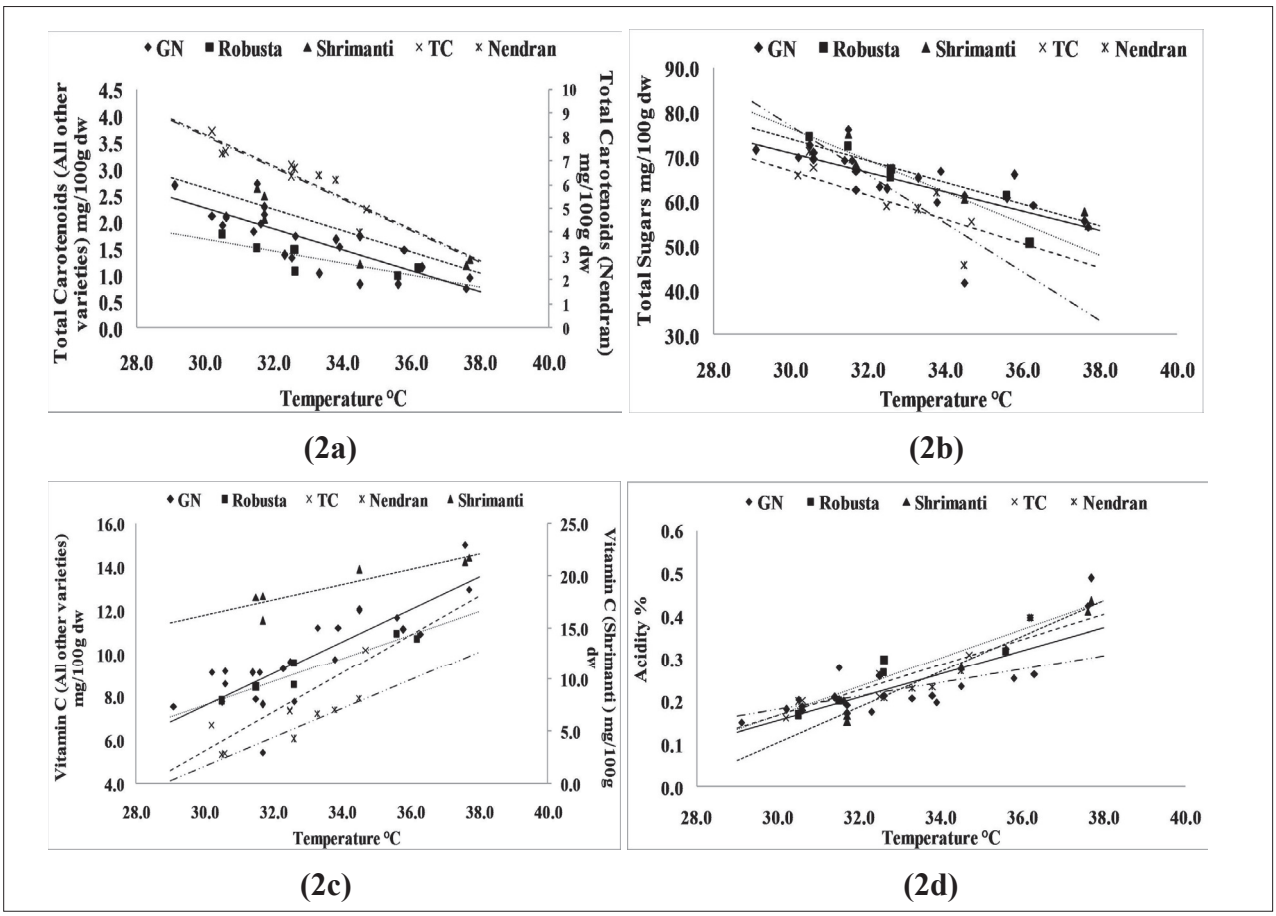

Figure 2. Relationship between different biochemical parameters with temperature in different cultivars of Banana across regions; (a) Total carotenoids, (b) Total sugars, (c) Vitamin C, and (d) Acidity.

Table 3. Carotenoid pigments in different cultivars of Banana grown at various regions.

Regions	Varieties	α-Cryptoxanthin	Auroxanthin	Mutatoxanthin	Luteoxanthin	β-Carotene	α-Carotene	Phytoene
Gujarat	Grand Naine	3,318.0±17.5	4.7±0.0	86.1±0.7	218.4±1.7	6,153.0±22.3	58.7±0.5	919.1±4.5
	Robusta	3,413.9±15.6	4.2±0.0	114.8±0.5	230.5±1.3	8641.7±0.0	117.7±0.9	993.3±2.6
Maharashtra	Grand Naine	2,219.6±42.7	61.3±0.9	279.7±1.5	489.9±4.0	11,669.2±43.0	175.8±1.7	833.4±7.4
	Shrimanti	2,106.2±0.76	76.7±2.2	214.6±2.4	484.7±1.3	7,952.7±105.4	163.1±3.4	1,027.0±3.4
Andhra Pradesh	Grand Naine	4,031.3±29.1	14.1±0.3	91.9±0.7	276.5±1.7	4,397.1±13.3	62.2±1.1	1,247.1±0.5
	TellaChekkerakeli	1,109.5±4.38	27.6±1.3	164.5±0.3	209.3±8.2	25,632.6±170.4	452.5±5.1	6,62.5±2.8
Kerala	Grand Naine	3,283.6±60.8	49.8±0.7	142.4±0.7	375.0±26.8	6,088.0±32.4	59.5±0.7	1,107.5±6.0
	Nendran	5,399.8±26.5	593.1±8.5	709.5±3.6	1,602.2±43.0	56,832.0±308.6	456.6±7.8	657.1±12.2
Mean		**3,110.3±37.2**	**103.9±1.3**	**225.4±1.3**	**485.8±11.0**	**15,920.8±86.9**	**193.3±2.6**	**930.9±4.2**

All values are expressed in μg kg^{-1} DW.

Table 4. Fructose, glucose and sucrose content in Banana cultivars grown in various regions and harvested at different months.

Regions	Month of harvest																	
	2013 June			2013 October			2014 February			2014 June			2014 October			2015 February		
	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose	Fructose	Glucose	Sucrose
Gujarat-GN	25.4±0.89	37.8±0.19	48.4±1.50	46.3±6.7	49.7 ±0.8	65.1±3.3	25.0±3.3	42.2±1.4	74.2±1.1	26.6±1.6	33.0±6.1	48.9±5.3	31.5±1.7	31.9±2.8	54.3±4.5	40.0±9.3	39.2±5.2	62.4±6.5
Maharashtra -GN	43.4±1.86	31.7±0.10	57.3±0.96	53.5±1.4	53.2±0.8	62.3±6.8	42.8±3.3	49.5±3.0	52.8±5.4	33.5±0.8	36.7±2.3	51.3±3.8	36.2±2.5	43.6±0.9	78.2±1.1	38.7±0.9	39.6±1.0	60.8±0.2
Andhra Pradesh-GN	35.0±2.41	36.5±0.07	42.6±0.60	34.1±1.5	42.7±0.8	57.3±0.6	46.8±0.3	39.8±3.1	55.0±10.6	43.2±0.0	45.9±1.1	51.3±2.1	30.2±0.8	25.3±1.5	57.5±2.6	47.2±0.0	40.0±1.4	59.9±2.1
Kerala-GN				42.6±1.8	46.5±0.8	50.3±1.3	31.7±0.4	26.7±3.0	61.0±2.9	42.5±5.4	39.9±5.2	52.6±4.2	30.7±1.2	42.7±0.5	97.8±14.4	43.9±0.7	47.2±3.7	55.2±0.9
Gujarat-Robusta	34.1±0.74	48.6±0.23	63.6±0.79	56.2±7.8	57.0±0.8	66.6±2.7	32.4±2.0	44.3±0.3	66.6±3.0	29.4±0.3	38.2±3.5	43.0±0.8	34.6±0.2	37.7±0.4	63.7±0.6	40.8±2.3	34.4±0.5	53.1±4.3
Maharashtra-Shrimanti	33.5±3.32	39.3±0.04	52.4±1.91	47.6±5.5	48.6±0.7	51.6±0.8	40.4±0.7	42.7±3.5	86.6±0.5	35.9±9.5	40.1±6.2	66.7±5.7	27.8±1.5	42.9±5.4	71.7±4.3	47.5±1.8	47.5±1.9	65.0±0.3
Andhra Pradesh-TC				48.5±1.2	44.1±0.8	62.9±2.2	54.4±3.5	45.0±5.3	74.7±6.1	46.4±1.5	39.6±1.5	70.7±9.1	39.8±3.1	36.0±0.0	84.4±6.4	55.6±4.7	51.9±5.6	66.1±2.2
Kerala-Nendran				76.8±1.0	104.9±0.6	10.5±0.8	71.1±6.1	100.1±9.9	20.3±0.2	74.3±3.1	100.4±6.7	13.2±0.2	68.0±2.4	103.3±8.4	19.3±1.2	71.3±0.6	102.1±5.0	19.5±1.3

All values are expressed in g kg^{-1} FW.

tra and Andhra Pradesh and October in Gujarat and Kerala, indicating the varietal variations in temperature response for carotenoid accumulation. June harvested fruits showed lower quality in terms of carotenoids in all the regions. Therefore, for producing good quality fruits planting date should be planned in such a way that the harvest will be in February or October. High temperature not only leads to the degradation of lycopene in tomato fruits (Demiray *et al*., 2013) but also reduced synthesis itself (Helyes *et al*., 2007). Temperatures of more than 30 °C lead to inhibition of lycopene synthesis in normal red cultivars of tomato and synthesis is restored when temperature drops below 30 °C (Garcia and Barrett, 2006).

Carotenoids profile

Seven carotenoids, namely cryptoxanthin, auroxanthin, mutatoxanthin, luteoxanthin, *β*-carotene, *α*-carotene, and phytoene, were identified in all the cultivars studied, and the major pigments were *β*-carotene and cryptoxanthin. 'Nendran' was the richest source of *β*-carotene and cryptoxanthin, whereas 'GN' and 'TC' recorded the lowest levels of carotenoids (Table 3). Germplasm screening of 10 Indian banana cultivars showed that 'Nendran' (3,011.94 µg 100 g^{-1} dry weight) and 'Rasthali' (105.35 µg 100 g^{-1} dry weight) contained the highest and lowest amounts of *β*-carotene, respectively in ripe fruit-pulp. A positive correlation was observed between the expression of *MaPSY1* and *β*-carotene accumulation in the ripe fruit-peel and pulp of 'Nendran'. Phytoene synthase (*PSY*) regulates carotenoid metabolic flux in the downstream enzymatic steps for the biosynthesis of lycopene, *α*-carotene and *β*-carotene (Fu *et al*., 2013). Some of the carotenoids reported in banana fruit are *α*-carotene, *β*-carotene, lutein, and zeaxanthin (Ekesa *et al*., 2012). All-trans-lutein, all-trans-*β*-carotene and all-trans-*α*-carotene were the major carotenes in cultivars Prata and Nanicao (Facundo *et al*., 2015). Red banana was found to be the rich source of carotenoids in banana (Arora *et al*., 2008) with a concentration of 4 µg g^{-1} dry weight and *β*-carotene with 1.17 µg g^{-1} dry weight. However, they have not analysed 'Nendran' which recorded 5.6 µg g^{-1} dry weight in our study indicating that this is one of the rich sources of *β*-carotene in banana. In tomatoes high temperature (35 °C) can inhibit the accumulation of lycopene by stimulating the conversion of lycopene into *β*-carotene (Hamauzu *et al*., 1998). Temperatures below 12 °C and above 32 °C strongly inhibit and completely block lycopene biosynthesis, respectively (Dumas *et al*., 2003). The banana peel ripened at high temperature (35 °C) had a significantly higher carotenoid content compared to those at around 20 °C. High temperature during ripening up-regulated the transcript levels of genes involved in the *α*- and *β*-carotene biosynthesis pathways and the activities of their encoded enzymes (Fu *et al*., 2019). High fruit temperatures can destroy lycopene and slow lycopene synthesis by converting to ζ-carotene through the enzyme lycopene *β*-cyclase whereas fruit shaded by plant foliage has the best color development (Robertson *et al*., 1995).

Total sugars

In the present study, total sugar content was higher at low temperatures and followed a similar trend as that of total carotenoids. In 'GN', the highest content was recorded at the temperature of 29.1 °C and in 'Robusta' at the temperature of 30.5 °C (Figure 2b). The content of total sugars was significantly and negatively correlated to temperature in all cultivars: 'GN' (r = -0.689), 'Robusta' (r = -0.926), 'Shrimanti' (r = -0.908), 'TC' (r = -0.905), and 'Nendran' (r = -0.840). However, regression analysis between the total sugars and temperature indicated that greater reduction in sugars per degree elevation in temperature was observed in 'Nendran' ($y = -5.468x + 240.9$; $R^2 = 0.711$) and 'Robusta' ($y = -3.575x + 183.7$; $R^2 = 0.890$). Lesser reduction was observed in 'TC' ($y = -2.742x + 149.1$; $R^2 = 0.907$), followed by 'GN' ($y = -2.177x + 136.2$; $R^2 = 0.498$) and 'Shrimanti' ($y = -0.199x + 8.605$; $R^2 = 0.775$). A similar study, where banana was grown in different times of the year, clearly indicated that the high temperature during fruit growth period was reported to reduce the total dry matter, total soluble solids, total sugar and also glucose and fructose content in banana fruits (Bugaud *et al*., 2009). This was found to be related to lower starch synthesis in fruits during their growth under higher temperature conditions. Apart from growth temperatures, low temperature during storage also reduced total sugars due to lower starch metabolism by the reduced *α*-amylase activity. Composition of starch was also modified due to low temperature storage (Kaur *et al*., 2017). The results of these studies indicated that fruit sugar content is modified by the growth as well as ripening temperatures. In both cases, the reduction in sugar content was mostly due to modified starch content, its composition, and the rate of metabolism. Lower sugars found in all varieties during the high growth temperature month of June indicated the need for planning the planting time to get the good quality fruits which is observed in February and October in our study.

Sugar profiling

Sugars are an important component of plant responses to high temperatures and to other forms of abiotic stresses. Changes in temperature affect fruit maturation and growth by influencing the enzymes acid invertase and sucrose synthase and also the sugar transport into the fruit. Fukuoka *et al*. (2009) reported that glucose and fructose concentration in the fruit were reduced under elevated temperatures due to the increased rate of respiration. High temperature during fruit growth period reduced the total soluble solids in banana; however sucrose, glucose and fructose content did not show significant differences between the hot rainy days, cold dry conditions and intermediate conditions during the fruit growth period (Bugaud *et al*., 2009). We identified a total of fifteen sugars in the fruits with the help of LC-MS/MS. Three major sugars, namely sucrose, fructose, and glucose, were present in all the cultivars, whereas the rest, namely galactose, xylose, mannose, ribose, lactose, maltose, arabinose, sorbitol, inositol, trehalose, fucose, and rhamnose, were variously distributed among the cultivars. Sucrose was the highest sugar in 'GN', 'Shrimanti', 'Robusta', and 'TC', whereas in 'Nendran', glucose was the highest, followed by fructose (Table 4). The levels of glucose, fructose, and sucrose were maximum at lower temperatures in all the locations, a finding consistent with that of Utsunomiya (1992), who reported that sugar content of the juice of purple passion fruit was highest when temperatures during the growing stage were low and that, among sugars, the accumulation of sucrose was more than that of any other sugars at low temperatures. Regression lines of total carotenoids and sugars with temperature indicate the cultivar differences in temperature response. 'Nendran' showed greater reduction in both sugar and carotenoids for the elevated temperature. 'Robusta' and 'GN' exhibited lower response to the temperature. Therefore these varieties can be cultivated in different regions without much effect on the fruit biochemical and antioxidant parameters when compared to 'Nendran'.

The three main sugars of banana fruit are fructose, glucose and sucrose. In both the peel and pulp of bananas fruits ripened at 20 and 30 °C, sucrose is the predominant sugar in the pre and at climacteric stages; in the post-climacteric period, glucose and fructose are the predominate sugars (Yang *et al*., 2009). Effect of ripening temperatures on biosynthesis of different sugars has been studied by many workers; however, our study was mainly to indicate the effect of higher temperature during fruit growth period on various sugars. The ripening temperature was constant for all the samples. Therefore the variation in sugar profile was less but the reduction in total sugars was noticed with increase in temperature, which was mainly due to reduced accumulation of starch at the time of harvest.

Vitamin C (Ascorbic acid)

Banana fruits are not known to be the good source of vitamin C. Ascorbic acid content of banana varieties ranged between 1.52–5.35 mg 100 g^{-1} whereas highest was recorded in red banana (Siji and Nandini, 2017). Significant variability among the cultivars for vitamin C content was also observed in this study with cv. Shrimanti exhibiting a fairly good quantity (22 mg 100 g^{-1} dw) (Figure 2c). Hernandez *et al*. (2018) reported that vitamin C content was increased when the high temperature stress was imposed during flowering and fruit set stages, indicating that its plant metabolism adapted to high temperature. Dumas *et al*. (2003) reported that high temperature enhances ascorbic acid accumulation in tomato fruit. Similarly, our results revealed that the highest levels of vitamin C were recorded at higher temperatures: in 'GN' in Gujarat, Andhra Pradesh, and Kerala, and in 'Shrimanti' in Maharashtra (Figure 2c). A similar effect of temperature on vitamin C content was reported in tomato fruits (Dewanto *et al*., 2002). However, an increase in temperature by 2 °C from 33.5 °C did not show significant effect on vitamin C content in a few tomato genotypes (Shivashankara *et al*., 2015). In the present study, fruits harvested in June were richer in vitamin C content in all the cultivars in Gujarat, Maharashtra, and Andhra Pradesh regions, whereas in Kerala, February proved better for 'GN' and 'Nendran' cultivars. Vitamin C content was significantly and positively correlated to temperature in all cultivars: 'GN' (r = 0.819), 'Shrimanti' (r = 0.912), 'Robusta' (r = 0.847), 'TC' (r = 0.902), and 'Nendran' (r = 0.941). The increase was more closely related in 'Nendran'. Regression lines indicated that the temperature effect on vitamin C was more in 'TC' (y = 0.895x - 21.37; R^2 = 0.840) and 'GN' (y = 0.748x - 14.89; R^2 = 0.688). 'Shrimanti' (y = 0.725x - 5.497; R^2 = 0.815), 'Robusta' (y = 0.544x - 8.746; R^2 = 0.916), and 'Nendran' (y = 0.664x - 15.13; R^2 = 0.929) were less affected. Cultivars experienced the maximum temperature up to 38 °C during the fruit growth period and showed an increase in the vitamin C content; beyond this temperature vitamin C content may decrease. High temperature exposure reduced vitamin C content significantly in kiwifruits (Richardson *et al*., 2004). Lee and Kader (2000) reported higher vitamin C content in tomato grown under low temperature than in that grown under high temperature.

Titratable acidity

Acidity was also significantly and positively correlated to temperature in all cultivars: 'GN' (r=0.809), 'Shrimanti' (r=0.934), 'Robusta' (r=0.985), 'TC' (r=0.929), and 'Nendran' (r=0.861). With increase in temperature, acidity increased in all the cultivars and the effect was more on 'Shrimanti' and least effect was on 'Nendran'. Increase in titratable acidity with increase in temperature was also reported in tomato by Khanal (2012). However, in banana higher acidity was reported when grown under cool dry conditions when compared to hot rainy conditions (Bugaud *et al*., 2009). The different result observed in our study was due to the higher growth temperatures compared to the study by Bugaud *et al*. (2009) where the temperature during hot rainy conditions ranged from 24 to 28 °C only. The acidity was higher in 'GN', 'Robusta' and 'Shrimanti' compared to 'Nendran' and 'TC'. Fruits of all the cultivars harvested in June showed the highest acidity (Figure 2d). High titratable acidity is responsible for the stability of ascorbic acid in fruits (Toor and Savage, 2006). In our study, higher acidity showed a relatively stable ascorbic acid content during high temperature. Regression lines indicated that the temperature effect on acidity was more in 'Shrimanti' (y=0.041x-1.137; R^2=0.971) and 'Robusta' (y=0.033x-0.850; R^2=0.87), whereas cultivars 'TC' (y=0.029x-0.726; R^2=0.860), 'GN' (y=0.027x-0.665; R^2=0.654), and 'Nendran' (y=0.015x-0.295; R^2=0.753) were less affected.

Total phenols and total flavonoids

Total phenols showed a similar pattern as that of acidity: all the cultivars recorded higher levels of total phenols at higher temperatures, and the highest levels were observed in 'Robusta', 'Shrimanti', 'TC', and 'GN' in Kerala (Figure 3a). Total phenols reflect the antioxidant capacity of fruits and were significantly and positively correlated to temperature in all cultivars: 'GN' (r = 0.816), 'Shrimanti' (r = 0.813), 'Robusta' (r = 0.965), 'TC' (r = 0.977), and 'Nendran' (r = 0.903). Wang and Zheng (2001) also observed increased concentrations of phenolics in growing fruits that had been exposed to high temperatures. An accumulation of phenolics at higher temperatures during growth is reported in other crops also, and is probably a response to stress (Wang, 2006). Total flavonoids content also increased with increase in temperature in all the cultivars and was highest in 'GN' in Gujarat and Maharashtra at higher temperatures, whereas the same cultivar also recorded the lowest levels of phenolics in Andhra Pradesh and Kerala (Figure 3b). Total flavonoids were significantly and positively correlated to temperature in all cultivars: 'GN' (r = 0.900), 'Shrimanti' (r = 0.887), 'Robusta' (r = 0.928), 'TC' (r = 0.867), and 'Nendran' (r = 0.931). Regression lines clearly indicated that the temperature influence on total phenols and flavonoids was more in 'Nendran' (y = 6.35x - 156.4; R^2 = 0.819); (y = 1.696x - 48.12; R^2 = 0.869), 'TC' (y = 4.724x - 99.56; R^2 = 0.986); (y = 1.876x - 53.76; R^2 = 0.864), and 'Robusta' (y = 5.893x - 141.1; R^2 = 0.796); (y = 1.650x - 47.10; R^2 = 0.932), and was less in 'Shrimanti' (y = 2.864x - 37.76; R^2 = 0.789); (y = 1.307x - 35.76; R^2 = 0.885) and 'GN' (y = 4.203x - 87.12; R^2 = 0.746); (y = 1.143x - 29.21; R^2 = 0.686) respectively. Wang and Zheng (2001) found that high temperatures increased the content of flavonols significantly in strawberry. Higher temperatures increase the rate of biosynthesis of phenolics and flavonoid content in tomato as these factors increase the enzymatic activities of phenyl propanoid pathway and thereby enhance the synthesis of phenolic compounds in plants (Toor and Savage, 2006). Miller and Rice Evans (1997) concluded that phenolic substances have a protective effect on ascorbic acid. Therefore, the presence of phenolics and flavonoids helps to maintain the level of ascorbic acid content in tomato fruit. This might be one of the reasons for higher vitamin C at elevated temperatures in all the cultivars used in our study. Fruits harvested in June were found to have higher total phenols and flavonoids in all the cultivars in Gujarat, Maharashtra, and Andhra Pradesh,

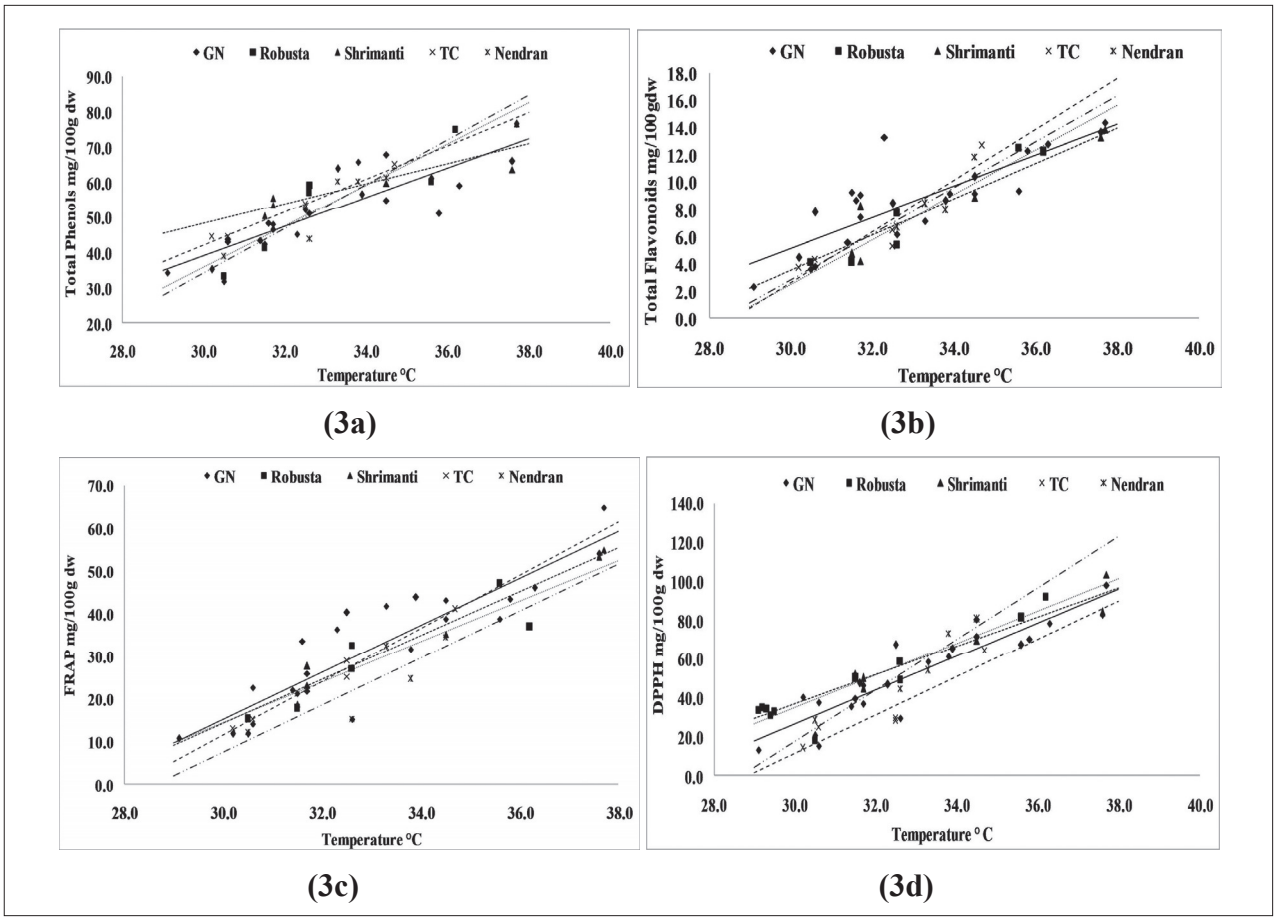

Figure 3. Relationship between different biochemical parameters with temperature in different cultivars of Banana across regions; (a) Total phenols, (b) Total flavonoids, (c) FRAP, and (d) DPPH.

whereas in Kerala, February was the best for 'GN' and 'Nendran', indicating the regional influence on total phenolics in addition to the cultivar differences. Increased day and night temperatures (30 °C/25 °C) reduced the total phenolic content in apple (Pan and Shu, 2007). Total phenolics were higher in fruits which were grown under higher temperature conditions as seen in the fruits harvested during June when compared to February and October harvested fruits in all the cultivars.

Antioxidant activity

Bananas should be considered as a good source of natural antioxidants for foods (Someya *et al*., 2002). Antioxidant activity expressed in terms of radical-scavenging activity usually varies as fruits ripen because of the differences in concentrations of antioxidant compounds (Raffo *et al*., 2002). Fatemeh *et al*. (2012) informed that cultivars 'Cavendish' and 'Dream' from Malaysia, showed average radical scavenging capacity in both peel and pulp of banana fruits. Shian and Abdullah (2012), also from Malaysia, found percent removal of DPPH radicals (colour) ranging from 3.2 to 63.1% in the ripe pulp of 'Berangan', 'Mas' and 'Raja' bananas. In the present study too, antioxidant activity varied significantly in all cultivars at different temperatures. As the temperature increased, so did FRAP in all cultivars, and the highest FRAP was recorded in 'GN' at all the locations (Figure 3c). FRAP were significantly and positively correlated to temperature in all the cultivars: 'GN' ($r = 0.890$), 'Shrimanti' ($r = 0.879$), 'Robusta' ($r = 0.981$), 'TC' ($r = 0.981$), and 'Nendran' ($r = 0.844$). The same was true of DPPH as well. 'Robusta', 'Shrimanti', and 'Nendran' showed higher DPPH at all the locations whereas 'TC' and 'GN' recorded low levels (Figure 3d). DPPH was significantly and positively correlated to temperature in all the cultivars: 'GN' ($r = 0.902$), 'Shrimanti' ($r = 0.941$), 'Robusta' ($r = 0.958$), 'TC' ($r = 0.896$), and 'Nendran' ($r = 0.905$). Regression lines indicated that the temperature effect on FRAP was more in 'TC' ($y = 6.251x - 176.0$; $R^2 = 0.986$) and 'GN' ($y = 5.520x - 150.4$; $R^2 = 0.810$), whereas 'Nendran' ($y = 5.501x - 157.5$; $R^2 = 0.718$), 'Shrimanti' ($y = 5.142x - 139.9$; $R^2 = 0.967$), and 'Robusta' ($y = 4.784x - 129.2$; $R^2 = 0.810$) were less affected. Regression lines indicated that the temperature effect on DPPH was more in 'Nendran' ($y = 13.24x - 380.3$; $R^2 = 0.904$) and 'TC' ($y = 9.813x - 283.2$; $R^2 = 0.853$) while cultivars 'GN' ($y = 8.726x - 235.7$; $R^2 = 0.830$), 'Robusta' ($y = 8.254x - 212.7$; $R^2 = 0.872$), and 'Shrimanti' ($y = 7.505x - 188.8$; $R^2 = 0.920$) were less affected. Higher FRAP and DPPH were probably due to the higher levels of phenolics and flavonoids (Kondo *et al*., 2005). Kondo *et al*. (2004) reported that the radical-scavenging activity of DPPH was associated with the content of total phenolics in plant tissues. Fruits harvested in June from all the regions recorded higher total antioxidant capacity and higher radical-scavenging abilities irrespective of cultivars. Regression lines indicated that the influence of temperature on DPPH, total phenols and flavonoids was more in 'Nendran', and 'GN' and 'Shrimanti' showed less effect. Whereas, for acidity, 'Shrimanti' was affected more by the temperature, and the least effect was in 'Nendran'. Higher acidity and total phenols in the ripe fruits indicate the negative effect of temperature on fruit biochemical and antioxidant parameters due to impairment in the ripening process.

Conclusion

The fruit biochemical and antioxidant parameters were affected by the growing temperatures. Antioxidant capacity, radical scavenging ability, phenols, flavonoids, vitamin C content and acidity of all the five cultivars of banana were higher in fruits harvested in June where the fruits were exposed to higher growth temperatures in all the regions. On the other hand, total carotenoids and total sugars decreased under high temperature conditions. Growth temperature differences altered the total sugars and carotenoids more compared to other parameters, indicating the sensitivity of these parameters. Study indicated the best harvest time for maximising the fruit biochemical and antioxidant parameters mainly in terms of sugars and carotenoids and also the less sensitive cultivar to temperature. Bunches harvested in February and October exhibited better quality than those harvested in June. This will help in planning the planting time to coincide with the low temperatures during the fruit growth period which varies with region and cultivar.

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