

Article

Climate-Induced Heat Stress Responses on Indigenous Varieties and Elite Hybrids of Mango (*Mangifera indica* L.)

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Abstract

Mango is highly sensitive to heat stress, which directly affects the yield and quality. The extreme heat waves of 2024, with temperatures reaching 41–47 °C over 25 days, caused significant impacts on sensitive cultivars. The impact of heat waves on ten commercial cultivars from subtropical regions viz., ‘Dashehari’, ‘Langra’, ‘Chausa’, ‘Bombay Green’, ‘Himsagar’, ‘Amrapali’, ‘Mallika’, ‘Sharda Bhog’, ‘Kesar’, and ‘Rataul’, and thirteen selected elite hybrids H-4208, H-3680, H-4505, H-3833, H-4504, H-1739, H-3623, H-1084, H-4264, HS-01, H-949, H-4065, and H-2805, is reported. The predominant effects that were observed include the following: burning symptoms or blackened tips, surrounded by a yellow halo, with premature ripening in affected parts and, in severe cases, tissue mummification. Among commercial cultivars, viz., ‘Amrapali’ (25%), ‘Mallika’ (30%), ‘Langra’ (30%), ‘Dashehari’ (50%), and ‘Himsagar’ and ‘Bombay Green’ had severe impacts, with ~80% of fruits being affected, followed by ‘Sharda Bhog’. In contrast, mid-maturing cultivars like ‘Kesar’, ‘Rataul’, and late-maturing elite hybrids, which were immature during the stress period, showed no symptoms, indicating they are tolerant. Biochemical analyses revealed significantly elevated total soluble solids (TSS > 25 °B) in affected areas of sensitive genotypes compared to non-affected tissues and tolerant genotypes. Aroma profiling indicated variations in compounds such as caryophyllene and humulene between affected and unaffected parts. The study envisages that the phenological maturity scales are indicators for the selection of climate-resilient mango varieties/hybrids and shows potential for future breeding programs.

Keywords: mango; climate resilience; heat wave; India; phenology; phenol; GC-MS



Academic Editors: Xiaoyong Xu, Lijuan Jiang and Lun Wang

Received: 22 April 2025

Revised: 9 June 2025

Accepted: 10 June 2025

Published: 26 July 2025

Citation: Kushwaha, A.K.; Thukkaram, D.; Rastogi, D.; Singh, N.S.; Beer, K.; Debnath, P.; Dayal, V.; Yadav, A.; Das, S.S.; Bajpai, A.; et al. Climate-Induced Heat Stress Responses on Indigenous Varieties and Elite Hybrids of Mango (*Mangifera indica* L.). *Agriculture* **2025**, *15*, 1619. <https://doi.org/10.3390/agriculture15151619>

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1. Introduction

Climate change significantly impacts fruit production systems by altering temperature patterns, precipitation levels, and the frequency of extreme weather events, which collectively influence flowering, fruit set, and yield quality [1,2]. Elevated temperatures can disrupt phenological stages, such as bud break and pollination, while increased CO₂ levels may accelerate growth but compromise nutritional quality. Heat stress poses a major challenge to fruit production systems by disrupting physiological and developmental processes in fruit-bearing plants. Prolonged heat exposure can also cause sunburn, dehydration, and

abnormal ripening, affecting marketability and post-harvest shelf life [3]. Sensitive crops like mango, grape, and citrus are particularly vulnerable, with significant economic losses due to poor physiological efficiency [4]. Adaptive strategies such as heat-tolerant cultivars and microclimate management are increasingly important for sustainable fruit production.

Mango (*Mangifera indica* L.) is cultivated across approximately 6 million hectares, predominantly in tropical and subtropical regions of the world [5,6]. Despite its wide adaptation, the cultivation is increasingly challenged by a range of biotic and abiotic stressors associated with large-scale production systems [7,8]. While genotypic variability imparts differential stress tolerance among cultivars, monocropping with commercial cultivars has heightened the crop's vulnerability. Among abiotic factors, temperature extremes, water scarcity, nutrient imbalances, and heavy metal accumulation significantly disrupt physiological, reproductive, and developmental processes, thereby adversely affecting both yield and fruit quality in mango [9].

In heat-sensitive mango cultivars such as 'Dashehari', exposure to elevated temperatures results in internal tissue breakdown, while in 'Alphonso', it manifests as spongy tissue formation; both render the fruits unfit for consumption [10,11]. Heat stress also disrupts key physiological processes, including photosynthesis and respiration [12], and adversely affects critical developmental stages such as fruit set, fruit enlargement, and ripening. When compounded by water scarcity, these effects can lead to fruit cracking [13]. Elevated temperatures accelerate the ripening process through increased ethylene production and heightened respiration rates, which in turn alter the biosynthesis of flavor and pigment-related compounds, thereby impacting the fruit's taste, aroma, and visual appeal [14,15]. Even fruits that develop without visible defects often suffer reduced postharvest shelf life under such conditions [16]. Collectively, these effects contribute to diminished fruit quality and a significant decline in the economic value of mango production.

To cope with heat stress, plants employ a range of avoidance strategies, such as transpirational cooling, modifications in membrane lipid composition, and altered phenology. The tolerance mechanisms involve ion transporters, heat shock proteins, and the accumulation of osmoprotectants [17–23]. Incorporating heat-tolerant genotypes into breeding programs holds promise for developing resilient cultivars. In subtropical regions, several mango genotypes display inherent avoidance and tolerance responses to heat stress; however, systematic screening under controlled heat stress conditions is not possible. For perennial species like mango, establishing uniform on-farm heat stress regimes poses significant challenges. Identifying natural heat-stress hotspots and capitalizing on sporadic extreme weather events offer practical opportunities for field-based evaluation and selection of heat-resilient genotypes.

Heat-induced changes in metabolite profiles have been widely documented across various fruit and vegetable crops, offering valuable insights into the molecular mechanisms underpinning tolerance to extreme heat stress [24–26]. Metabolites play a crucial role in maintaining cellular homeostasis under stress conditions by preserving membrane integrity, supporting metabolic function, and regulating protective and repair-related biosynthetic pathways [27,28]. Among these, phenolic compounds have emerged as key contributors to heat stress resilience. Phenolics confer protection by scavenging reactive oxygen species (ROS), enhancing the activity of antioxidant enzymes, stabilizing cellular membranes, and activating stress-responsive signaling pathways [29–32]. These multifaceted roles position phenolics as central components in the adaptive response to thermal stress in plants.

In response to the Indian Meteorological Department's advisory on extreme heat events during the summer of 2024, a focused assessment was undertaken to evaluate the impact of heat stress on a diverse set of mango genotypes, including popular cultivars, released hybrids, and elite hybrids under development. To facilitate systematic observation,

representative trees were marked across locations experiencing elevated temperatures. This study seeks to deepen understanding of genotype-specific responses to climate-induced heat stress, particularly in relation to fruit maturity groups, and to identify potential physiological and biochemical markers associated with heat tolerance. The findings aim to contribute to the identification and development of climate-resilient mango cultivars suited for future production challenges.

2. Materials and Methods

2.1. Site and Sampling

Field experimentation and sampling were carried out at ICAR-Central Institute for Sub-tropical Horticulture (ICAR-CISH), Lucknow, Uttar Pradesh, India (“26°30′ N, 80°30′ E”), which represents a typical subtropical climate. The varieties and hybrids used for the study were maintained in the field gene bank of the National Active Germplasm Site, ICAR-CISH, Lucknow, India. Three ripened fruits from each genotype, replicated thrice in the block, were taken for analysis. The plot of commercial varieties and hybrids was considered a randomized block design.

2.2. Meteorological and Phenology Data Recording

Meteorological data were collected from the institute’s meteorological observatory on temperature (minimum and maximum), sunshine hours, humidity, rainy days, and rainfall (mm). Data on different phenological stages were recorded from bud swelling to maturity by following the extended BBCH scale [33]. The two-year data, i.e., 2023 and 2024, were compared for days to maturity from full bloom. The stage of fruit of different genotypes at maximum temperature and THA during June was also taken into consideration to classify heat-avoiding genotypes. Under subtropical conditions in India, generally, flowering mango starts from February and it lasts till March end while the fruiting stage starts post-pollination, starting from March to April first week. The onset of physiological maturity for early varieties starts from mid-May, while for medium maturing varieties it is the second week of June to the first week of July, and late maturing varieties start maturing from Mid-July till August first week.

2.3. Total Heat Accumulation (THA)

Heat sum units (HSU) and total heat accumulation (THA) were calculated using the following formulas:

$$HSU = \frac{T_{max} + T_{min}}{2} - T_{base}$$

$$THA = \sum HSU$$

The base temperature for mango is 17.9 °C [34].

2.4. Varieties and Hybrids

Traditional cultivars viz., ‘Bombay Green’, ‘Himsagar’, ‘Dashehari’, ‘Sharda Bhog’, ‘Langra’, ‘Kesar’, ‘Rataul’ and hybrid varieties viz., ‘Mallika’ and ‘Amrapali’ along with elite hybrids viz., ‘H-4208’, ‘H-3680’, ‘H-4505’, ‘H-3833’, ‘H-4504’, ‘H-1739’, ‘H-3623’, ‘H-1084’, ‘H-4264’, ‘HS-01’, ‘H-949’, ‘H-4065’, and ‘H-2805’ were assessed for their tolerance to heat stress. These varieties and hybrids are categorized as early, mid, and late groups based on time of physiological maturity (Table S1). These hybrids were derived from the pedigree involving ‘Dashehari’, ‘Amrapali’, ‘Neelam’, ‘Tommy Atkins’, and ‘Eldon’ (Table S2).

2.5. Estimation of Percent Incidence of Sunburn Symptoms

Sunburn symptoms were considered as the predominant symptom of heat wave effect, and it was expressed in terms of Percent incidence, which was recorded on a tree basis and calculated using the following formula:

$$\text{Percent incidence} = \{(\text{No of affected fruits}) / \text{Total No of Fruits}\} \times 100$$

2.6. Biochemical Characterization

2.6.1. Assessment of Maturity Index

Maturity index is assessed in mango based on two traits, viz., TSS and firmness. Total soluble solids (TSS) of heat stress-affected vs. non-affected parts of the fruits were recorded from fresh samples using a hand refractometer in °Brix, and firmness was observed using a GXV Firmness Meter in n/ms.

2.6.2. Estimation of Total Acidity

Total acidity was measured from a fresh sample by the titration method where 2 g samples were dissolved in 20 mL of water and 5 mL of this was taken and 2–3 drop of phenolphthalein were added and titrated against 1 N NaOH and reading of used NaOH was recorded till the color of sample changed to pink.

2.6.3. Quantification of Phenolic Compounds Using High-Pressure Liquid Chromatography (HPLC)

Phenolic compounds quantification was performed using HPLC using the following protocol. Exactly 5 g sample from each fruit was dissolved in a mixture of methanol/water (80:20 *v/v*) to optimize the final concentration to 5–20 g/mL. Homogenization of samples was performed by vortexing, and finally, the samples were centrifuged, and the supernatant was filtered to discard particulate matter. Phosphate buffer of pH 3.05 was used as mobile phase A, while 75% acetonitrile with 25% water was considered as mobile phase B. Before running the sample, the HPLC system was well equilibrated with both mobile phases. Calibration of the system was performed by running a series of dilutions of standard polyphenolic compounds, viz., gallic acid, chlorogenic acid, catechin, epi-catechin, and p-coumaric acid, using the same solvent mixture used for homogenization of fruit samples. A calibration curve was plotted against the concentration of the standards, which was further utilized for the quantification of phenolic compounds. 20 µL of prepared samples were injected into the HPLC system, and identification of polyphenolic compounds was performed by comparing the retention time against standards.

2.6.4. Aroma Profiling

Aroma profiles of all the genotypes were assessed following the headspace-GC method. Samples from affected and non-affected fruit parts were taken into a headspace vial and air-locked, and the compounds from the library were detected by chromatography.

2.6.5. Volatile Organic Compound Profiling Using Gas Chromatography-Mass Spectrometry (GC-MS) Analysis

TMS derivatives of the sample extracts were prepared. Approximately 5 mg of the sample was suspended in 40 µL of the solution of methoxylamine hydrochloride in pyridine (20 mg/mL). The mixture was shaken for 2 h at 37 °C before adding 70 µL of the 2,2,2-trifluoro-N-methyl-N-trimethylsilylacetamide (MSFTA) for 30 min. The resulting derivatized mixture of metabolites was subjected to analysis on GC-MS, and data analysis was performed using standard procedures [35].

2.6.6. Statistical Analysis

The change in affected part vs. non-affected part was assessed by *t*-test, and GC-MS results were analyzed using R program version 4.3.1 to generate PCA, Scree plots, heatmaps, and Venn diagrams.

3. Results

3.1. Comparative Evaluation of Meteorological Parameters During 2023 and 2024

The year 2024 was marked as hotter, which is evident from the fact that the average maximum temperature during the months of May and June was 41.13 °C with a maximum temperature of 47 °C as compared to 38.17 °C and 43.5 °C, respectively, for the year 2023 (Figure 1). The same was the case with the average minimum temperature, which was 24.6 °C and 23.09 °C for the years 2023 and 2024, respectively (Figure 2b). Heat sum units (HSU), which is a function of daily temperature adjusted for the base temperature of every crop, which for mango is 17.9 °C. Total heat accumulation (THA) is the cumulative of HSU over a period. HSU decides the phenological stages, which range from flowering to ripening.

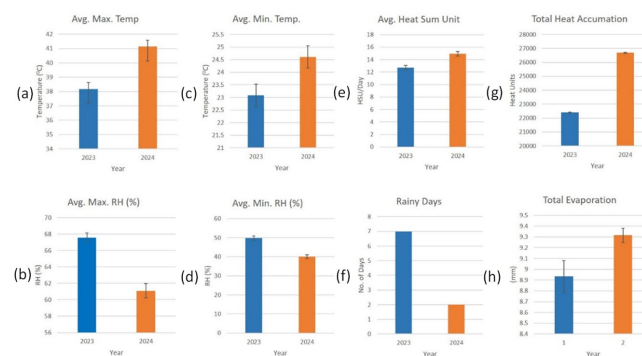


Figure 1. Comparison of different meteorological parameters ((a) mean maximum temperature, (b) mean minimum temperature, (c) mean total heat accumulation, (d) mean maximum relative humidity, (e) average heat summation units, (f) mean minimum relative humidity, (g) mean number of rainy days, and (h) mean total evaporation) observed during May–June month of the years; 2023 and 2024.

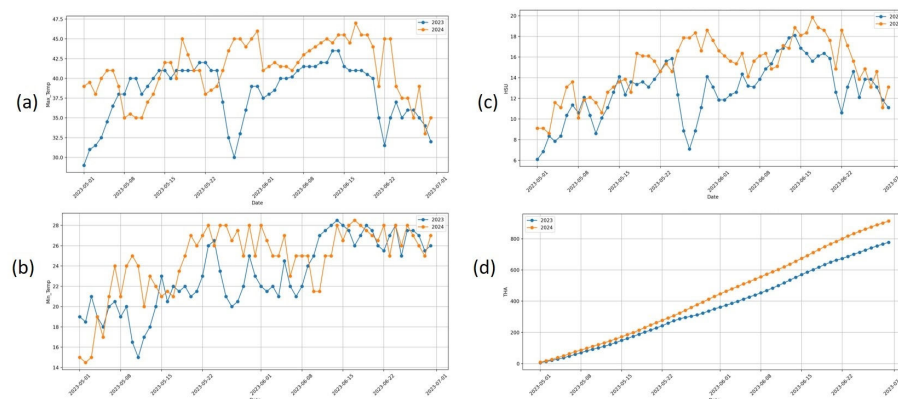


Figure 2. Trendline of (a) maximum and (b) minimum temperature observed, (c) heat unit/day, and (d) total heat accumulation observed during the May–June months of two consecutive years, 2023 and 2024.

HSU and THA during the fruit development phase, viz., May and June of the year 2024, were significantly higher (14.97/day and 22,395) than in the year 2023 (12.73/day and 26,684) (Figure 2a,b), indicating that crops in 2024 were exposed to heat stress during fruit development. Along with temperature, moisture conditions also differed, as these months in 2024 experienced a drier period, with only two rainy days compared to seven in 2023. The

average relative humidity during this period was 50.5% in 2024 and 58.68% in 2023, with higher evaporation in 2024 (9.3 mm) compared to 8.9 mm in 2023 (Figure 1).

3.2. Impact of Excessive Heat on the Phenology of Mango

For the flowering-related phenophases, viz., bud emergence (BBCH-510), bud swelling (BBCH-511), bud burst (BBCH-513), flower opening (BBCH-611), full bloom (BBCH-615), and fruit set (BBCH-701), the difference between the two years was significant for most genotypes, except for ‘Amrapali’, ‘H-3680’, ‘H-3833’, ‘H-4208’, ‘H-4504’, and ‘H-4509’, where only one phenophase showed a significant difference. This suggests that these genotypes buffer against seasonal differences in such magnitude. The other hybrids, as well as the commercial varieties, viz., ‘H-1739’, ‘H-3623’, ‘H-4065’, ‘H-4264’, ‘Himsagar’, ‘Dashehari’, ‘Langra’, ‘Chausa’, ‘Mallika’, ‘Kesar’, and ‘Rataul’, exhibited significant differences. During the second fortnight of June 2024, prominent differences were observed between early-maturing varieties, which had reached BBCH-809, and mid-late varieties, which were at BBCH-709. The varieties ‘Himsagar’, ‘Bombay Green’, ‘Dashehari’, and ‘Langra’ were fully mature and at the ripening stage (BBCH-809), while among elite hybrids, ‘H-2805’ (Dashehari × Eldon) was at the same stage. Fruits of the hybrid varieties ‘Amrapali’ and ‘Mallika’ were at full size with fully developed shoulders but were still unripened (BBCH-709). Other hybrids, viz., ‘H-4208’, ‘H-3680’, ‘H-4505’, ‘H-3833’, ‘H-4504’, ‘H-1739’, ‘H-3623’, ‘H-1084’, ‘H-4264’, ‘HS-01’, ‘H-949’, and ‘H-4065’, were also at the same stage.

3.3. Incidence of the Symptoms

Highest percent incidence of heat stress symptoms based on visual observation was recorded in ‘Bombay Green’ and ‘Himsagar’ (>80%) followed by ‘Dashehari’, ‘Langra’, ‘Sharda Bhog’ and ‘Mallika’ (40–55%) while ‘Rataul’, ‘Kesar’ had shown no impact of heat stress since no fruit with the necrotic symptom was observed (Figure 3a). The elite hybrids viz., ‘H-4208’, ‘H-3680’, ‘H-4505’, ‘H-3833’, ‘H-4504’, ‘H-1739’, ‘H-3623’, ‘H-1084’, ‘H-4264’, ‘HS-01’, ‘H-949’, ‘H-4065’ have shown no such symptoms although they were at the same phenological stage that of ‘Mallika’ and ‘Amrapali’. Assessment of parents of the hybrids revealed that one of the parents in all of these hybrids has shown symptoms, whereas the other parent, viz., ‘Tommy Atkins’ (TA) and ‘Eldon’, had no incidence of such symptoms during the maximum heat incidence period. During this period, these two genotypes were also at the same phenological stage as ‘Mallika’ and ‘Amrapali’. In addition, Arunika variety, which is a mid-late maturing variety, was severely affected by heat stress (although no blackening of the tip, but only discoloration and yellow halo prominent Figure 3a). It has been observed that all the early varieties were severely impacted because they were at the ripening stage when heat struck them (Figure 3b).

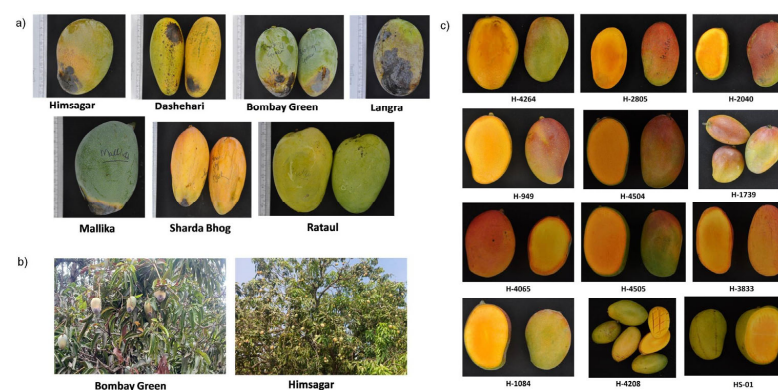


Figure 3. Damage symptoms observed on fruits due to excessive heat in (a) different cultivars, (b) tree view of incidence on sensitive cultivars (Bombay Green and Himsagar), (c) hybrids exhibited no symptoms.

3.4. TSS and Firmness in Affected vs. Non-Affected Tissue

The TSS in the affected part of the fruit was abnormally high, indicating the hastening of the ripening process by conversion of starch to sugar. In the affected part of the variety ‘Himsagar’, the mean TSS was significantly higher, 30 °Brix, as compared to the non-affected part, 19 °Brix; a similar pattern was the case in ‘Bombay Green’, where it was 25 and 15 °Brix, respectively (Figure 4a). In late maturing variety, i.e., ‘Mallika’, although the fruits were not mature but the affected part of the fruit showed a significantly higher TSS value of 24 °Brix. While in the non-impacted variety, the TSS ranged from 11 to 15 °Brix at the time of sampling. Similarly, the firmness was also impacted in stressed cultivars; the least mean firmness was observed in ‘Bombay Green’ (0.07 kg/cm²), followed by ‘Himsagar’ (0.12 kg/cm²) (Figure 4b). In case of Sharda Bhog, the lack of irrigation in the block led to immature shrinkage of fruits and apical burning, and hence, the firmness was not as low as observed in ‘Himsagar’ and ‘Bombay Green’. Heat stress impact on acidity percentage was assessed in sensitive cultivars in affected as well as non-affected tissues, along with non-impacted cultivars. Significant reduction in acidity was observed in affected tissues of the sensitive cultivars, i.e., in affected tissues of ‘Himsagar’, the acidity was 0.05% while in healthy tissue it was 0.16% (Table S5).

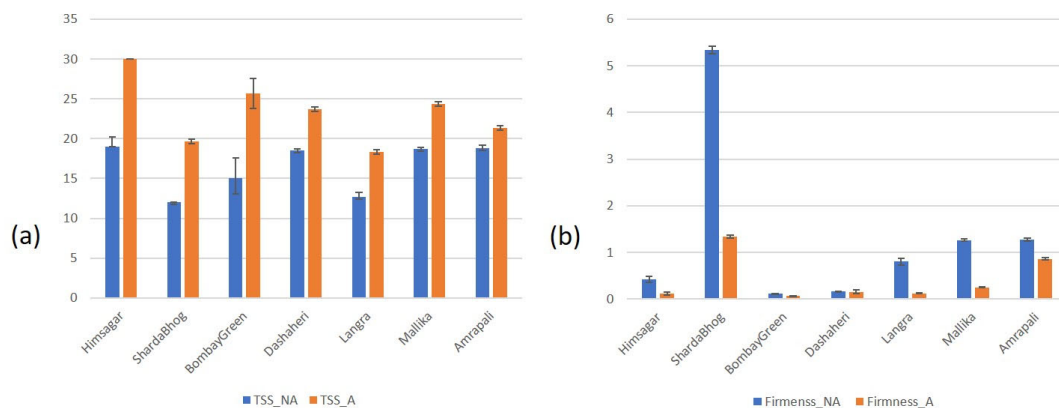


Figure 4. Comparison of the effect of heat stress on (a) TSS and (b) firmness between affected and non-affected tissues.

3.5. Change in Phenolic Compound Content

Differences in phenolic compounds were observed among affected and non-affected tissues of the fruit (Figure 5). The difference in gallic acid content in affected and non-affected parts was significant across the varieties except for ‘Mallika’. In severely affected varieties, viz., ‘Bombay Green’ and ‘Himsagar’, the gallic acid concentration in affected tissue was significantly higher, 66.28 and 46.33 µg/g, respectively, as compared to non-affected tissues, 27.28 and 19.41 µg/g. Catechin content difference was also significant in sensitive cultivars, except for the variety ‘Dashehari’, where the difference was inconsistent. Under stressed conditions, the catechin content reduced significantly from 29.64, 7.52, 16.36, and 40.47 to 5.5, 5.17, 5.97, and 8.42 in ‘Himsagar’, ‘Bombay Green’, ‘Sharda Bhog’, and ‘Langra’ varieties, respectively. Although the differences were inconsistent in varieties viz., ‘Mallika’ and ‘Dashehari’, Coumaric acid content was not observed in most of the cultivars except ‘Mallika’ in non-affected tissues, while in the case of affected tissues, the presence of the compound is observed in ‘Langra’ and ‘Sharda Bhog’ as well (Tables S3 and S4).

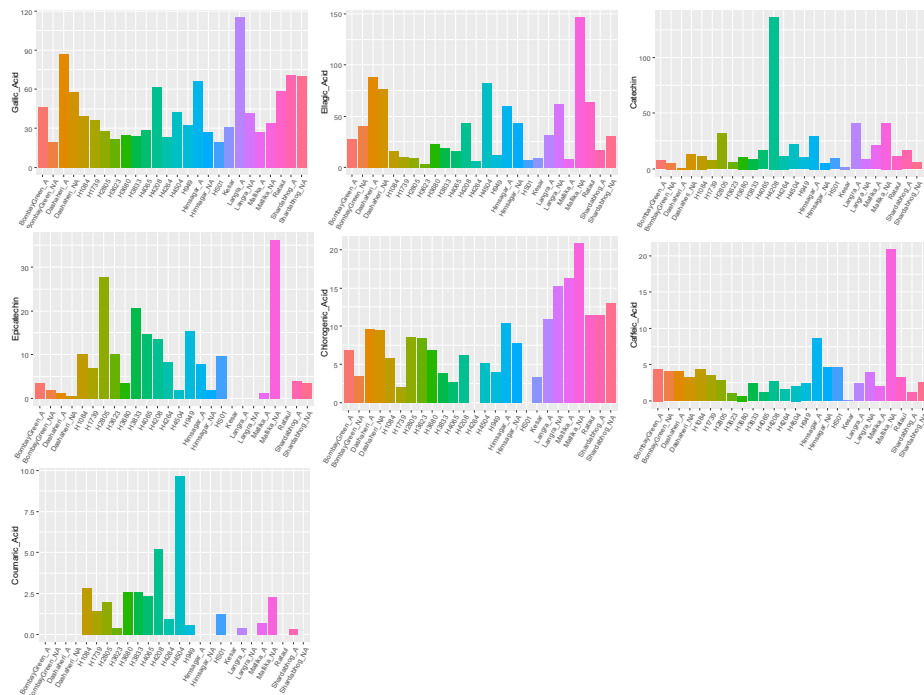


Figure 5. Mean concentration of phenolic compounds observed in different mango genotypes (A = affected tissue and NA = non-affected tissues).

Since Mallika is late maturing hybrid cultivar, the concentration of all phenolic compound in non-affected tissues were significantly higher as compared to affected tissues while opposite trend was observed in early maturing and highly sensitive varieties viz., Himsagar and Bombay Green as there was marked increase in all phenolic compound in affected tissues as compared to non-affected tissues.

3.6. Change in Aroma Profile of Severely Affected Genotypes

Comparative assessment of aroma between affected and non-affected tissue led to the identification of a differential aroma profile. Caryophyllene was consistently present in affected tissues as compared to non-affected tissues, irrespective of the cultivars under investigation. A similar trend was observed in the case of humulene, except it was not detected in the Himsagar variety. In addition, the cultivar-specific aroma profile was identified based on analysis of fresh fruit samples, and alpha-pinene and limonene were found specific to variety Langra and Dashehari, respectively, while in Himsagar, both aroma profiles were present.

3.7. Differentially Expressed Compound Detection via GC-MS Profiling

GC-MS profiling led to the identification of a total of 171 compounds from the NIST library search. Comparison based on compounds detected in all samples between affected and non-affected tissues led to identification of 50 compounds specific to the non-affected part, while 25 to the affected part, and 28 were found common (Figure 6). Based on differential grouping of compounds from affected and non-affected parts of the sensitive as well as tolerant hybrids, the compounds viz., Talose, 2,3-Dihydroxybutanedihydrazide, D-glucopyranose, Rosiridin, D-(+)-Mannopyranose 1-O-(3-O-(2-methylbutanoyl)-D-glucopyranose, and citric acid were found specific to non-affected parts and were absent in the affected tissues. When only sensitive cultivars were considered, Sucrose, D-(−)-Fructofuranose, pentakis(trimethylsilyl) ether (isomer), D-Allofuranose, pentakis(trimethylsilyl) ether, 2,3,4,5,6-Pentahydroxyhexanal, and 2,3-Dihydroxybutanedihydrazide were differentially expressed between affected and non-affected tissues. Compounds viz., Glycerol 3TMS derivative, D-

Galactopyranoside, methyl 2,6-bis-O-(trimethylsilyl)-, cyclic, 2,3-Dihydroxybutanedihydrazide, Stearic acid, Arachidic acid, rac 1-Oleoyl-2-palmitoylglycerol, 3-Hydroxy-3-(methoxycarbonyl) pentanedioic acid, L-aspartic acid and L-glutamic acid were specifically expressed in non-affected tissues while Sucrose, D-(−)-Fructofuranose, pentakis(trimethylsilyl) ether (isomer), D-Glucopyranose, 2,3,4,5,6-Pentahydroxyhexanal, 2,3-Dihydroxybutanedihydrazide were specific to affected tissues. Sucrose, 8TMS derivative, was expressed at varied significantly between affected and non-affected tissue, as its expression in Himsagar rose from 6.46 in non-affected tissues to 35.08 in affected and the same pattern was observed in Bombay Green, where this was 2.37 to 14.02. From the volatile organic compound (VOC) profile, it was evident that sucrose is expressed in all the mango genotypes and hybrids. Comparative VOC profiles of all mango hybrids indicate that a higher sucrose production was recorded in heat wave-affected mangoes compared to non-affected mangoes at that specific stage of the heat wave.

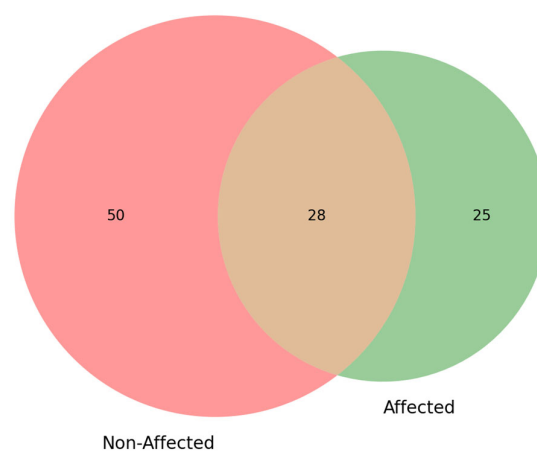


Figure 6. Venn Diagram of differentially expressed compounds between affected and non-affected tissue detected through GC-MS analysis.

Further, a heat map combined with hierarchical clustering was prepared on the basis of the GC-MS profile of heat-wave affected and non-affected tissues of sensitive cultivar along with tolerant hybrids of mango (Figure 7). Among the 171 expressed metabolites across the heat-tolerant and susceptible mango genotypes, the top 30 metabolites were differentially expressed across the genotypes.

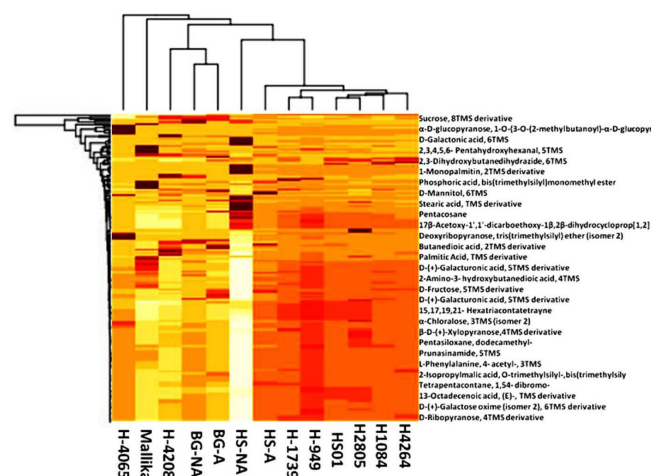


Figure 7. Heat map of sensitive and selected hybrids based on GC-MS analysis.

Principal component analysis was performed among mango genotypes and hybrids on the basis of identified metabolites by using GC-MS (Figure 8a,b). Data revealed that components 1 to 13 produce a cumulative variation of 100%. Only components with eigen value >1 were considered. As eigen values represent the total amount of variance that can be explained by a given principal component. It was seen that evalule is found higher in PC1, which is 7.85, followed by PC2 (1.84), after that the value started decreasing, which is also shown in the screen plot. However, dim1 was contributing 60.43% of the variation, and dim.2 was contributing 14.21% of the variation. Together, PC1 and PC2 contributed 74.6% of the variation from the total variation. In case of PC1 higher positive correlation was found in H4264 (0.9805), followed by Himsagar (affected) (0.9796) and HS01 (0.9788). However, in the case of Dim2 highest positive correlation was found in Bombay Green (non-affected) (0.8176), followed by ‘Amrapali’ (0.7473) and ‘Bombay Green’ (affected) (5043), and ‘Mallika’ (non-affected) (0.2688). Contrastingly H1739, H2805, H1084, H949, and H4065 were negatively correlated with PC2 (Figure 8a,b).

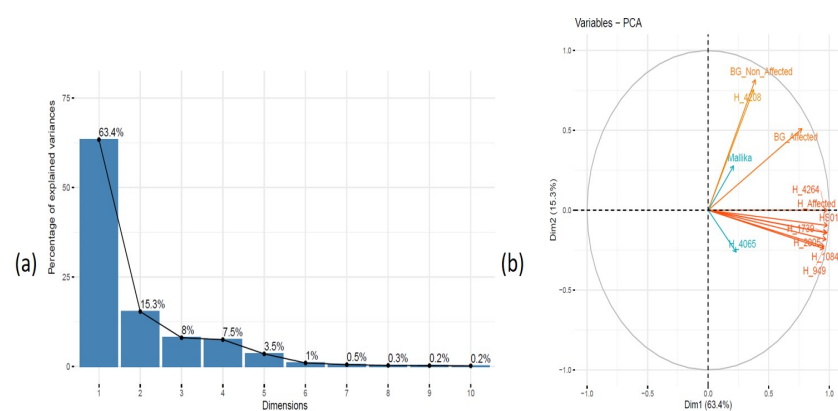


Figure 8. Principal component analysis revealed two major PCs: (a) scree plot and (b) bi-plot depicting grouping of genotypes based on GC-MS compounds.

4. Discussion

The World Meteorological Organization observed 2024 as the warmest year, which was 1.55 °C warmer than 1850–1900, and the period between 2015 and 2024 was conferred to be the warmest decade than the pre-industrial period [36]. Tropical and sub-tropical regions of the world are the most affected parts, and agriculture as well as horticultural production systems have been the most vulnerable business ventures. Here, in the subtropics of India significantly elevated temperature during 2024 was observed compared to the year 2023. This led to increased heat unit incidence on the mango crop, which impacted the crop in various ways, i.e., change in time of occurrence of pheno-phases, physiological disorders, metabolites expression, etc.

Phenological shifts have been observed across plant species due to climate change across the world [37,38]. The mango is a perennial species, and phenology is under the influence of temperature [39,40]. If the temperature fluctuates, the primordial emergence is delayed or advanced from the regular timing [41]. The flowering phenophases observed during 2023 and 2024 showed significant variations, with fluctuating temperatures during these years. In 2023, which experienced relatively cooler conditions, mango trees followed a more typical flowering pattern, with synchronized bloom periods and a gradual progression through pheno-phases such as bud formation, flowering, and fruit set. The flowering period extended over a longer duration, allowing for better pollination and a higher fruit set. In contrast, the hotter temperatures in 2024 accelerated the phenophases of mango flowering. The heat led to an earlier onset of flowering, with a compressed timeline for the

progression from bud initiation to full bloom. Overall, the hotter conditions in 2024 highlighted the impact of temperature fluctuations on mango phenology. The changes observed underscored the sensitivity of mango trees to climatic variations, with higher temperatures potentially shortening flowering phases and having a greater impact on yields.

The changes in mango fruit development and maturity observed during 2023 and 2024 revealed the influence of temperature variations on these crucial pheno-phases. In 2023, the relatively cooler conditions allowed for a steady and prolonged fruit development period. This moderate temperature range supported the gradual accumulation of sugars, acids, and other essential compounds in the fruit, resulting in high-quality mangoes with desirable size, taste, and nutritional value. The extended maturity phase also provided growers with a predictable harvest window. In contrast, the hotter conditions of 2024 significantly impacted fruit development and maturity. Elevated temperatures accelerated the rate of fruit growth, leading to a shorter development period. While the rapid growth produced fruits more quickly, it often compromised their size and quality. The intense heat during the maturation phase caused hastened ripening, increased water loss, and a higher incidence of physiological disorders such as blackening of the mango tip, producing fruit burn symptoms. The incidence of the symptoms varied with different genotypes, in early maturing varieties where there was a coincidence of high temperature with.

With higher temperatures at the time of ripening, there was increased production of sugars and their components in varieties 'Himsagar' and 'Bombay Green'. This higher conversion of starch to sugars leads to increased TSS and reduced firmness. There was a significant difference for these two marketing-related traits between affected tissues and non-affected tissues of the other sensitive cultivars as well except for the late ripening varieties, viz., 'Amrapali' and 'Mallika', since these were not at the ripening stage but at the maturity stage. Mummification of the tissue in these cases has been observed. In most of the hybrid pedigrees involve crosses of late maturing with late maturing types, viz., 'Amrapali' and 'Tommy Atkins', which led to increased flexibility to such temperatures as these escape heat due to by late ripening period. The difference in phenology is striking from a pedigree perspective, as hybrids involving 'Amrapali' $\times$ 'Tommy Atkins' showed non-significant differences, where both parents are classified as mid-maturing under subtropical conditions. In contrast, crosses involving 'Dashehari' $\times$ 'Tommy Atkins' exhibited significant differences, likely because 'Dashehari' is an early-maturing genotype. This suggests that hybrids derived from mid-late $\times$ mid-late crosses are more adaptive to temperature fluctuations. Abrupt weather changes were observed during May and June, with phenological stages during this period ranging from BBCH-703 to BBCH-709. The corresponding varieties started showing differences between the two years. Late ripening features may be regarded as one of the selection criteria to combat these fluctuations in temperature. This presents a future lead in which types of genotypes with late maturity traits are to be included in developing climate-resilient hybrids.

Upon critical observation, it was found that certain secondary metabolites were only expressed in the non-affected or tolerant genotypes and hybrids of the mango. Plant secondary metabolites are compounds found sporadically across the plant kingdom. These metabolites, classified based on their chemical constituents, serve various functions in plants. Due to their role in defending against biotic and abiotic stresses, they are considered key defensive compounds. Secondary metabolites contribute to plant protection by safeguarding against insects, herbivores, and harsh environmental conditions [42]. Plants devote more energy to the synthesis of secondary metabolites than primary metabolites, which specifies the important nature of secondary metabolites [43]. Plant secondary metabolites have huge diversity in chemical and structural patterns. They also appear as either

non-volatile compounds or volatile compounds. Secondary metabolites are also part of plants' innate immunity [44].

These secondary metabolites may play a crucial role in explaining the tolerance of certain hybrids or genotypes to heat waves. The process of homeostasis, specifically the balance in the biosynthesis and compartmentalization of metabolites, is impaired by high temperatures mainly through water relations [45,46] and direct influence on osmolytes production (proline, glycine betaine, soluble sugars, etc.) as the primary metabolites [47–49]. The heat waves rapidly impacted heat-susceptible mango genotypes, disrupting internal metabolic processes and hastening biochemical changes within the cells. As a result, the stored starch in heat-wave-affected fruits failed to convert into simple sugars, remaining primarily as sucrose. In contrast, heat wave-tolerant genotypes and hybrids underwent normal physiological and biochemical processes, including typical fruit senescence, where complex sugars were naturally broken down into simple sugars during ripening. This could be a probable reason for the lower sucrose levels observed in heat-tolerant mango genotypes and hybrids. Osmolytes directly influence proteins, both free and bound in membrane structures, together with lipids [50]. Furthermore, the secondary metabolites, phenolics, play an important role in the heat stress response as soluble phenolics and substrates in the enzymatic activity of peroxidases and other enzymes involved in an antioxidative response [51].

Quinic acid is a ubiquitous metabolite found in various plants, which plays a role in plant defense against abiotic stress through the formation of Caffeoylquinic acid [52]. It can also be recognized as an important biogenetic precursor for the biosynthesis of aromatic natural products through the shikimate pathways [53,54]. In addition to the above activity, it has also been found to show several therapeutic properties as an antimicrobial, antifungal, cytotoxic, and antioxidant [55]. Oxidative stress causes the formation of reactive oxygen species and reactive nitrogen species and triggers several destructive mechanisms. Quinic acid mediated antioxidant property supports the synthesis of tryptophan and nicotinamide, leading to the increase in DNA repair and inhibition of NF-KB [56].

The increase in TSS during fruit ripening is primarily driven by enzymatic hydrolysis of starch and sucrose, while the reduction in acidity results from organic acid degradation and respiration. From these results, it is evident that there is a negative correlation of heat stress with acidity and a positive relation with TSS. Earlier, it has been reported that reduction in fruit acidity could be attributed to increased respiration and enzymatic activity of citric acid cycle and glycolysis, and reduction in vacuolar storage citrate and tartrate due to membrane permeability and proton pump activities [57]. Terpenes and terpenoids are common secondary metabolites produced in mango, which have been reported to serve as defense compounds that combat pathogens, herbivores, and abiotic stresses. The biosynthesis of terpenes and terpenoids occurs through two major pathways: the mevalonate (MVA) pathway and the methylerythritol phosphate (MEP) pathway. In particular, the former pathway is primarily involved in the production of sesquiterpenes that are predominantly reported in leaves and fruits of perennials. For instance, Caryophyllene, α -Humulene, α -Santalene, α -Bergamotene, and β -Bergamotene, etc., are sesquiterpenes that are reported to have broad-spectrum resistance to biotic and abiotic stresses, especially cold and heat stress [58].

Another compound encountered in the GC-MS profiling, L-glutamic acid, may be a key factor contributing to heat wave tolerance in certain mango varieties and hybrids. Glutamic acid can act as the precursor of other amino acids such as aspartic acid, serine, alanine, lysine, and Proline [59,60]. Glutamic Acid reduced the oxidative stress level of ion leakage, MDA and superoxidase radical by enhanced activities of SOD, POD, CAT enzymes capable of detoxifying ROS [61]. Gallic acid has a positive influence on plants

under abiotic stress, especially heat stress, by stimulating the biosynthesis of Chlorophyll and proline as an osmo-protectant [60]. Glutamic acid also improves the defense signaling under stress. Since heat causes damage to a range of cellular components, a large number of mutagenic protective pathways and complex regulatory networks are expected to be involved in the acquisition of thermo-tolerance. Besides, another compound has been identified as one of the key components in the mitigation of stress, which is Glutamine, a plentiful free amino acid that could be a potential organic VOC to mitigate heat stress in mango. Earlier, exogenous application of Glutamine has been reported as a salinity stress mitigator [62].

Another compound revealed in the non-affected part of 'Himsagar' was α -tocopherol, having a positive impact on stress mitigation by using its lipophilic antioxidant properties. The same has been reported earlier in tobacco [63]. Additionally, Gallic acid (GA), a phenolic compound found in the unaffected parts of 'Himsagar', may help the plant tolerate abiotic stress, including heat stress, by enhancing its antioxidant capacity and stimulating enzymatic and non-enzymatic antioxidant defense systems. Further, it has also been reported that Gallic acid application increases antioxidant activity and regulates ion uptake in *Lepidium sativum* L. under salt stress conditions [64]. Gallic acid improved sunflower seeds' resistance and/or tolerance against Cd stress [65]. Gallic acid treatment led to higher resistance in soybean plants to cold stress via its ability to scavenge free radicals, improve water status, and photosynthetic capacity [66].

The possible mechanisms of Glutamic acid improved resistance and/or tolerance of plants to heat stress have not been fully elucidated. Glutamic acid positively impacts by limiting the excess excitation energy in chlorophyll for the photosynthetic apparatus during stress, reducing ROS and lipid peroxidation, and enhancing antioxidant capacity depending on the number and position of hydroxyl groups in glutamic acid structure [67]. Shikimic acid (SA) has also been monitored in heat-tolerant mango genotypes and hybrids, highlighting its potential role in mitigating heat stress. SA is a natural organic compound derived from the seeds of the Chinese staranise plant (*Illicium verum*) [68]. Studies indicate that SA can significantly reduce oxidative stress markers in lactate diet-induced diarrhea in rat models, affecting indicators such as superoxide dismutase (SOD), glutathione peroxidase (GSH-Px), catalase (CAT), malondialdehyde (MDA), NADPH oxidase activity (NOX), conjugated dienes (CD), and the oxidative stress index (OS) [69]. However, secondary metabolite-based plant defense mechanisms alone are often insufficient to provide adequate protection against high temperature stress, underscoring the need for innovative agronomic strategies to enhance plant thermos tolerance.

5. Conclusions

Climate resilience in fruit crops refers to their capacity to withstand and adapt to adverse environmental conditions, including extreme temperatures, erratic rainfall, prolonged droughts, salinity, and pest outbreaks. Among these, heat stress has emerged as a major abiotic challenge, particularly for mango (*Mangifera indica* L.), a prominent fruit crop in tropical and subtropical regions. In 2024, subtropical India experienced an intense heatwave, with daily temperatures ranging between 41 °C and 47 °C for approximately 25 consecutive days, from the latter half of May through mid-June.

A systematic field assessment was conducted to evaluate the natural response of commercial cultivars and advanced mango hybrids under these extreme conditions. Most North Indian early- to mid-season cultivars were severely affected, coinciding with critical maturity stages during peak heat. Commonly observed symptoms included fruit tip burning, premature ripening, and tissue mummification, alongside notable biochemical alterations such as elevated total soluble solids (>25 °B) and changes in phenolic profiles.

Comparative analysis between 2023 and 2024 revealed a marked shift in phenology under elevated temperature regimes. In 2024, accelerated flowering and shortened fruit maturation periods were accompanied by increased incidence of heat-induced disorders such as tip blackening and fruit burn. Cultivars with late maturity traits, such as ‘Amrapali’ and hybrids involving late-maturing parents, demonstrated better tolerance by avoiding peak heat periods, suggesting the utility of late maturity as a potential selection trait in breeding climate-resilient mango varieties.

Metabolomic profiling revealed the accumulation of specific secondary metabolites, such as quinic acid, glutamic acid, gallic acid, γ -tocopherol, and shikimic acid in heat-tolerant genotypes and unaffected tissue zones. These compounds play key roles in osmoprotection, antioxidative defense, and cellular homeostasis under heat stress. However, while secondary metabolite-based defense mechanisms contribute significantly to thermotolerance, they alone may not suffice to protect mango under extreme heat conditions. Thus, integrating metabolic insights with adaptive agronomic strategies and targeted breeding approaches is essential to develop cultivars resilient to future climate extremes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/agriculture15151619/s1>, Table S1: Hybrids and their parentage; Table S2: Phenological differences between 2023 and 2024 for different flowering related phenological traits; Table S3: Profile of different Phenolic compounds among affected vs non-affected fruit tissues of heat wave sensitive mango commercial varieties/hybrids; Table S4: Profile of different phenolic compounds in non-affected mango genotypes (hybrids); Table S5: Comparison of effect of heat stress on (a) TSS and (b) firmness among affected and non affected fruit tissues of different popular commercial mango varieties/hybrids.

Author Contributions: Conceptualization, A.K.K. and D.T.; methodology, A.K.K. and V.D.; software, D.R.; validation, S.S.D., A.K.K., K.B. and D.T.; formal analysis, D.R., N.S.S. and P.D.; investigation, A.K.K., D.R., N.S.S., A.Y. and K.B.; resources, D.T. and A.B.; data curation, A.K.K. and V.D.; writing—original draft preparation, A.K.K., K.B., M.M. and P.D.; writing—review and editing, A.B., D.T., M.M. and S.S.D.; visualization, D.T. and P.D.; supervision, D.T.; project administration, D.T. and A.Y.; funding acquisition, D.T. All authors have read and agreed to the published version of the manuscript.

Funding: Protection of Plant Varieties and Farmer’s Right Authority (PPVFRA), New Delhi (Fund Code: DUS-Mango).

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The original contributions presented in this study are included in the article/Supplementary Materials. Further inquiries can be directed to the corresponding author.

Acknowledgments: The authors acknowledge the funds received from PPVFRA, New Delhi, for the project at the National DUS center for the mango crop. The authors are thankful to the Honorable DG and DDG (Horticulture), ICAR, New Delhi, India, for their constant support and motivation for carrying out research on climate resilience horticulture.

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

BBCH	Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie
GC-MS	Gas Chromatography-Mass Spectrometry

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