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Transcriptomic, physiological, and biochemical responses of turmeric (Curcuma longa) to heat stress

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Turmeric (*Curcuma longa*) is an economically important crop native to hot and humid regions of India. The current study aims to establish the basis for a multifaceted understanding of turmeric plants' cellular and physiological responses to heat stress. We combined transcriptomic (RNA-seq) analysis, real-time photosynthesis data, and profiles of emissions of biogenic volatile organic compounds (BVOCs) to interpret the responses of turmeric plants to heat stress. RNAseq data indicated significant differential expression in 41.8% of genes, with photosynthesis-related genes overrepresented. Photosynthetic rate measurements demonstrated an almost complete failure of photosynthesis at 41 °C, followed by incomplete recovery at a normal temperature of 21 °C. Emissions of almost all detected BVOCs increased considerably during periods of heat treatment. The data establishes the ontological gene groups most affected, estimates the temperature tolerance of turmeric, and provides insights into plant responses to climate change.

Curcuma longa, commonly known as turmeric, is a perennial plant in the same family (*Zingiberaceae*) as ginger and cardamom. Turmeric products have been used for centuries, mostly in China, India, and Southeast Asia, as a spice and traditional medicine[1]. Recently, however, research on curcumin—a bioactive compound – propelled turmeric to one of the most sought-after herbal products in the US. The market value of curcumin was estimated at US$ 98.74 million in 2023 and is forecasted to increase to US$ 221.2 million by 2032, with a slight majority of the demand associated with pharmaceutical applications (Global Market Insights)[2]. Turmeric is a market-ready crop with growing demand in multiple applications such as culinary, cosmetics, and medicinal[3]. Cultivation of turmeric in the U.S. would allow for better quality control, lower transportation costs, and greater oversight of grower practices[4].

Existing research related to turmeric is overwhelmingly focused on the biological activity of curcumin and curcuminoids in animals, their biochemistry[5] and methods of their extraction and processing; studies are rarely focused on turmeric as a crop. In fact, most studies of curcumin do not mention turmeric, its main source. Even then, the majority of PubMed® search results featuring the word "turmeric" do not directly deal with the plant's physiology.

Turmeric, being native to the hot and humid tropics and subtropics of South and East Asia, is cultivated in a habitat that is at a particular risk of heat waves, which are predicted to intensify due to climate change. Increased ambient temperature in tropical climates is generally associated with decreased crop productivity[6]. Global warming may result in an increase in global temperature by as much as 5 °C by the end of the century, with the tropical and subtropical regions projected to be affected the most[7]. While turmeric crop generally thrives in hot climates, there is little data available on their resistance to unusually high heat, a condition that is predicted to become more common in the near future.

While heat stress in turmeric has not been thoroughly investigated, abundant research is available on the general mechanisms of heat stress in other plants. Possible cellular injuries caused by excessive heat include disruption of membrane integrity, protein denaturation and inactivation (particularly in chloroplasts and mitochondria), and interruption of cell division through malformation of microtubules[8]. This can manifest, among other symptoms, as an accumulation of reactive oxygen species (ROS)[9] and inhibition of photosynthesis, the latter observation being widely described in the literature[6,10–12].

During heat stress, photosynthesis is affected through several interconnected mechanisms. The net photosynthetic rate suffers from increased photorespiration at higher temperatures[6]. This process does not produce useful energy for the plant, as classic respiration would, and metabolically competes with photosynthesis.

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A class of compounds featured in this project is known as biogenic volatile organic compounds (BVOCs). These compounds are readily emitted from plants in a regulated manner and play a role in communication and signaling[13], defense[14], and, importantly for us, temperature regulation[15]. Regulation of emission of BVOCs is largely controlled by gene expression but also varies with environmental conditions that affect metabolism, such as stress[16]. The main categories of plant-originating BVOCs are isoprene, terpenes, alkanes, alkenes, alcohols, esters, carbonyls, and acids[17]. Our project detected 24 compounds in the emission profile of turmeric plants, including an aldehyde, an alcohol, monoterpenoids, and a sesquiterpene. Interestingly, many BVOCs can be perceived by human olfactory organs and are responsible for the distinct scents of plant species.

The purpose of our research was to lay the broad groundwork for understanding the mechanisms of heat stress response in turmeric. Combining biochemical and physiological data with a transcriptomic profile allows us to explore the physiological processes taking place during heat stress. With our multipronged approach to the methodology, we hope this work will contribute to research in other plant species as well as the wider fields of molecular biology, atmospheric chemistry, and, importantly, agriculture.

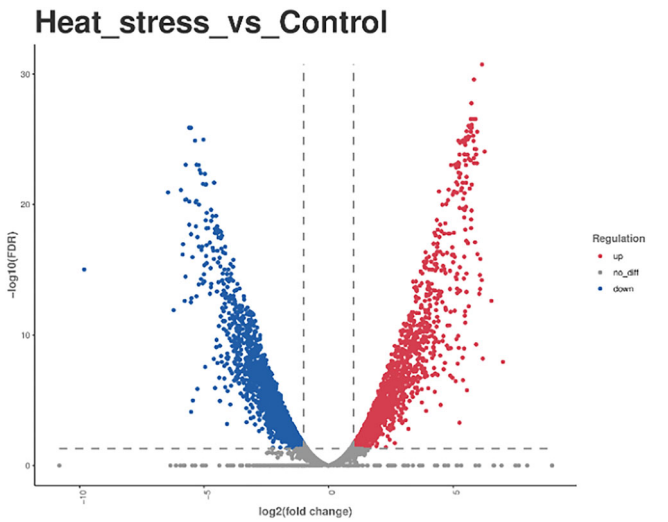

Fig. 1 | Volcano plot of gene expression, highlighting differentially expressed genes (DEGs). The false discovery rate (FDR) cutoff is set to 0.05 on the vertical axis – differential expression below this cutoff, marked in grey, is not considered significant. Under heat stress, the genes shown in blue and to the left are downregulated, and the genes shown in red and to the right are upregulated. Differential expression of the genes that are higher on the vertical axis is more significant. The figure was generated by LC Sciences (Supplementary File).

Results

Heat stress causes significant differential gene expression

Out of 10,103 genes identified during RNA sequencing, 4222 (41.8%) were differentially expressed to a significant degree, i.e., with the false discovery rate (FDR) below 0.05. Of those, 1957 (46.4%) genes were upregulated, and 2265 (54.6%) genes were downregulated under heat stress (Fig. 1 and Supplementary File).

Expression of light-harvesting-related genes is disproportionately affected by heat stress

In the Gene Ontology (GO) scatterplot (Fig. 2), two ontology terms have a rich factor of 1.0, meaning that all known and detected genes responsible for the specified function are expressed differentially. Those ontology terms are "light harvesting in photosystem I" and "pigment binding" – another function associated with light-harvesting complexes (LHCs) of photosystems I and II[18]. The next most enriched ontology term is "chlorophyll binding," also associated with photosynthesis. In contrast, genes specifically

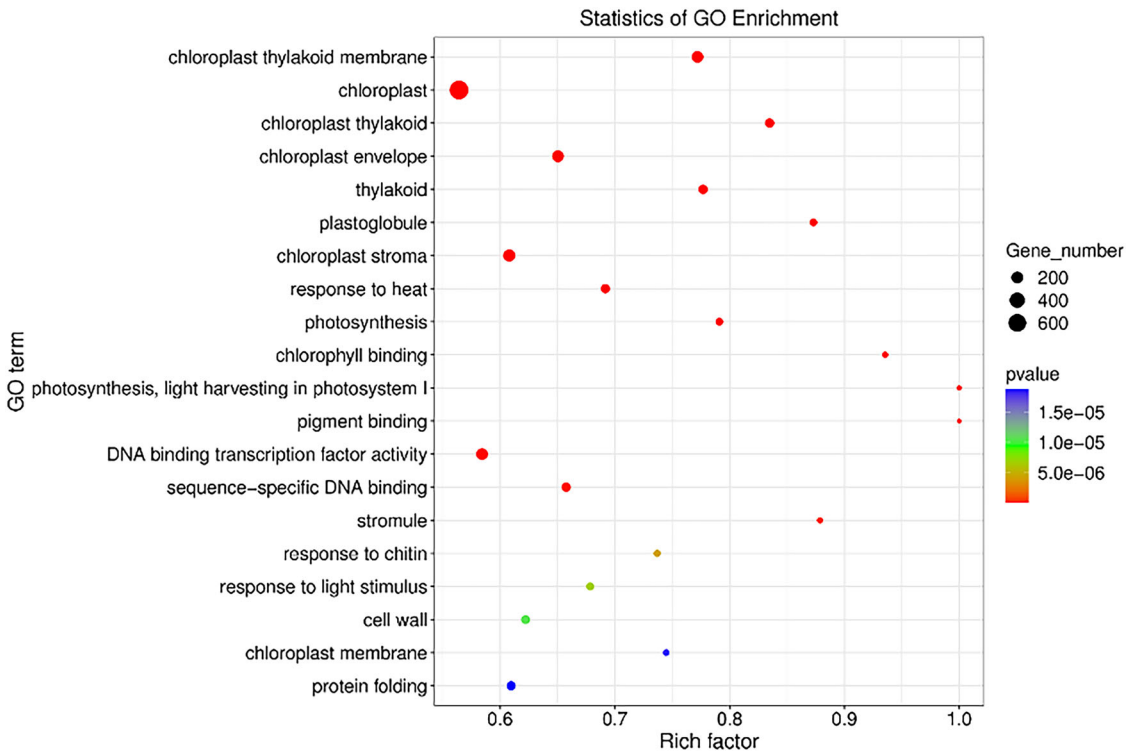

Fig. 2 | Gene Ontology (GO) scatterplot reflecting the rich factor, number, and significance of differential expression of genes for each of the ontology terms. A higher rich factor indicates a larger proportion of genes within a GO term are being differentially expressed. Gene number is the total number of genes in an ontology term. Significance is represented by *p* value, with higher confidence shown in red. This figure was generated by LC Sciences (Supplementary File).

Fig. 3 | KEGG pathways enrichment analysis scatterplot reflecting rich factors, number, and significance of differential expression of genes associated with each pathway. A higher rich factor indicates a larger proportion of genes in the pathway are differentially expressed. Gene number refers to the total number of genes associated with each pathway. Significance is represented by p-values, with higher confidence color-coded as red; note that the two bottom pathways are above 0.05 and therefore not significant—diagram generated by LC Sciences (Supplementary File).

associated with heat stress response (ontology term "response to heat") are only enriched to less than 0.7.

A similar conclusion can be drawn from Fig. 3: "photosynthesis—antenna proteins" pathway is also enriched to 1.0, indicating that all known genes associated with this pathway are expressed differentially under heat stress. Another interesting pathway identified in this analysis is plant–pathogen interaction. Pathogen-induced stress is known to share commonality with other types of stress, including abiotic and oxidative[19].

Two sets of 20 genes are shown to further examine differential expression patterns: the most downregulated genes (Table 1) and the most upregulated genes (Table 2). Out of the 20 most downregulated genes, nine (45%) are directly associated with light harvesting according to KEGG Orthology database (Table 1). Their downregulation ranges from −5.14 to −9.82 $\log_2$ fold change (35.25-fold to 903.51-fold downregulation, correspondingly). Photosynthesis-related, and specifically light-harvesting-related genes are highly overrepresented in this category and are underexpressed to a high degree. At the other extreme of differential expression, the 20 most upregulated genes included 15 genes (75%) for heat shock proteins of various families (Table 2), ranging from 5.57 to 5.92 $\log_2$ fold change (47.44-fold to 60.67-fold upregulation, correspondingly). Interestingly, the most upregulated gene was identified as *psaB*, an important photosynthesis-related gene, at 7.00 $\log_2$ fold change (127.77-fold upregulation).

Photosynthesis ceases abruptly under heat stress, while respiration increases

The real-time photosynthesis/respiration rate, derived from the exchange rates of water vapor and carbon dioxide between the plant and its environment, as seen in Fig. 4, demonstrated the following:

The heat-stressed plants had the ability to initiate photosynthesis when first exposed to light after a period of cool "nighttime" temperature, but only for a short time. The net photosynthetic rate collapsed to near zero after 3–4 h of "daylight" (and the accompanying heat). Interestingly, when the light exposure ends at the end of the "day," the heat-stressed plants immediately start to respire at a much higher rate than the control group. This higher respiration rate decreases over 3–4 h of the "night" and eventually almost reaches the normal value as temperatures cool (Fig. 4).

Over the period of three days, as the plants presumably deplete carbohydrate storage due to their inability to photosynthesize effectively, as well as accumulate damage from heat stress, the peak photosynthetic rate decreases day-to-day.

Gas chromatography detected higher volatile emissions under heat stress

A total of 24 unique biogenic volatile organic compounds (BVOCs) were identified in the foliar emission profiles of the turmeric plants, including 14 monoterpenes, 5 oxygenated monoterpenes (e.g., eucalyptol, linalool, α-terpineol, piperitone), 2 alkylbenzenes (p-cymene, p-cymenene), and 1 sesquiterpene (β-caryophyllene). Our results indicate that turmeric leaves are not significant BVOC emitters under normal conditions, with peak emissions ranging from only 40 to 60 pmol m^{-2} s^{-1} (Fig. 5). However, when exposed to heat stress, BVOC emissions increased significantly to 500–1200 pmol m^{-2} s^{-1} (Fig. 5). The magnitude of induction varied considerably between different BVOCs. 3-hexenol showed the highest degree of induction, with heat-stressed emission values being approximately 1500 times greater than the control (Table 3). 3-hexenol is a green leaf volatile synthesized via the lipoxygenase pathway, and its emission has been linked to cell wall damage arising from leaf injury or heat stress[20]. The magnitude of induction for the other compounds ranged from 3.0 (α-fenchene) to 57 (α-terpineol). With the exception of α-fenchene, the emission rates of the other 23 BVOCs were significantly higher ($P < 0.05$) in the heat-stressed plants (Table 3).

The relative abundance of most BVOCs did not change notably with heat stress (Table 3). The dominant BVOC emitted by turmeric was α-phellandrene, accounting for 30% and 36% of the total emissions from control and heat-stressed plants, respectively. This was followed by

Table 1 | Twenty of the most downregulated UniGenes out of 2064 identified during assembly

Gene_ID	Name	KODescription	log2FC
TRINITY_DN43042_c0_g6	CAB2R	light-harvesting complex II chlorophyll a/b binding protein 1	−9.8194*
*TRINITY_DN43042_c0_g8	CAB1	light-harvesting complex II chlorophyll a/b binding protein 1	−6.2294*
TRINITY_DN47351_c1_g2	–	carbonic anhydrase	−5.9316
TRINITY_DN33946_c0_g1	ANT18	bifunctional dihydroflavonol 4-reductase/flavanone 4-reductase	−5.8645
TRINITY_DN38676_c0_g2	–	pyrimidine and pyridine-specific 5'-nucleotidase	−5.7592
TRINITY_DN46509_c0_g1	–	carbonic anhydrase	−5.7499
TRINITY_DN45965_c1_g1	CAB40	light-harvesting complex II chlorophyll a/b binding protein 1	−5.7414*
TRINITY_DN36526_c0_g2	CAB36	light-harvesting complex II chlorophyll a/b binding protein 2	−5.6042*
TRINITY_DN41557_c0_g4	ANS	anthocyanidin synthase	−5.5976
TRINITY_DN35028_c0_g1	LHCA4	light-harvesting complex I chlorophyll a/b binding protein 4	−5.5376*
TRINITY_DN35330_c2_g2	CRR7	glycerophosphoryl diester phosphodiesterase	−5.5350
TRINITY_DN31638_c0_g1	GSTF12	glutathione S-transferase	−5.5305
TRINITY_DN45288_c0_g1	–	glutamine synthetase	−5.3111
TRINITY_DN34770_c0_g2	GDCSH	glycine cleavage system H protein	−5.3065
TRINITY_DN45965_c1_g4	CAB40	light-harvesting complex II chlorophyll a/b binding protein 1	−5.2227*
TRINITY_DN34023_c0_g1	GA2OX1	gibberellin 2-oxidase	−5.2207
TRINITY_DN34151_c1_g2	LHCB4.2	light-harvesting complex II chlorophyll a/b binding protein 4	−5.2082*
TRINITY_DN43042_c0_g9	CAB-151	light-harvesting complex II chlorophyll a/b binding protein 2	−5.1846*
TRINITY_DN40213_c2_g2	LHCA1	light-harvesting complex I chlorophyll a/b binding protein 1	−5.1394*
TRINITY_DN38065_c1_g1	RFS2	raffinose synthase	−5.0858

Genes were filtered for significance at p value < 0.05. Column "KODescriptions" indicates the functional associations provided by KEGG Orthology database. Genes directly associated with light harvesting are indicated with asterisks (*). Column "Gene_ID" indicates the ID of the UniGene as assigned during assembly and corresponds to gene IDs in the Supplementary Data file.

Table 2 | Twenty of the most upregulated UniGenes out of 2064 identified during assembly

Gene_ID	Name	KODescription	log2FC
TRINITY_DN38788_c2_g4	psaB	photosystem I P700 chlorophyll a apoprotein A2	6.9974**
TRINITY_DN45155_c0_g1	FTIP1	5-methyltetrahydropteroyltriglutamate--homocysteine methyltransferase	6.0743
TRINITY_DN12617_c0_g1	DIR2	isoleucyl-tRNA synthetase	5.9778
TRINITY_DN40021_c0_g1	HSC-I	heat shock 70 kDa protein 1/2/6/8	5.9230*
TRINITY_DN45380_c0_g5	Os03g0179900	lipoxygenase	5.8795
TRINITY_DN42348_c2_g1	–	HSP20 family protein	5.8339*
TRINITY_DN33228_c0_g1	HSP18	HSP20 family protein	5.8316*
TRINITY_DN46966_c1_g3	hsp16.9A	HSP20 family protein	5.8179*
TRINITY_DN46878_c0_g6	HSP70	heat shock 70 kDa protein 1/2/6/8	5.7499*
TRINITY_DN41747_c1_g1	HSP22.7	HSP20 family protein	5.7454*
TRINITY_DN36255_c3_g2	HSP26.7	HSP20 family protein	5.7421*
TRINITY_DN42243_c0_g4	DIR11	isoleucyl-tRNA synthetase	5.7375
TRINITY_DN47317_c3_g7	HSP70	heat shock 70 kDa protein 1/2/6/8	5.7219*
TRINITY_DN36501_c0_g2	hsp16.9A	HSP20 family protein	5.7101*
TRINITY_DN46581_c3_g6	HSP18.1	HSP20 family protein	5.6512*
TRINITY_DN40021_c0_g2	HSP70	heat shock 70 kDa protein 1/2/6/8	5.6335*
TRINITY_DN46581_c3_g4	–	HSP20 family protein	5.6203*
TRINITY_DN46966_c1_g2	HSP18.1	HSP20 family protein	5.6101*
TRINITY_DN39464_c0_g1	HSP24.1	HSP20 family protein	5.5795*
TRINITY_DN42175_c2_g3	HSP21	HSP20 family protein	5.5679*

Genes were filtered for significance at p value < 0.05. Column "KODescriptions" indicates the functional associations provided by KEGG Orthology database. Genes corresponding to heat shock proteins are indicated with asterisks (*). The gene directly associated with photosynthesis is indicated with a double asterisk (**). Column "Gene_ID" indicates the ID of the UniGene as assigned during assembly and corresponds to gene IDs in the Supplementary Data file.

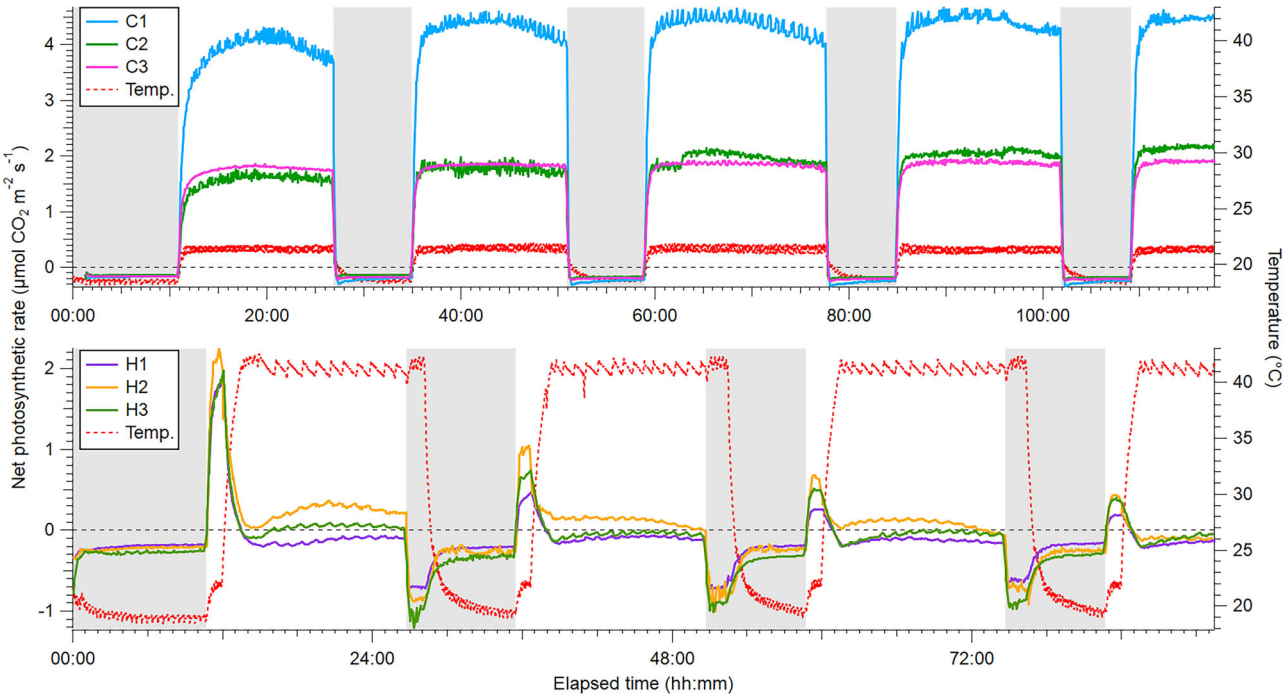

Fig. 4 | Real-time photosynthesis/respiration measurements. Normal photosynthetic cycle (top) and interrupted photosynthesis under heat stress (bottom). C1, C2, and C3 are the control plants, while H1, H2, and H3 are the heat-stressed plants. The gray-shaded regions indicate nighttime. Note the higher respiration rate in heat-stressed plants in the absence of light. Zero on the vertical axis implies that photosynthesis and respiration are balanced or non-existent.

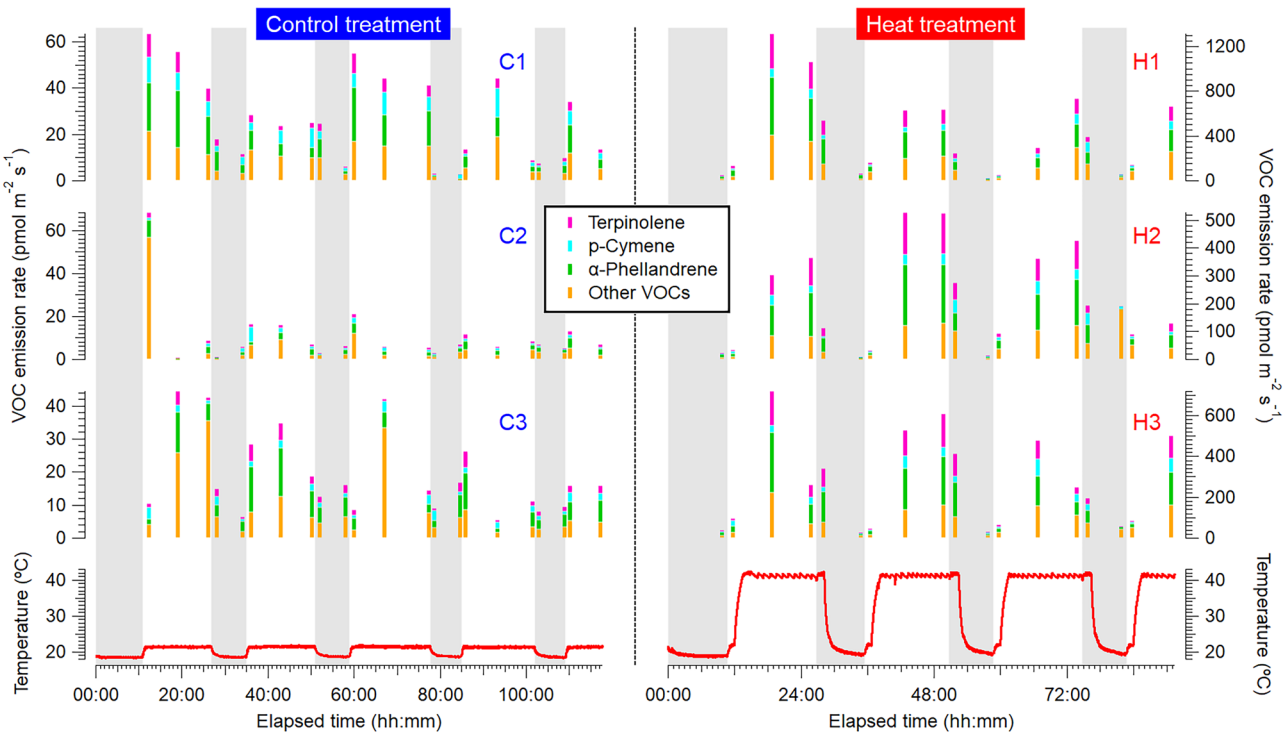

Fig. 5 | Time series of biogenic volatile organic compound (BVOC) emissions, as measured by gas chromatography from 3 control (C1, C2, C3) and 3 heat-stressed (H1, H2, H3) turmeric plants. The diurnal temperature profiles for both sets of plants are shown in the bottom panels. The gray-shaded regions indicate nighttime (i.e., no light).

terpinolene and p-cymene. The contribution of terpinolene doubled from 12% in control plants to 23% in heat-stressed plants, while p-cymene's contribution decreased marginally from 14% in control plants to 9% in heat-stressed plants (Table 3).

Discussion

To our knowledge, this is one of the first transcriptomic studies and probably one of the first interdisciplinary studies involving heat stress in turmeric. While a shotgun sequencing-derived genome assembly exists[21], it is

Table 3 | Daytime emission rates (Mean ± SD) and the relative percentages of 24 unique biogenic volatile organic compounds (BVOCs) emitted by control (C) and heat-stressed (H) turmeric plants ($N = 3$)

Compound	Emission rate (pmol m^{-2} s^{-1})		H/C	*P* value	Relative abundance (%)	
	C	H			C	H
Methacrolein	0.237 ± 0.364	6.41 ± 6.26	27	2.72×10^{-4} (**)	0.99	1.2
3-Hexenol	0.0148 ± 0.0219	22.6 ± 23.2	1500	3.14×10^{-4} (**)	0.062	4.2
α-Thujene	0.165 ± 0.290	0.676 ± 0.794	4.1	1.07×10^{-2} (*)	0.69	0.13
α-Pinene	0.579 ± 0.370	4.22 ± 2.55	7.3	3.08×10^{-6} (***)	2.4	0.78
Sabinene	0.0493 ± 0.0955	0.499 ± 0.449	10	2.34×10^{-4} (**)	0.21	0.093
β-Myrcene	0.807 ± 0.769	16.7 ± 7.33	21	5.00×10^{-9} (***)	3.4	3.1
β-Pinene	0.381 ± 0.334	4.90 ± 2.87	13	7.88×10^{-7} (***)	1.6	0.91
Unk MT 19.22	0.101 ± 0.160	0.911 ± 0.969	9.0	1.33×10^{-3} (*)	0.42	0.17
α-Phellandrene	7.23 ± 6.09	195 ± 105	27	1.15×10^{-7} (***)	30	36
δ-3-Carene	0.399 ± 0.299	4.14 ± 2.28	10	4.14×10^{-7} (***)	1.7	0.77
α-Terpinene	0.654 ± 0.966	9.66 ± 4.55	15	1.95×10^{-8} (***)	2.7	1.8
Limonene	0.597 ± 0.524	14.5 ± 6.58	24	7.69×10^{-9} (***)	2.5	2.7
p-Cymene	3.39 ± 3.03	50.7 ± 21.0	15	2.36×10^{-9} (***)	14	9.4
β-Phellandrene	0.680 ± 0.886	10.5 ± 4.70	15	8.99×10^{-9} (***)	2.9	1.9
Eucalyptol	0.453 ± 0.327	19.7 ± 18.6	44	1.60×10^{-4} (**)	1.9	3.7
γ-Terpinene	0.393 ± 0.309	9.42 ± 4.52	24	2.04×10^{-8} (***)	1.6	1.8
p-Cymenene	1.40 ± 2.98	10.0 ± 6.36	7.1	5.78×10^{-6} (***)	5.9	1.9
Linalool	0.363 ± 0.630	4.89 ± 4.00	13	5.87×10^{-5} (***)	1.5	0.91
Unk OxyMT 23.18	0.216 ± 0.277	9.19 ± 5.64	42	6.69×10^{-7} (***)	0.91	1.7
α-Terpineol	0.140 ± 0.146	7.95 ± 5.68	57	5.28×10^{-6} (***)	0.59	1.5
Piperitone	0.0719 ± 0.119	0.755 ± 0.435	10	7.08×10^{-7} (***)	0.30	0.14
β-Caryophyllene	0.524 ± 0.675	3.56 ± 3.49	6.8	9.38×10^{-4} (**)	2.2	0.66
α-Fenchene	2.20 ± 6.53	6.60 ± 14.0	3.0	1.93×10^{-1} (n.s.)	9.2	1.2
Terpinolene	2.81 ± 2.38	124 ± 64.6	44	5.25×10^{-8} (***)	12	23

H/C indicates the average ratio of the emissions between heat-stressed and control plants (i.e., magnitude of BVOC induction). The emission differences between heat-stressed and control plants were statistically tested using independent samples *t* tests, and the resulting *P* values and significance levels are reported (* :$P < 0.05$, **: $P < 0.001$, ***: $P < 0.0001$, n.s.: not significant).
Unk MT unknown monoterpene, *Unk OxyMT* unknown oxygenated monoterpene.

not annotated. Transcriptomic analysis was required to be performed de novo – in that respect, our approach is one of the first of its kind.

Gene ontology (GO) and pathway analysis provided an important insight into the effect of heat stress on photosynthetic activity – almost all of the genes in specific categories (as assigned by the respective software) related to photosynthesis were expressed differentially (Figs. 2 and 3). This is supported by the real-time photosynthesis/respiration data (Fig. 4) that demonstrates an almost complete shutdown of photosynthesis after a specific temperature is reached during the gradual "morning" warm-up. Therefore, we conclude that photosynthesis is the most vulnerable physiological process to heat stress. Photosynthesis is also one of the vital biochemical pathways of any plant, and therefore any potential treatment intended to compensate for the effects of heat stress will have to consider protecting photosynthetic machinery as an important therapeutic target.

Gas chromatography (GC) data indicated a significant increase in the amount of biogenic volatile organic compounds (BVOCs) emitted by the plants under heat stress. Considering that 46.4% of significantly differentially expressed genes were upregulated, it is unlikely that this reflects a complete disruption of the plants' biochemical pathways. Instead, we propose that this represents a deliberate response by the plant. BVOCs are known to be involved in temperature control[15], and the two compounds emitted at the highest quantities, α-phellandrene and terpinolene, are also studied for antioxidant properties[22]. Incidentally, heat stress might also induce oxidative stress in plants[23], and oxidative stress increases the expression of heat shock proteins (HSPs)[24], suggesting a link between the mechanisms for responses to oxidative stress and heat stress. Therefore, the increased emission of BVOCs is likely a controlled response of the plants to either heat stress directly or other stress caused by heat damage.

Looking at the data for individual differentially expressed genes (DEGs), 47 entries out of 4222 total DEGs were tagged as related to the synthesis of terpenes and terpenoids by KEGG (Supplementary File). Twelve of them were upregulated, and 35 were downregulated. With only one exception out of 30 cases, the genes associated with chloroplasts were overwhelmingly downregulated. To rephrase, out of 47 genes tagged with relation to terpene or terpenoid synthesis pathway, 30 were also tagged with an association with chloroplast – one of them was upregulated, and 29 were downregulated. This hints at two possible explanations, described below.

First, as evident from the GC-MS data, the total emissions of terpenes and terpenoids have increased; therefore, the downregulation of most DEGs associated with these pathways suggests that the plants synthesize BVOCs irrespective of gene expression, e.g., release the pre-stored compounds from glands or undertake de novo synthesis during heat stress.

Alternatively, the downregulation could be explained by the disproportionate suppression of chloroplast activity that would be consistent with our claim that the machinery involved in photosynthesis is particularly vulnerable to heat stress, even with reduced gene expression, the remaining protein translation is enough to sustain, increase and diversify the synthesis of terpenes and terpenoids; in other words, these particular enzymes are not the limiting factor in the synthesis pathway.

A decisive role in the apparent suppression of photosynthesis may be played by the plant's response to oxidative stress. Since the metabolic reactions (particularly the electron transport chain) involved in

photosynthesis are a major source of reactive oxygen species[25], it is reasonable that the organism might deliberately suppress them in order to alleviate oxidative stress. The excess emission of terpenes during heat stress also hints at the activation of the mechanisms involved in the mitigation of oxidative stress since these compounds exhibit antioxidative and membrane-stabilizing properties[26].

The gene most overexpressed under heat stress was found to be *psaB*, the gene coding for the protein psaB—a subunit of photosystem I (PSI), involved in the electron transport chain (ETC)[27]. According to recent research, psaB acts as an attenuator of excessive electron transfer between photosystems II and I[28]. In this case, overexpression of *psaB* would be consistent with being a deliberate mechanism for containing oxidative stress.

We propose that an interdisciplinary approach to studying crop physiology is preferred for developing abiotic stress-resilient crops. In this study, we employed principles of atmospheric chemistry, plant physiology, and transcriptomics to understand how turmeric plants respond to heat stress. We outline three main effects of heat stress on turmeric plants. First, the photosynthetic rate drops dramatically during periods of heat, to the point that photosynthesis cannot compete with respiration. Second, the plant significantly increases the magnitude of biogenic volatile organic compound (BVOC) emissions. Lastly, significant differential gene expression was observed in 41.8% of the detected genes, with genes directly related to photosynthesis being vastly overrepresented. Therefore, the plant's capability to photosynthesize is significantly affected by heat stress. Since photosynthesis is necessary for biomass acquisition—a desirable trait in crops—excessive heat can lead to reduced yields or even total biomass loss due to plant death. We hope the data presented in this research will stimulate interdisciplinary efforts to develop heat-resilient crop lines.

Methods

Plant materials

Young plants (eight weeks old) of the CL11 genotype (high yield, high curcumin content)[29] of *Curcuma longa* were received from Alabama Agricultural and Mechanical University (AAMU) and transplanted into 1-gallon pots. The plants were watered generously every third day and were kept at a near-constant temperature of 25 °C. The light cycle consisted of 14 h of 4000 lux light and 10 h of darkness. Six of the healthiest plants were selected for the project. Experimental or heat-stressed (H1, H2, and H3) and control (C1, C2, and C3) groups of three each were assigned randomly immediately prior to the start of the first experiment.

Heat stress

The control group (plants C1, C2, and C3) was kept at a constant 21 °C ambient temperature for the entirety of the data collection period; however, variations in the tissue temperature are possible due to irradiation by intense light during the period designated "day." The heat stress group (plants H1, H2, and H3) was also kept at 21 °C during the period designated "night" – since after the collection of the "twilight" sample and up to the collection of the "morning" sample; otherwise, the specimen was exposed to the heat stress temperature of 41 °C, with short transitional periods (Supplementary File). The control group was monitored for four full days, with the experiment terminating at the following "noon" of the cycle, 117 h in total. Heat stress group experiment was terminated early, on the "noon" of its fourth day, 91 h in total, due to concerns for the specimen's health and therefore a risk of lower RNA yield for future sequencing.

The light cycle for both groups was identical, with 16 h of light and 8 hours of dark in a 24-h period. All specimens were watered with 500 mL of water every second day at the time point right after the collection of the "noon" sample.

Plant volatile sampling and analysis by gas chromatography

Volatile sampling of the turmeric plants was conducted in the Fluxtron facility[30] at the University of California, Irvine. The facility consists of a temperature-controlled walk-in environmental chamber. Two sets of experiments were conducted, control and heat stress, with each set lasting about 4 days. For each experimental set, three plant replicates were sampled concurrently. Each plant was individually enclosed in a transparent Teflon bag. The bags were continuously flushed with BVOC-free air sourced from a zero air generator (Model 747-30; Aadco Instruments). CO_2 from a pure CO_2 cylinder was added to the influent air stream to maintain a CO_2 mixing ratio of approximately 400 μmol mol^{-1} inside the Teflon bags. The temperature inside the bags was continuously measured using thermocouple sensors. Part of the effluent air from each bag was periodically sampled onto sorbent tubes for offline BVOC analysis. The BVOC analysis was performed on a thermal desorption-gas chromatography with time-of-flight mass spectrometry and a flame ionization detector (TD-GC-TOFMS/FID) system (Markes International). Further details about the TD-GC-TOFMS/FID and its analytical protocols can be found in Nagalingam et al. (2022)[31]. In addition to BVOC sampling via sorbent tubes, a portion of the air from each bag was also sampled onto an infrared gas analyzer (LI-840A; LI-COR Biosciences) for semi-continuous measurements of CO_2 and water vapor. These measurements were then used to calculate the net photosynthetic rates of the turmeric plants.

RNA sequencing

The control group tissue samples were collected 117 h after the start of the experiment. Heat stress group tissue samples were collected early, 91 h after the start of the experiment, due to deteriorating health of the specimen and a risk of lower RNA yield.

All leaves inside the enclosing bags were collected separately for each of the six specimens at the end of the experimental period during the "day." Soft leaf tissue was snap-frozen in liquid nitrogen, transported on dry ice, and stored at −80 °C for RNA extraction.

RNA extractions was carried out as described by Ramadoss and Basu (2018) and Deepa et al. (2014) with modifications (Supplementary File), separately for each tissue sample. RNA samples were quantified using a Nanodrop spectrophotometer (Supplementary File).

The six RNA samples, corresponding to each specimen, were sent to LC Sciences, LLC (Houston, TX), shipped with dry ice, where an electropherogram was performed to assess RNA integrity (Supplementary File). Due to sample quality concerns, samples C1 and H1 were excluded from sequencing.

Library preparation for RNA-sequencing was performed by LC Sciences as described below (Personal communication). RNA samples were used to construct a poly(A) RNA sequencing library as per the TruSeq Stranded mRNA (Illumina) sample preparation protocol and purified by two rounds of oligo-(dT) magnetic beads purification. The strands were fragmented in a divalent cation buffer at elevated temperature, and the dsDNA library was prepared and barcoded. Paired-end sequencing was then performed on the NovaSeq 6000 (Illumina) system to produce a theoretical maximum of one hundred million reads per RNA sample, 150 base pairs per read, or 15 billion reads of individual base pairs.

De novo transcriptome assembly and analysis

Since no reference genome is available for turmeric, de novo transcriptome assembly was conducted by LC Sciences in the following ways (Personal communication). Reads were filtered for quality and adaptor contamination using the Cutadapt Perl script[32] and FastQC software. Clean data was used in Trinity software[33] to generate a series of virtual transcripts based on mutual alignment of the reads. These were clustered by similarity, and the longest transcript in the cluster would be labeled the UniGene.

The UniGenes, representing the transcripts that are expected to be found in the samples, were used to model the proteins that are being expressed using NCBI non-redundant protein database and SwissProt, to construct a map of gene ontology (GO) using Gene Ontology Resource, to associate with pathways using KEGG Pathway, and associate with functions using EggNOG orthology database. Differential expression analysis was performed using Salmon software[34] and exported as an Excel file.

RNA-sequencing and data generation from the sequences were performed by LC Sciences, LLC, and Figs. 1, 2 and 3 were generated by the company.

Data availability

Minimal dataset that would be necessary to interpret, replicate and build upon the methods or findings reported in the article are available upon request.

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Author contributions

K.M. wrote the manuscript, with contributions from S.N. A.G. designed and provided guidance for the GC-MS studies. K.M. maintained the plants and performed RNA extractions. K.M. and S.N. conducted the GC-MS experiments and analyses. S.M. and L.D. grew and maintained the turmeric plants at AAMU and shipped them to C.B. C.B. conceptualized the project, and S.M. contributed to its design. C.B. and S.M. secured funding for the project.

C.B. supervised the overall project and edited the manuscript. All authors read and approved the final version of the manuscript.

Competing interests
The authors declare no competing interests.

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