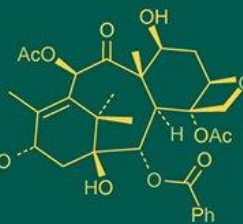
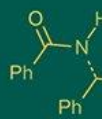


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Genotype-dependent modulation of photosynthesis and oxidative dynamics by directional light in mango

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Abstract

Light distribution within the canopy plays a critical role in regulating physiological and biochemical processes in perennial fruit crops like mango (*Mangifera indica* L.). The present study evaluated the interactive effect of genotype and incident photosynthetic photon flux density (PPFD) direction on chlorophyll content, biochemical attributes and antioxidative responses under field conditions during 2022-23 and 2023-24. The results revealed a significant genotype $\times$ direction interaction for all parameters. Among the cultivars, Amrapali recorded the highest leaf chlorophyll content (up to 43.0 SPAD) and panicle chlorophyll content (18.94 SPAD), followed by Langra, whereas Fazli showed the lowest values. Similarly, total phenols (34.18 mg GAE 100 g⁻¹ FW) and total soluble sugars (163.78 mg 100 g⁻¹ FW) were maximum in Amrapali under south exposure. Across directions, the south-facing orientation resulted in the highest values for chlorophyll, phenols, sugars and catalase activity (up to 19.42), followed by east, while north and west recorded comparatively lower values. However, higher irradiance under south and east directions also increased lipid peroxidation (up to 8.46 μ mol g⁻¹ FW), indicating elevated oxidative stress. The concurrent increase in catalase activity suggests an efficient antioxidative response to mitigate oxidative damage. Overall, the study demonstrates that optimal light orientation, particularly south and east, combined with responsive genotypes like Amrapali and Langra, enhances photosynthetic efficiency, biochemical quality and stress tolerance in mango, providing important implications for orchard management and productivity enhancement.

Keywords: Photosynthetic photon flux density, Genotype $\times$ environment interaction, Chlorophyll content, Antioxidative enzyme activity, Mango

1. Introduction

Mango (*Mangifera indica* L.) is one of the most economically important fruit crops in tropical and subtropical regions and holds a prominent position in global horticulture due to its high nutritional value, consumer preference and export potential (Evans *et al.*, 2017) [7]. India, being the largest producer, contributes significantly to global mango production, where the crop plays a vital role in livelihood security and agricultural sustainability (Balaganesh and Makarabbi, 2023) [4]. In addition to its economic importance, mango fruits are rich in sugars, vitamins, minerals and bioactive compounds such as phenolics and antioxidants, which enhance both nutritional quality and health benefits (Ganguly *et al.*, 2025) [8].

Plant growth, productivity and fruit quality in mango are strongly influenced by environmental factors, among which light is one of the most critical determinants. Photosynthetic photon flux density (PPFD), representing the intensity of photosynthetically active radiation, directly affects photosynthesis, chlorophyll synthesis and carbon assimilation (Patel *et al.*, 2026; Coelho *et al.*, 2025) [6, 18]. In perennial fruit trees like mango, light distribution within the canopy is often uneven due to tree architecture, planting geometry and solar movement, resulting in differential exposure of plant parts to incident radiation (Cheesman *et al.*, 2025) [5]. This heterogeneity in light availability significantly influences physiological and biochemical processes at both vegetative and reproductive levels (Wang *et al.*, 2023) [24].

The direction of incident light plays a crucial role in determining canopy light interception patterns. South-facing canopy surfaces generally receive higher solar radiation, while east-facing sides benefit from moderate morning light conditions and west-facing sides are

exposed to relatively intense afternoon radiation. In contrast, north-facing orientations receive comparatively lower irradiance (Nel *et al.*, 2024) ^[17]. Such directional variations can lead to significant differences in photosynthetic performance, pigment accumulation and metabolite synthesis within the plant (Simkin *et al.*, 2022) ^[23]. Optimizing light distribution through canopy orientation and management has therefore been recognized as an important strategy for improving fruit quality and productivity in orchard systems (Kishore *et al.*, 2023) ^[13].

Chlorophyll content is a key physiological indicator of photosynthetic efficiency and plant health. It reflects the plant's ability to capture and utilize light energy for carbon fixation. Variations in chlorophyll content under different light environments are closely associated with changes in photosynthetic capacity and biomass production (Yu *et al.*, 2024) ^[26]. Moreover, reproductive structures such as panicles can also contribute to photosynthesis and their chlorophyll content plays an important role in supporting fruit development through additional assimilate supply (Garrido *et al.*, 2023) ^[9].

Light availability also regulates important biochemical constituents such as phenolic compounds and soluble sugars. Phenolics are essential secondary metabolites involved in plant defense and antioxidative mechanisms and their synthesis is often stimulated under higher light conditions (Ahlawat *et al.*, 2024) ^[1]. Similarly, soluble sugars, which are the primary products of photosynthesis, directly influence fruit quality attributes such as sweetness and flavor (Aslam *et al.*, 2026) ^[3]. However, excessive light exposure may lead to the generation of reactive oxygen species (ROS), resulting in oxidative stress and lipid peroxidation (Zandi & Schnug, 2022) ^[27]. To mitigate such stress, plants activate antioxidative enzymes such as catalase, which plays a crucial role in detoxifying hydrogen peroxide and maintaining cellular homeostasis (Pirasteh-Anosheh *et al.*, 2023) ^[19].

Genotypic variation further influences plant responses to light environments. Different mango cultivars vary in their photosynthetic efficiency, metabolite accumulation and stress tolerance, which affects their adaptability under varying irradiance conditions (Khalil *et al.*, 2025) ^[12]. Despite the importance of light direction and genotype, limited information is available on their interactive effects on physiological and biochemical traits in mango. Therefore, the present study was undertaken to evaluate the combined influence of genotype and incident PPFD direction on chlorophyll content, phenolics, soluble sugars, lipid peroxidation and catalase activity with the aim of improving understanding of light-mediated responses and optimizing orchard management strategies.

2. Materials and Methods

2.1 Experimental Site

The experiment was conducted at the Fruit Research Farm, Imalia, Department of Horticulture, Jawaharlal Nehru Krishi Vishwa Vidyalaya (JNKVV), Jabalpur, Madhya Pradesh, India. The experimental site is geographically located at 23.90° N latitude and 79.58° E longitude, at an altitude of 411.78 m above mean sea level. The region is characterized by a subtropical climate with distinct seasonal variations.

2.2 Experimental Design and Treatments

The experiment was conducted using an asymmetrical factorial randomized block design (RBD) with three replications. A total of 20 treatment combinations were evaluated, comprising two factors: varieties and incident photosynthetic photon flux density (PPFD) directions. The first factor included five mango varieties, namely Dashehari (V₁), Langra (V₂), Amrapali (V₃), Fazli (V₄) and Sunderja (V₅). The second factor consisted of four directions of incident PPFD, viz., North (D₁), South (D₂), East (D₃) and West (D₄).

2.3 Measurement of Physiological Parameters

2.3 Leaf Chlorophyll Content Index (SPAD)

Leaf chlorophyll content was measured using a portable SPAD chlorophyll meter. Observations were recorded from the middle portion of fully expanded leaves while avoiding the midrib region. For each plant, ten readings were taken and averaged to represent the chlorophyll content index.

2.4 Panicle Chlorophyll Content Index (SPAD)

Chlorophyll content of panicles was recorded using the same SPAD meter. Measurements were taken from the green portion of emerging and fully developed panicles. An average of ten readings per plant was used to determine the panicle chlorophyll index.

2.5 Estimation of Biochemical Parameters

2.5.1 Total Phenolic Content

Total phenolic content was estimated using the Folin-Ciocalteu method. Fresh leaf tissue (0.5 g) was homogenized in 80% ethanol and centrifuged at 10,000 rpm for 15 min. The supernatant was reacted with Folin-Ciocalteu reagent followed by sodium carbonate and absorbance was measured at 765 nm using a UV-Vis spectrophotometer. Results were expressed as mg gallic acid equivalents (GAE) per g fresh weight.

2.5.2 Total Soluble Sugars

Total soluble sugars were determined using the anthrone method. Fresh leaf tissue (0.5 g) was extracted in 80% ethanol and centrifuged. The supernatant was treated with anthrone reagent and absorbance was recorded at 620 nm. Sugar content was expressed as mg g⁻¹ fresh weight.

2.5.3 Lipid Peroxidation (MDA Content)

Lipid peroxidation was estimated by measuring malondialdehyde (MDA) content using the thiobarbituric acid (TBA) method. Leaf tissue (0.5 g) was homogenized in 0.1% trichloroacetic acid (TCA) and centrifuged. The supernatant was mixed with TBA reagent and heated at 95°C for 30 min, followed by rapid cooling. Absorbance was measured at 532 nm and corrected for nonspecific absorbance at 600 nm.

2.5.4 Catalase Activity

Catalase activity was determined following the method of Chance and Maehly (1955). Fresh leaf tissue (0.5 g) was homogenized in phosphate buffer (pH 7.0) and centrifuged. The enzyme extract was incubated with 3% hydrogen peroxide (H₂O₂) and the decrease in absorbance was monitored at 240 nm. Enzyme activity was expressed as $\mu\text{mol H}_2\text{O}_2$ decomposed min⁻¹ g⁻¹ fresh weight.

2.6 Statistical Analysis

The data were analyzed using analysis of variance (ANOVA) appropriate for factorial randomized block design. The significance of treatment effects was tested at the 5% probability level ($p = 0.05$) and critical difference (CD) values were calculated for comparing treatment means. Data analysis and graphical visualization were performed using R statistical software.

3. Result

3.1 Physiological parameter

3.1.1 Genotype $\times$ incident PPFD direction interaction affecting leaf chlorophyll content (SPAD) in mango

The pooled analysis (2022-23 and 2023-24) revealed a significant interactive effect of genotype and incident PPFD direction on leaf chlorophyll content index (SPAD) in mango (Table 1). Among the evaluated varieties, V3 (Amrapali) consistently recorded the highest chlorophyll content across all directions, followed by V2 (Langra), indicating superior photosynthetic pigment accumulation in

these genotypes, whereas V4 (Fazli) exhibited the lowest chlorophyll content irrespective of direction (Fig. 1a).

Across incident PPFD directions, the South-facing direction (PPFD2) resulted in the highest leaf chlorophyll content for all varieties, followed by East (PPFD3), whereas West (PPFD4) and North (PPFD1) directions recorded comparatively lower values (Fig. 1a). The chlorophyll content ranged from 33.4 to 43.0 SPAD units under south exposure with the maximum observed in Amrapali (43.0 ± 2.3), while the lowest value (28.2 ± 1.4) was recorded in Fazli under west exposure.

The interaction effect ($V \times D$) was statistically significant (CD at $p = 0.05$: 4.40), indicating that varietal response to light direction differed significantly. Amrapali showed a pronounced increase in chlorophyll content under south and east exposures compared to north and west, whereas Fazli exhibited relatively limited variation across directions. The overall distribution pattern across genotypes and directions is further illustrated by the heatmap (Fig. 2a).

Table 1: Interactive effects of genotype and incident PPFD direction on chlorophyll content index (SPAD) in mango: pooled analysis across 2022-23 and 2023-24

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	32.1 ± 1.6	36.7 ± 1.9	35.2 ± 1.8	31.0 ± 1.5
V2 (Langra)	35.9 ± 1.8	40.4 ± 2.1	38.7 ± 2.0	34.3 ± 1.7
V3 (Amrapali)	38.3 ± 2.0	43.0 ± 2.3	41.5 ± 2.2	37.2 ± 1.9
V4 (Fazli)	29.8 ± 1.5	33.4 ± 1.7	32.5 ± 1.6	28.2 ± 1.4
V5 (Sunderja)	31.4 ± 1.6	35.2 ± 1.8	33.9 ± 1.7	29.6 ± 1.5
SEm $\pm$	Variety (V): 0.85	Direction (D): 0.76	$V \times D$: 1.52	
CD ($p = 0.05$)	Variety (V): 2.45	Direction (D): 2.20	$V \times D$: 4.40	

3.1.2 Genotype $\times$ incident PPFD direction interaction affecting panicle chlorophyll content (SPAD) in mango

The pooled analysis (2022-23 and 2023-24) revealed a significant interactive effect of genotype and incident PPFD direction on panicle chlorophyll content index (SPAD) in mango (Table 2). Among the studied varieties, V3 (Amrapali) recorded the highest panicle chlorophyll content across all directions, followed by V2 (Langra), indicating superior chlorophyll retention in reproductive structures, whereas V4 (Fazli) exhibited the lowest SPAD values under all directional exposures (Fig. 1b).

With respect to incident PPFD direction, the South-facing direction (PPFD2) resulted in the highest panicle chlorophyll content, followed by East (PPFD3), while West

(PPFD4) and North (PPFD1) recorded relatively lower values (Fig. 1b). The SPAD values under south exposure ranged from 11.54 to 18.94 with the maximum observed in Amrapali (18.94 ± 1.18), whereas the minimum value (10.02 ± 0.72) was recorded in Fazli under west exposure.

The interaction between genotype and direction was statistically significant (CD at $p = 0.05$: 2.83), indicating differential varietal responses to incident light direction. Amrapali showed a marked increase in panicle chlorophyll content under south and east exposures compared to north and west, whereas Fazli exhibited comparatively smaller variation across directions. The overall pattern across treatments is further illustrated by the heatmap (Fig. 2b).

Table 2 Interactive effects of genotype and incident PPFD direction on panicle chlorophyll content index (SPAD) in mango: pooled analysis across 2022-23 and 2023-24

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	12.71 ± 0.83	14.48 ± 0.94	13.92 ± 0.88	12.11 ± 0.79
V2 (Langra)	15.38 ± 0.97	16.89 ± 1.08	16.21 ± 0.99	14.82 ± 0.91
V3 (Amrapali)	17.62 ± 1.06	18.94 ± 1.18	18.28 ± 1.10	17.03 ± 1.02
V4 (Fazli)	10.63 ± 0.76	11.54 ± 0.85	11.28 ± 0.81	10.02 ± 0.72
V5 (Sunderja)	12.18 ± 0.84	13.22 ± 0.92	12.87 ± 0.88	11.56 ± 0.80
SEm $\pm$	Variety (V): 0.57	Direction (D): 0.49	$V \times D$: 0.98	
CD ($p = 0.05$)	Variety (V): 1.64	Direction (D): 1.41	$V \times D$: 2.83	

3.2 Biochemical Parameters

3.2.1 Effect of genotype and incident PPFD direction on total phenol content in mango: The pooled analysis (2022-23 and 2023-24) indicated a significant influence of genotype and incident PPFD direction on total phenol content (mg GAE 100 g⁻¹ FW) in mango (Table 3). Among the different varieties, V3 (Amrapali) recorded the highest

total phenol content across all directions, followed by V2 (Langra), reflecting their superior capacity for phenolic accumulation, whereas V4 (Fazli) consistently exhibited the lowest phenol content (Fig. 1c).

Regarding the direction of incident PPFD, the South-facing direction (PPFD2) resulted in the highest total phenol content, followed by East (PPFD3), while North (PPFD1)

and West (PPFD4) recorded comparatively lower values (Fig. 1c). The phenol content under south exposure ranged from 21.07 to 34.18 mg GAE 100 g⁻¹ FW with the maximum observed in Amrapali (34.18±1.66), whereas the minimum value (18.33±0.93) was recorded in Fazli under west exposure.

The interaction between genotype and direction was statistically significant (CD at $p = 0.05$: 3.75), indicating

that varieties responded differently to changes in light direction. Amrapali showed a marked increase in total phenol content under south and east exposures compared to north and west, whereas Fazli exhibited relatively smaller variation across directions. The overall distribution pattern across treatments is further illustrated by the heatmap (Fig. 2c).

Table 3 Influence of variety and direction of incident photosynthetic photon flux density (PPFD) on total phenols (mg GAE 100 g⁻¹ FW) in mango (pooled over 2022-23 and 2023-24)

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	23.28±1.12	25.94±1.28	24.63±1.19	22.41±1.05
V2 (Langra)	28.41±1.34	30.72±1.48	29.58±1.39	27.26±1.27
V3 (Amrapali)	32.08±1.51	34.18±1.66	33.02±1.55	30.74±1.42
V4 (Fazli)	19.26±0.98	21.07±1.08	20.41±1.02	18.33±0.93
V5 (Sunderja)	21.54±1.05	23.42±1.16	22.68±1.09	20.36±0.99
SEm ±	Variety (V): 0.74	Direction (D): 0.65	V × D: 1.30	
CD ($p = 0.05$)	Variety (V): 2.14	Direction (D): 1.88	V × D: 3.75	

3.2.2 Effect of genotype and incident PPFD direction on total soluble sugars in mango

The pooled analysis (2022-23 and 2023-24) revealed a significant effect of genotype and incident PPFD direction on total soluble sugars (mg 100 g⁻¹ FW) in mango (Table 4). Among the evaluated varieties, V3 (Amrapali) recorded the highest total soluble sugar content across all directions, followed by V2 (Langra), indicating enhanced carbohydrate accumulation in these genotypes, whereas V4 (Fazli) consistently exhibited the lowest sugar content (Fig. 1e).

With respect to incident PPFD direction, the South-facing direction (PPFD2) resulted in the highest total soluble sugar content, followed by East (PPFD3), whereas North (PPFD1) and West (PPFD4) recorded comparatively lower values

(Fig. 1e). The sugar content under south exposure ranged from 146.85 to 163.78 mg 100 g⁻¹ FW with the maximum observed in Amrapali (163.78±3.98), while the minimum value (142.63±2.88) was recorded in Fazli under west exposure.

The interaction between genotype and direction was statistically significant (CD at $p = 0.05$: 8.92), indicating differential varietal responses to light direction. Amrapali showed a pronounced increase in sugar content under south and east exposures compared to north and west, whereas Fazli exhibited relatively smaller variation across directions. The overall pattern across treatments is further illustrated by the heatmap (Fig. 2e).

Table 4 Influence of variety and direction of incident photosynthetic photon flux density (PPFD) on total soluble sugars (mg 100 g⁻¹ FW) in mango (pooled over 2022-23 and 2023-24)

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	148.62±3.12	152.84±3.46	151.03±3.28	147.56±3.05
V2 (Langra)	154.88±3.38	158.96±3.72	157.41±3.55	153.72±3.26
V3 (Amrapali)	159.42±3.65	163.78±3.98	162.11±3.82	158.34±3.51
V4 (Fazli)	143.21±2.94	146.85±3.18	145.32±3.06	142.63±2.88
V5 (Sunderja)	146.02±3.05	149.74±3.32	148.26±3.18	145.48±2.97
SEm ±	Variety (V): 1.78	Direction (D): 1.54	V × D: 3.08	
CD ($p = 0.05$)	Variety (V): 5.15	Direction (D): 4.46	V × D: 8.92	

3.2.3 Effect of genotype and incident PPFD direction on lipid peroxidation in mango

The pooled analysis (2022-23 and 2023-24) revealed a significant effect of genotype and incident PPFD direction on lipid peroxidation (μmol g⁻¹ FW) in mango (Table 5). Among the different varieties, V3 (Amrapali) recorded the highest lipid peroxidation levels across all directions, followed by V2 (Langra), indicating comparatively higher oxidative stress in these genotypes, whereas V4 (Fazli) consistently exhibited the lowest lipid peroxidation values (Fig. 1d).

With respect to incident PPFD direction, the South-facing direction (PPFD2) resulted in the highest lipid peroxidation, followed by East (PPFD3), whereas North (PPFD1) and

West (PPFD4) recorded comparatively lower values (Fig. 1d). The lipid peroxidation under south exposure ranged from 5.22 to 8.46 μmol g⁻¹ FW with the maximum observed in Amrapali (8.46±0.45), while the minimum value (4.64±0.27) was recorded in Fazli under west exposure.

The interaction between genotype and direction was statistically significant (CD at $p = 0.05$: 1.05), indicating that varieties differed in their response to light direction in terms of oxidative damage. Amrapali showed a noticeable increase in lipid peroxidation under south and east exposures compared to north and west, whereas Fazli exhibited relatively smaller variation across directions. The overall variation across treatments is further illustrated by the heatmap (Fig. 2d).

Table 5: Influence of variety and direction of incident photosynthetic photon flux density (PPFD) on lipid peroxidation ($\mu\text{mol g}^{-1}$ FW) in mango (pooled over 2022-23 and 2023-24)

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	5.94±0.32	6.48±0.36	6.16±0.34	5.68±0.30
V2 (Langra)	7.06±0.38	7.58±0.41	7.29±0.39	6.78±0.35
V3 (Amrapali)	7.98±0.42	8.46±0.45	8.18±0.43	7.68±0.40
V4 (Fazli)	4.82±0.28	5.22±0.31	5.04±0.29	4.64±0.27
V5 (Sunderja)	5.34±0.30	5.86±0.33	5.68±0.31	5.18±0.29
SEm ±	Variety (V): 0.21	Direction (D): 0.18	V × D: 0.36	
CD (p = 0.05)	Variety (V): 0.61	Direction (D): 0.52	V × D: 1.05	

3.2.4 Effect of genotype and incident PPFD direction on catalase activity in mango

The pooled analysis (2022-23 and 2023-24) demonstrated a significant effect of genotype and incident PPFD direction on catalase activity in mango (Table 6). Among the studied varieties, V3 (Amrapali) recorded the highest catalase activity across all directions, followed by V2 (Langra), indicating a stronger antioxidative defence system in these genotypes, whereas V4 (Fazli) consistently exhibited the lowest catalase activity (Fig. 1f).

Regarding incident PPFD direction, the South-facing direction (PPFD2) resulted in the highest catalase activity, followed by East (PPFD3), whereas North (PPFD1) and

West (PPFD4) recorded comparatively lower values (Fig. 1f). Catalase activity under south exposure ranged from 14.62 to 19.42 with the maximum observed in Amrapali (19.42 ± 0.94), while the minimum value (13.88 ± 0.63) was recorded in Fazli under west exposure.

The interaction between genotype and direction was statistically significant (CD at $p = 0.05$: 2.25), indicating differential varietal responses to light direction. Amrapali exhibited a marked increase in catalase activity under south and east exposures compared to north and west, whereas Fazli showed relatively smaller variation across directions. The overall pattern across treatments is further illustrated by the heatmap (Fig. 2f).

Table 6 Influence of variety and direction of incident photosynthetic photon flux density (PPFD) on catalase activity in mango (pooled over 2022-23 and 2023-24)

Variety	North (PPFD1)	South (PPFD2)	East (PPFD3)	West (PPFD4)
V1 (Dashehari)	16.18±0.72	16.74±0.79	16.36±0.75	15.88±0.70
V2 (Langra)	17.62±0.81	18.08±0.87	17.76±0.83	17.28±0.78
V3 (Amrapali)	18.94±0.88	19.42±0.94	19.08±0.90	18.56±0.84
V4 (Fazli)	14.18±0.65	14.62±0.71	14.36±0.68	13.88±0.63
V5 (Sunderja)	15.04±0.69	15.48±0.74	15.18±0.71	14.70±0.66
SEm ±	Variety (V): 0.45	Direction (D): 0.39	V × D: 0.78	
CD (p = 0.05)	Variety (V): 1.30	Direction (D): 1.12	V × D: 2.25	

4. Discussion

The present investigation clearly demonstrates that both genotype and incident photosynthetic photon flux density (PPFD) direction significantly influence chlorophyll content in mango, as reflected by SPAD values in both leaves and panicles. The observed significant interaction between genotype and light direction indicates that varietal performance is not uniform across canopy orientations, highlighting the combined role of genetic makeup and micro-environmental light distribution.

The higher chlorophyll content recorded in south- and east-facing directions can be attributed to enhanced light interception and optimal radiation exposure. In tropical and subtropical regions, south-facing canopy surfaces generally receive greater cumulative solar radiation, particularly during midday, while east-facing surfaces benefit from moderate morning light with relatively lower thermal stress. This balanced irradiance likely promotes chlorophyll biosynthesis and reduces photooxidative damage, thereby improving pigment stability and accumulation (Wang *et al.*, 2021) [25]. Conversely, north- and west-facing orientations receive either limited or more intense afternoon radiation, which may lead to suboptimal photosynthetic conditions or increased photoinhibition, ultimately reducing chlorophyll content (Karunakaran *et al.*, 2026) [11].

Genotypic differences in chlorophyll content further suggest inherent variability in photosynthetic efficiency and adaptability to light environments. Among the studied cultivars, Amrapali consistently exhibited the highest SPAD values in both leaves and panicles, followed by Langra. This superior performance may be associated with enhanced chloroplast development, higher nitrogen assimilation efficiency and better regulation of light-harvesting complexes under varying irradiance conditions (Jutamanee & Onnom, 2016) [10]. In contrast, Fazli recorded the lowest chlorophyll content across all directions, indicating comparatively lower photosynthetic capacity or reduced efficiency in utilizing available light (Khalil *et al.*, 2025) [12]. The pronounced increase in chlorophyll content of Amrapali under south and east exposures suggests a strong genotype × environment interaction, where this cultivar is particularly responsive to favorable light conditions. Such responsiveness may be linked to its canopy architecture, leaf orientation and efficient photoprotective mechanisms, which enable better utilization of incident PPFD (Simkin *et al.*, 2022; Coelho *et al.*, 2025) [6, 23]. On the other hand, the relatively stable but lower chlorophyll content observed in Fazli across directions indicates limited plasticity in response to light variation, which may restrict its photosynthetic performance under suboptimal orientations (Khalil *et al.*, 2025) [12].

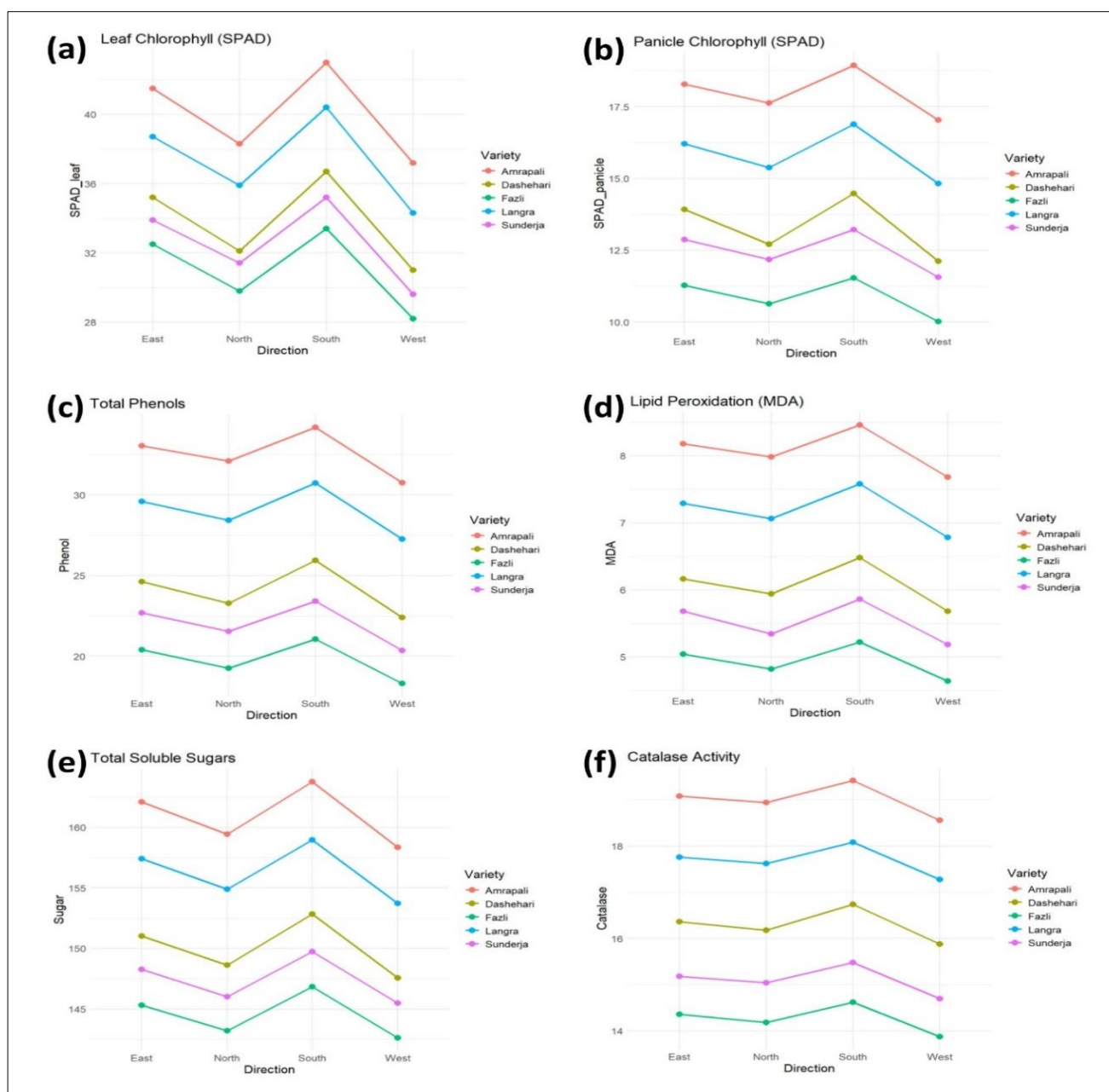


Fig 1: Interaction plots showing the effects of genotype and incident PPFD direction on (a) leaf SPAD, (b) panicle SPAD, (c) total phenols, (d) lipid peroxidation, (e) total soluble sugars and (f) catalase activity in mango (pooled over 2022-23 and 2023-24).

Similar trends observed in both leaf and panicle chlorophyll content indicate that the influence of light direction extends beyond vegetative tissues to reproductive structures. Higher panicle chlorophyll content under south and east exposures suggests improved photosynthetic contribution of panicles, which can play a crucial role in assimilate supply during fruit development (Garrido *et al.*, 2023) [9]. This is particularly important in perennial fruit crops like mango, where reproductive organs can contribute significantly to carbon assimilation (Wang *et al.*, 2023) [24].

The significant interaction effects ($V \times D$) observed for both parameters further confirm that the response of mango cultivars to incident light direction is genotype-dependent. Such interactions have also been reported in other fruit crops, where canopy orientation and light distribution significantly affect physiological traits, including chlorophyll content, photosynthesis and ultimately yield (Cheesman *et al.*, 2025; Kishore *et al.*, 2023) [5, 13].

Overall, the findings emphasize that optimizing canopy light interception through proper orchard orientation and selection of responsive genotypes like Amrapali and Langra can enhance chlorophyll content and photosynthetic efficiency in mango. This has important implications for orchard management practices, including planting geometry, pruning strategies and training systems aimed at maximizing light utilization (Kishore *et al.*, 2023; Nel *et al.*, 2024) [13, 17]. The higher accumulation of total phenols under south- and east-facing directions suggests that increased light availability enhances the activity of the phenylpropanoid pathway. Phenolic compounds are known to play a critical role in photoprotection and antioxidative defense and their increased accumulation under higher irradiance conditions is often associated with improved tolerance to light-induced oxidative stress (Rao and Zheng, 2025) [20]. The consistently superior performance of Amrapali and Langra indicates that these genotypes possess a greater capacity for light-induced

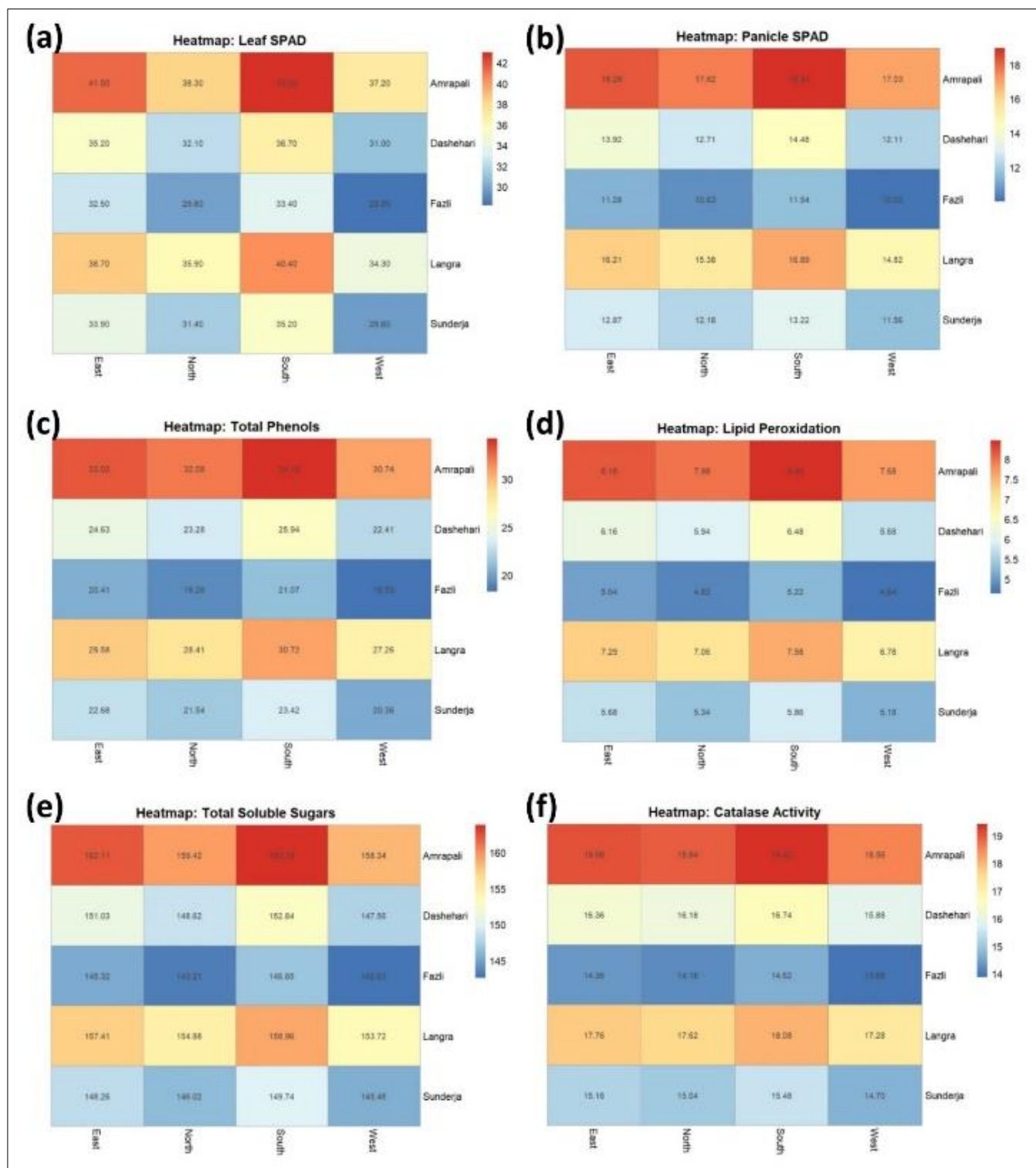


Fig 2: Heatmaps showing the interactive effects of genotype and incident PPFD direction on (a) leaf SPAD, (b) panicle SPAD, (c) total phenols, (d) lipid peroxidation, (e) total soluble sugars and (f) catalase activity in mango (pooled over 2022-23 and 2023-24). Colour scale indicates low (blue) to high (red) values across varieties and directions.

phenolic biosynthesis, whereas the lower levels in Fazli reflect comparatively weaker responsiveness to irradiance (Rosli *et al.*, 2025) ^[21].

A similar trend observed in total soluble sugars indicates that enhanced light interception improves photosynthetic efficiency and carbon assimilation. South and east exposures likely provide optimal irradiance conditions that support sustained photosynthetic activity, thereby promoting carbohydrate synthesis and accumulation (Morales & Kaiser, 2020) ^[16]. The superior sugar accumulation in Amrapali and Langra suggests more efficient source-sink

relationships and assimilate partitioning under favorable light conditions. In contrast, the comparatively lower sugar levels in Fazli may indicate reduced photosynthetic efficiency or less effective assimilate translocation (Malundo *et al.*, 1996) ^[15].

The increase in lipid peroxidation under higher light exposure reflects enhanced oxidative stress due to the overproduction of reactive oxygen species (ROS). High irradiance can lead to excess excitation energy within chloroplasts, resulting in ROS generation and subsequent membrane damage (Wang *et al.*, 2021) ^[25]. The relatively

higher lipid peroxidation observed in Amrapali and Langra suggests that these genotypes experience greater oxidative pressure, likely as a consequence of their higher metabolic activity. However, this increase may also reflect a higher rate of physiological processes rather than inherent susceptibility (Sharma *et al.*, 2012)^[22].

In response to increased oxidative stress, catalase activity was also enhanced under south and east exposures, indicating activation of the antioxidative defense system. Catalase plays a key role in detoxifying hydrogen peroxide and maintaining cellular redox balance under stress conditions (Anjum *et al.*, 2016)^[2]. The higher catalase activity observed in Amrapali and Langra suggests a more efficient antioxidative defense mechanism, enabling these genotypes to cope effectively with elevated ROS levels. Conversely, the lower catalase activity in Fazli may reflect a comparatively weaker defense system (Khalil *et al.*, 2025)^[12].

The significant genotype $\times$ direction interaction across all biochemical parameters further confirms that varietal responses are highly dependent on light environment. Amrapali exhibited a coordinated response involving enhanced phenolic accumulation, increased sugar content, elevated oxidative stress markers and stronger antioxidative enzyme activity. This integrated response suggests an efficient balance between metabolic activity and stress mitigation, allowing better utilization of available light (Malekzadeh *et al.*, 2024)^[14]. In contrast, the relatively limited variation in Fazli indicates lower physiological plasticity under changing light conditions.

6. Conclusion

The findings of the present study clearly demonstrate that both genotype and incident photosynthetic photon flux density (PPFD) direction significantly influence physiological and biochemical characteristics of mango. The significant genotype $\times$ direction interactions observed across all parameters confirm that varietal performance is highly dependent on canopy light orientation. Among the evaluated genotypes, Amrapali emerged as the most superior cultivar, consistently recording the highest leaf and panicle chlorophyll content, total phenols, total soluble sugars, lipid peroxidation and catalase activity across all directions, followed by Langra. In contrast, Fazli exhibited the lowest values for most of the physiological and biochemical traits, indicating comparatively lower photosynthetic efficiency, metabolic activity and adaptability to varying light environments.

With respect to incident PPFD direction, the south-facing orientation proved to be the most favorable, resulting in maximum chlorophyll content (up to 43.0 SPAD in leaves and 18.94 SPAD in panicles), highest phenolic accumulation (up to 34.18 mg GAE 100 g⁻¹ FW) and greatest total soluble sugar content (up to 163.78 mg 100 g⁻¹ FW). The east-facing direction ranked second in promoting these traits, whereas north and west directions recorded comparatively lower values. These findings clearly indicate that enhanced light interception under south and east exposures improves photosynthetic pigment accumulation and carbon assimilation. However, higher irradiance under south and east directions was also associated with increased lipid peroxidation (up to 8.46 μ mol g⁻¹ FW), indicating elevated oxidative stress. This was accompanied by a corresponding increase in catalase activity (up to 19.42),

suggesting the activation of an efficient antioxidative defense system, particularly in high-performing genotypes like Amrapali and Langra. This coordinated response reflects a balance between enhanced metabolic activity and stress mitigation under favorable light conditions.

Overall, the study establishes that optimal light orientation (south and east) combined with responsive genotypes such as Amrapali and Langra significantly enhances photosynthetic efficiency, biochemical attributes and antioxidative capacity in mango. These findings highlight the importance of integrating genotype selection with orchard orientation and canopy management practices to maximize light utilization, improve fruit quality and enhance stress resilience under field conditions.

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