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Biochemical responses of a wild and a cultivated accession of *Momordica charantia* under contrasting soil moisture regimes

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Abstract. *Nguyen TV, Kasim M, Anggraini T, Doan LN, Duong NV, Vo TCT, Do ST. 2026. Biochemical responses of a wild and a cultivated accession of* Momordica charantia *under contrasting soil moisture regimes. Biodiversitas 27 (4): d270403. https://doi.org/10.13057/biodiv/d270403.* Water deficit is a major abiotic constraint affecting plant growth, functional traits, and genotype-level variation under field conditions. This study evaluated growth performance and antioxidant-related biochemical traits of a wild and a cultivated accession of bitter melon (*Momordica charantia*) under three soil moisture regimes (80%, 65%, and 50% field capacity) using a split-plot field design. Total Phenolic Content (TPC), Total Flavonoid Content (TFC), antioxidant activity (DPPH radical scavenging), and biomass-related traits were quantified in leaves at defined crop ages and in fruits at commercial maturity, and yield-based biochemical indices were calculated to integrate concentration and dry matter accumulation. Moderate moisture deficit (65% field capacity) was associated with increased TPC, TFC, and antioxidant activity in several instances, while severe deficit (50% field capacity) reduced biomass stability and biochemical performance, particularly in the cultivated accession. Fruits accumulated greater absolute biochemical yields per plant, whereas leaves exhibited stronger concentration-based responsiveness to moisture variation. The wild accession generally showed greater biochemical plasticity and higher yield-integrated metabolite production than the cultivated accession under moisture stress. These findings demonstrate a clear trade-off between metabolite concentration and biomass accumulation under drought conditions, with moderate stress generally supporting higher biochemical performance. The results highlight the importance of genotype selection and irrigation management in maximizing functional traits and support the use of wild germplasm in breeding strategies for improved drought adaptation in bitter melon.

Keywords: Accession-specific responses, bitter melon, crop wild relatives, phenolic and flavonoid responses, soil moisture regimes

INTRODUCTION

Water availability is a major environmental factor regulating plant growth, metabolism, and survival under increasing climate variability (FAO 2017, 2021; IPCC 2022). Water deficit disrupts cellular homeostasis and promotes Reactive Oxygen Species (ROS) formation, triggering antioxidant defense systems and metabolic adjustment that help protect cells under abiotic stress (Choudhury et al. 2017; Hasanuzzaman et al. 2020).

Bitter melon (*Momordica charantia* L.) is widely cultivated for its nutritional and medicinal value, whereas its wild relatives persist across diverse habitats, including water-limited environments. Previous work has mainly emphasized agronomic performance, growth, and yield responses under deficit irrigation (Nguyen et al. 2025). These studies revealed contrasting drought resilience between wild and cultivated accessions, indicating an important role of genetic background. However, comparative biochemical responses of wild and cultivated bitter melon under field soil-moisture gradients remain poorly understood.

Domestication reshapes plant traits through selection for productivity, uniformity, and yield stability, often modifying genetic diversity and stress-related regulatory architecture (Dwivedi et al. 2016; Gaut et al. 2018). Wild genotypes often retain broader phenotypic and biochemical plasticity, including more dynamic regulation of secondary metabolites under stress. This pattern relates to Intraspecific Trait Variation (ITV), an important component of biodiversity that contributes to plant adaptation under heterogeneous environments and can influence ecosystem functioning, species interactions, and resilience to climate variability (Westerband et al. 2021; Cope et al. 2022). In crops, domestication may alter this variation relative to wild relatives, making genotype-dependent biochemical plasticity an important aspect of crop adaptation.

Genetic evidence also supports divergence between wild and cultivated bitter melon. Population genomic analyses have shown substantial differentiation between wild and cultivated accessions (Cui et al. 2020; Matsumura et al. 2020). More broadly, studies in Cucurbitaceae indicate that domestication and breeding have reshaped structural variation and stress-related pathways, potentially influencing responses to abiotic constraints (Ma et al. 2022). These findings suggest that biochemical responses to water limitation may differ among bitter melon genotypes with contrasting domestication backgrounds.

Phenolic compounds and flavonoids are key secondary metabolites involved in plant defense, photoprotection, and redox balance. Their biosynthesis is regulated under abiotic stress through ROS signaling and phenylpropanoid metabolism (Hasanuzzaman et al. 2020; Dong and Lin 2021), and this regulation varies with stress intensity and developmental stage (Zhang et al. 2024; Ninkuu et al. 2025). Under drought, activation of the phenylpropanoid pathway, including phenylalanine ammonia-lyase, is often associated with increased polyphenol accumulation and ROS scavenging capacity (Sharma et al. 2019). Controlled studies also show that phenolic accumulation may be coordinated with antioxidant enzyme activity and oxidative stress modulation (Mohagheghian et al. 2025). However, higher phenolic or flavonoid concentrations under moisture deficit should not automatically be interpreted as improved nutritional value, because severe stress may also reduce biomass and overall plant performance.

Recent studies in *M. charantia* show that irrigation can affect growth, fruit yield, and biochemical traits, especially in interaction with nutrient supply and mycorrhizal inoculation (Dolatmand-Shahri et al. 2024). Additional evidence indicates that drought can modify antioxidant activity, phenolic responses, and growth performance in a genotype-dependent manner (Hatamian et al. 2026). Even so, field-based comparisons between wild and cultivated accessions across graded soil-moisture regimes remain limited.

Therefore, this study evaluated the biochemical responses of a wild and a cultivated accession of *M. charantia* under graded soil moisture in a field-based split-plot experiment. Total phenolic content, total flavonoid content, antioxidant activity, and biomass-related traits were quantified in leaves sampled at defined crop ages and in fruits harvested at commercial maturity. By integrating concentration-based measurements with yield-based biochemical indices at the whole-plant level, this study aimed to characterize accession-specific biochemical variation under moisture reduction and to provide empirical evidence relevant to genotype-level diversity and stress adaptation in bitter melon. We hypothesized that moderate moisture deficit (65% field capacity) would promote metabolite accumulation while maintaining sufficient biomass to maximize yield-integrated biochemical output, and that the wild accession would show greater biochemical plasticity and resilience than the cultivated accession under reduced moisture conditions.

MATERIALS AND METHODS

Experimental site and growing conditions

The experiment was conducted during the dry season of 2024-2025 at the experimental field of Kien Giang University, Chau Thanh District, Kien Giang Province, Vietnam (9°09′14″ N, 105°14′25″ E). A tropical monsoon climate with a pronounced dry period characterizes the site. The soil at the experimental site was classified as sandy loam, consisting of approximately 62% sand, 30% silt, and 8% clay, with a pH of 6.5±0.06 and electrical conductivity of 181.6 µS cm^{-1}. The Field Capacity (FC) of the soil was determined gravimetrically and averaged 34.7±1.8%. During the experimental period, mean daily air temperature and relative humidity were 28.8±0.6°C and 71.1±1.2%, respectively. The experiment was conducted under open-field conditions without rainfall interference, ensuring controlled maintenance of soil moisture levels through irrigation management.

Plant materials

Two accessions of bitter melon (*M. charantia*) were evaluated: a wild accession (TCCS VP-BT08/16) and a cultivated accession (TCCS VP-BT01/14). Seeds were provided by Van Phat Company (VAPHACO, Vietnam). Smaller fruits and greater phenotypic heterogeneity characterize the wild accession, whereas the cultivated accession represents a commercially selected type with larger fruits and more uniform growth. Seedlings were raised under nursery conditions and transplanted to the field on 4 December 2024 at the 3-4 true-leaf stage.

Experimental design and irrigation treatments

The experiment was arranged in a split-plot design with three replications. Accession (wild and cultivated) was assigned as the main-plot factor, and soil moisture regime as the subplot factor. Three irrigation levels were established based on fractions of field capacity: 80% FC (well-watered control), 65% FC (moderate deficit), and 50% FC (severe deficit). Each subplot measured 30 m^2 (3 m × 10 m) and consisted of two rows with 20 plants per subplot. Plants were spaced at 1.0 × 1.0 m. To minimize border effects, 10 centrally located plants per subplot were used for repeated measurements and fruit harvest. The experimental unit for statistical analysis was the subplot mean within each replication.

Crop management practices

All plots received uniform agronomic management throughout the growing season to minimize confounding effects unrelated to irrigation treatments. The soil was amended with well-decomposed organic manure prior to transplanting at rates consistent across all plots. Chemical fertilizers were applied following local recommendations for bitter melon cultivation on sandy loam soils, providing a total of 184 kg N, 112 kg P_2O_5, and 124 kg K_2O per ha. A basal application was incorporated before transplanting, followed by four split top-dressings at two-week intervals starting from the 4-6 leaf stage. To suppress weed growth and reduce soil evaporation, all plots were mulched uniformly with black polyethylene sheets. Plants were trained vertically using a triangular trellis system combined with a 20-cm mesh net to support climbing growth, improve canopy aeration, and facilitate uniform light interception and harvesting.

Irrigation management and soil moisture monitoring

Soil moisture levels were regulated using an automated drip irrigation system equipped with soil moisture sensors (DKAD03, Loc Phat Co., Vietnam) installed at a depth of

15-20 cm in each subplot. Field Capacity (FC) was determined gravimetrically at the beginning of the experiment following soil saturation and drainage equilibrium. Target moisture levels corresponding to 80%, 65%, and 50% of FC were maintained throughout the growing period. Soil moisture readings from the sensors were monitored continuously to ensure that each treatment remained within its predefined FC range. Sensor measurements were cross-checked every 10 days using a handheld soil moisture meter (DM-15, Takemura, Japan). Deviations exceeding ±3% of the target FC were corrected by adjusting irrigation frequency and duration. Although cumulative irrigation volumes were not quantified, continuous monitoring and periodic verification ensured consistent separation among the designated soil moisture regimes throughout the experimental period.

Sample collection and processing

Leaf samples

Within each subplot, six plants (separate from fruit-harvest plants) were randomly selected for leaf sampling at 60, 80, 100, and 120 Days After Transplanting (DAT). Mature, healthy leaves were collected from these plants. Leaves collected from the six plants within each subplot were pooled to form one composite biological sample per subplot at each sampling date. This composite sample represented the biological replicate for biochemical analysis. All biochemical assays were conducted in technical triplicate to ensure analytical precision. Leaves were washed, air-dried, sliced (1-2 mm), vacuum-dried at 65°C and -70 kPa for 48 h, and stored under vacuum at -20°C until analysis.

Fruit samples

Ten centrally located plants per subplot were designated for fruit harvest. Fruits were harvested immediately upon reaching commercial maturity, because bitter melon fruits remain at the optimal harvest stage for only a short period (approximately 2-3 days) before progressing toward ripening. Fruits were washed, air-dried at room temperature, and sliced into approximately 1-2 mm thickness prior to dehydration. Drying was conducted in a vacuum oven at 65°C under -70 kPa for 48 h, following the protocol described by Tan et al. (2014). After drying, samples were ground and passed through a 1-mm mesh sieve to obtain a homogeneous powder.

To obtain an integrated representation of seasonal biochemical performance, dried fruit samples collected throughout the growing period within each subplot were pooled and thoroughly homogenized prior to subsampling. Consequently, fruit biochemical measurements reflect cumulative seasonal responses rather than stage-specific variation. All powdered samples were stored under vacuum at -20°C until analysis.

Biochemical analyses

TPC was measured using the Folin-Ciocalteu method (Ainsworth and Gillespie 2007) and expressed as mg Gallic Acid Equivalents (GAE) g^{-1} Dry Weight (DW). TFC was determined by the aluminum chloride colorimetric method (Chang et al. 2002) and expressed as mg Quercetin Equivalents (QE) g^{-1} DW. Antioxidant activity was evaluated using the DPPH radical scavenging assay following Brand-Williams et al. (1995) with modifications. Extract solutions were prepared in methanol at five concentrations ranging from 0.5 to 2.5 mg mL^{-1}. A DPPH solution (1000 µg mL^{-1}) was prepared in methanol and stored in the dark at 4°C for 24 h prior to use. For each assay, 1 mL of extract solution was mixed with 1 mL of DPPH solution and incubated in the dark at room temperature for 30 min. Absorbance was measured at 517 nm using a UV-Vis Spectrophotometer (Shimadzu 1800, Japan). The control consisted of 1 mL of methanol mixed with 1 mL of DPPH solution.

Radical scavenging activity was calculated as:

$$\text{Inhibition (\%)} = \frac{A_0 - A}{A_0} \times 100$$

Where :

A_0 : The absorbance of the control

A : The absorbance of the extract

A linear regression model ($y = ax + b$) was constructed using Microsoft Excel 2016, where y represents percentage inhibition and x represents extract concentration (mg mL^{-1}).

The IC_{50} value **(**expressed as mg extract mL^{-1} required to achieve 50% inhibition**)** was calculated as:

$$IC_{50} = \frac{50 - b}{a}$$

The coefficient of determination (R^2) was used to evaluate the goodness-of-fit of the regression model. All measurements were conducted in technical triplicate for each biological replicate.

Calculation of yield-based biochemical traits

To integrate concentration-based measurements with biomass production, yield-based biochemical indices were calculated as:

$$\text{TPC\_yield (mg plant}^{-1}\text{)} = \text{Leaf dry weight (g plant}^{-1}\text{)} \times \text{TPC (mg GAE g}^{-1}\text{ DW)}$$

$$\text{TFC\_yield (mg plant}^{-1}\text{)} = \text{Leaf dry weight (g plant}^{-1}\text{)} \times \text{TFC (mg QE g}^{-1}\text{ DW)}$$

Equivalent calculations were applied for fruit biochemical yield. These indices represent the total biochemical output per plant by integrating metabolite concentration with biomass production.

Handling of missing data

Due to the earlier senescence of the cultivated accession under severe moisture deficit, measurements at 100 and 120 DAT were not available for this genotype in certain treatments. Therefore, statistical analyses were conducted separately for each sampling date using available valid observations. No data imputation was performed.

Statistical analysis

Data were analyzed using a split-plot ANOVA framework. Accession was treated as the main-plot factor, soil moisture regime as the subplot factor, and replication as a random effect.

For leaf traits measured across developmental stages, analyses were conducted separately for each sampling date to characterize stage-specific responses. Because fruit biochemical traits represented seasonal composites, time was not included as a repeated factor.

Normality and homogeneity of variance were assessed using Shapiro-Wilk and Levene's tests. When necessary, data were log- or square-root transformed prior to analysis. Mean comparisons were performed using Duncan's Multiple Range Test at $p<0.05$. All statistical analyses were conducted using SPSS version 20.0.

RESULTS AND DISCUSSION

Effects of soil moisture on leaf biomass

Leaf fresh weight and dry weight varied significantly among accessions and developmental stages, whereas the main effect of soil moisture was not consistently significant at early sampling times and became more pronounced at later stages (Tables 1 and 2). At 60 and 80 DAT, differences among soil moisture treatments were generally not statistically significant, although biomass differed between the two accessions. From 100 DAT onward, soil moisture significantly affected both fresh and dry leaf biomass, indicating stronger treatment effects during later stages of plant development.

Genotype effects were stage-dependent. Across most sampling dates, the wild accession produced substantially greater leaf biomass than the cultivated accession, particularly from 80 DAT onward. For example, at 80 DAT, the fresh leaf yield of the wild accession exceeded 135 g plant^{-1} under both 80% and 65% FC, whereas the cultivated accession produced approximately 67 g plant^{-1} under comparable moisture conditions (Table 1). Similar patterns were observed for dry leaf biomass (Table 2).

Responses to soil moisture differed between the two accessions, as indicated by significant genotype × moisture interactions at several sampling dates. In the wild accession, leaf biomass tended to decline under severe moisture deficit (50% FC), particularly at later developmental stages. In contrast, the cultivated accession showed a less consistent response pattern across moisture treatments, especially at earlier sampling stages.

Table 1. Effects of soil moisture levels on fresh leaf biomass (g plant^{-1}) of wild and cultivated bitter melon accessions at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	61.17ab C	135.87a A	123.33a AB	111.17a B	***
	65	63.30a C	135.40a A	126.17a A	101.77b B	***
	50	62.17ab B	102.03b A	101.03b A	85.33c A	**
Cultivated accession	80	46.13c A	66.83c A	54.10c A	-	ns
	65	45.53c B	67.60cb A	-	-	*
	50	49.47bc B	91.07bc A	-	-	***
Sig. (A)		**	***	***	***	
Sig. (B)		ns	ns	***	**	
Sig. (A×B)		ns	*	**	**	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences (P<0.05, Duncan's test). Significance levels: *: P<0.05, **: P<0.01, ***: P<0.001, ns: Not significant, Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence. Wild accession: TCCS VP-BT08/16, Cultivated accession: TCCS VP-BT01/14

Table 2. Effects of soil moisture levels on dry leaf biomass (g plant^{-1}) of wild and cultivated bitter melon accessions at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	11.58ab C	27.44a A	24.98a AB	23.50a B	***
	65	12.47a C	27.57a A	26.28a A	21.95b B	***
	50	12.40a B	20.81b A	20.97b A	19.04c A	**
Cultivated accession	80	8.74c A	12.88c A	10.59c A	-	ns
	65	8.87c A	13.49c A	-	-	ns
	50	9.75bc B	18.80b A	-	-	***
Sig. (A)		**	***	***	***	
Sig. (B)		ns	ns	**	**	
Sig. (A×B)		ns	*	**	**	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences (P<0.05, Duncan's test). Significance levels: *: P<0.05, **: P<0.01, ***: P<0.001, ns: Not significant, Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Although general trends were broadly similar between fresh and dry leaf biomass, some differences in treatment responses were observed between the two measurements. These discrepancies may partly reflect variation in leaf water content among treatments, because fresh biomass includes both structural biomass and tissue hydration, whereas dry biomass more directly represents accumulated dry matter.

Fruit yield response to soil moisture regimes

Fruit biomass per plant (Table 8) generally decreased under severe moisture deficit (50% FC), although the response across the moisture gradient was not strictly linear. Both accessions produced relatively high fruit biomass under well-watered and moderate moisture conditions (80% and 65% FC), whereas a marked reduction was observed at 50% FC.

Genotype effects were evident across moisture treatments. The cultivated accession generally produced slightly greater fruit biomass than the wild accession under comparable soil moisture regimes, particularly under well-watered conditions. However, both accessions exhibited reductions in fruit biomass under severe deficit, indicating that reproductive biomass production was sensitive to substantial moisture limitation.

Leaf concentration-based biochemical responses

Total Phenolic Content (TPC)

Leaf Total Phenolic Content (TPC) varied across developmental stages and accessions, whereas the influence of soil moisture differed among sampling dates (Table 3). At 60 DAT, differences among soil moisture treatments were not statistically significant, although variation among accessions was observed. At 80 and 100 DAT, soil moisture significantly affected TPC, with several treatments showing higher phenolic concentrations under reduced moisture conditions. However, the direction of this response was not uniform across accessions and stages.

Genotype differences became more evident during later developmental stages. At 100 and 120 DAT, the wild accession generally exhibited higher TPC values than the cultivated accession, particularly under moderate and severe moisture deficit. Significant genotype × moisture interactions observed at 100 DAT indicate that the magnitude of phenolic accumulation under different soil moisture regimes depended on accession-specific responses. Overall, TPC responses to soil moisture did not follow a simple monotonic trend, suggesting that both developmental stage and genotype-specific regulation influence phenolic accumulation in bitter melon leaves.

Total Flavonoid Content (TFC)

Leaf Total Flavonoid Content (TFC) varied significantly among accessions, soil moisture treatments, and developmental stages (Table 4). The wild accession consistently exhibited substantially higher flavonoid concentrations than the cultivated accession across all sampling dates. Soil moisture significantly affected TFC at all sampling times. However, the response pattern did not follow a simple monotonic trend across the moisture gradient. In several cases, moderate moisture deficit (65% FC) resulted in elevated flavonoid concentrations, whereas at other stages the highest values occurred under severe deficit (50% FC). For example, at 60 DAT the highest TFC in the wild accession occurred under 65% FC, whereas at 80 DAT the maximum values were observed under 50% FC.

Genotype × moisture interactions became significant at later developmental stages (100 and 120 DAT), indicating that the magnitude of flavonoid accumulation under different moisture regimes depended on accession-specific responses. These results suggest that both genetic background and environmental conditions influence flavonoid accumulation in bitter melon leaves.

Antioxidant activity

Antioxidant activity, evaluated using the DPPH assay (IC_{50}), varied among accessions and developmental stages, with soil moisture effects differing across sampling times (Table 5). Lower IC_{50} values indicate stronger radical scavenging activity.

Soil moisture significantly influenced IC_{50} at 60 and 80 DAT, whereas differences among moisture treatments were not statistically significant at later stages. In several cases, moderate moisture deficit (65% FC) was associated with lower IC_{50} values compared with the well-watered treatment, indicating enhanced antioxidant activity under moderate stress conditions. However, this pattern was not consistent across all stages, and in the wild accession, the lowest IC_{50} values at 100 DAT were observed under severe deficit (50% FC).

Genotype effects were evident at several sampling dates. The cultivated accession generally exhibited higher IC_{50} values than the wild accession, particularly at 60 and 100 DAT, indicating weaker antioxidant activity. Significant genotype × moisture interactions at 100 and 120 DAT further demonstrate that antioxidant responses to soil moisture varied between the two accessions during later developmental stages.

Fruit biochemical yield and seasonal performance

Seasonal fruit biochemical performance is summarized within the organ-level integrated analysis (Table 8). Fruit tissues contributed substantially to total biochemical output per plant due to their much greater biomass accumulation compared with leaves. Across both accessions, fruit biomass generally declined under severe moisture deficit (50% FC), resulting in lower integrated biochemical yields in several cases.

Moderate moisture deficit (65% FC) often maintained relatively high biochemical yields, particularly for flavonoid output, although the highest values were not consistently associated with a single moisture treatment across accessions. For example, the wild accession exhibited the highest seasonal TPC yield at 65% FC, whereas the cultivated accession showed the greatest phenolic yield under well-watered conditions (80% FC).

Table 3. Effects of accession and soil moisture on leaf total phenolic content (mg GAE g^{-1} DW) in bitter melon at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	24.98a A	17.89cd BC	23.51bc A	16.58b C	*
	65	22.27a B	25.70ab AB	30.73a A	24.20a AB	*
	50	25.18a AB	29.17a A	26.38ab AB	19.72ab B	*
Cultivated accession	80	23.75a A	15.82d B	19.78c C	-	**
	65	21.01a A	19.50bc A	-	-	ns
	50	26.25a A	22.53bc A	-	-	ns
Sig. (A)		ns	**	***	***	
Sig. (B)		ns	***	**	ns	
Sig. (A×B)		ns	ns	***	ns	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences ($P<0.05$, Duncan's test). Statistical significance is denoted as: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant, Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Table 4. Effects of accession and soil moisture on leaf total flavonoid content (mg QE g^{-1} DW) in bitter melon at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	16.44c A	14.37b A	6.47c B	8.45b B	**
	65	27.84a A	19.81a B	8.69b C	16.71a B	**
	50	22.63b A	22.91a A	10.50a C	15.01a B	***
Cultivated accession	80	9.22d A	7.68c A	6.76c A	-	ns
	65	14.61c A	8.92c A	-	-	ns
	50	13.29cd A	11.38bc A	-	-	ns
Sig. (A)		***	***	***	***	
Sig. (B)		**	**	***	***	
Sig. (A×B)		ns	ns	***	***	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences ($P<0.05$, Duncan's test). Statistical significance: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant. Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Table 5. Effects of accession and soil moisture on antioxidant activity (IC$_{50}$, mg extract mL^{-1}) of bitter melon leaves at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	1.92b A	1.59ab B	1.78a AB	1.66a B	*
	65	1.64b A	1.45b AB	1.46b AB	1.40b B	*
	50	1.91b A	1.51ab B	1.37b B	1.48b B	*
Cultivated accession	80	2.42a A	1.45b C	1.68a B	-	***
	65	1.93b A	1.44b A	-	-	ns
	50	2.31a A	1.75a B	-	-	**
Sig. (A)		***	ns	***	***	
Sig. (B)		**	*	***	*	
Sig. (A×B)		ns	ns	***	*	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences ($P<0.05$, Duncan's test). Statistical significance: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant. Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Genotype differences were evident for several fruit biochemical traits, with the wild accession generally exhibiting higher phenolic and flavonoid yields than the cultivated accession under comparable moisture regimes. These patterns indicate accession-specific differences in reproductive biochemical allocation under graded soil moisture conditions.

Leaf yield-integrated biochemical indices

To integrate concentration-based measurements with biomass production, yield-based biochemical indices were calculated for leaves (Tables 6 and 7). These indices revealed patterns that differed from concentration-only measurements because total biochemical yield per plant reflects both metabolite concentration and leaf biomass.

Across most sampling stages, the wild accession produced substantially greater phenolic and flavonoid yields than the cultivated accession, reflecting its higher leaf biomass production. Soil moisture effects on yield-integrated indices varied across developmental stages and did not follow a consistent monotonic pattern along the moisture gradient.

When considered together with concentration-based traits (Table 3) and biomass production (Table 2), these results indicate that yield-integrated biochemical performance is determined by the interaction between metabolite concentration and biomass accumulation. In several cases, moderate moisture deficit (65% FC) enhanced metabolite concentrations while maintaining relatively high biomass, resulting in elevated yield-based biochemical output. In contrast, under severe moisture deficit (50% FC), reductions in biomass often limited total biochemical yield despite moderate or increased metabolite concentrations. This pattern highlights a trade-off between concentration-based responses and biomass production across moisture regimes.

In several cases, moderate moisture deficit (65% FC) resulted in high biochemical yields, particularly when leaf biomass remained relatively stable. However, at other stages, the highest yields occurred under either well-watered or severe deficit treatments, indicating that yield-integrated biochemical output is jointly determined by the interaction between biomass dynamics and metabolite accumulation.

Significant genotype × moisture interactions observed at several sampling dates further demonstrate that accession-specific differences in leaf biomass production strongly influenced whole-plant biochemical performance under soil moisture variation.

Whole-plant and organ-level interactions

Whole-plant integrated biochemical traits and organ-level comparisons are summarized in Table 8. Plant organs exerted a strong main effect on biomass and biochemical yield, reflecting clear differences between vegetative (leaf) and reproductive (fruit) tissues in biomass allocation and biochemical accumulation. Fruit tissues consistently produced much greater biomass and consequently contributed more strongly to total biochemical yield per plant than leaves.

Three-way ANOVA (Accession × Moisture × Organ) revealed significant interaction effects for total biomass and seasonal TPC yield, whereas the interaction was not significant for TFC yield. These results indicate that responses to declining soil moisture differed not only between accessions but also between plant organs.

Overall, leaves showed greater variability in concentration-based biochemical traits across moisture regimes, whereas fruits contributed substantially to whole-plant biochemical output primarily through higher biomass accumulation.

Table 6. Effects of accession and soil moisture on leaf total phenolic yield (mg GAE plant^{-1}) in bitter melon at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	293.00ab C	490.33b AB	588.19b A	389.68b BC	***
	65	278.18ab C	711.95a AB	806.15a A	532.48a B	**
	50	314.28a C	615.05ab A	557.45b AB	379.63c AB	*
Cultivated accession	80	206.18ab A	204.17e A	209.71c A	-	ns
	65	187.74b A	259.03de A	-	-	ns
	50	253.96ab A	423.97cd A	-	-	ns
Sig. (A)		*	***	***	***	
Sig. (B)		ns	*	*	ns	
Sig. (A×B)		ns	***	***	***	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences ($P<0.05$, Duncan's test). Significance levels: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant. Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Table 7. Effects of accession and soil moisture on leaf total flavonoid yield (mg QE plant^{-1}) in bitter melon at different growth stages

Accession (A)	Soil moisture (B, %)	Day After Transplanting (DAT)				Sig.
		60	80	100	120	
Wild accession	80	190.21c B	390.86b A	162.34b B	199.46c B	***
	65	342.93a BC	537.22a A	228.64a C	366.79a B	**
	50	281.57b B	476.43ab A	219.15a B	284.41b B	***
Cultivated accession	80	80.41d A	98.64 c A	71.41c A	-	ns
	65	129.54d A	120.12c A	-	-	ns
	50	129.58d B	212.60 c A	-	-	*
Sig. (A)		***	***	***	***	
Sig. (B)		**	ns	ns	**	
Sig. (A×B)		***	***	**	**	

Note: Different letters within columns (small letter) or rows (capital letter) indicate significant differences ($P<0.05$, Duncan's test). Significance levels: *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant. Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (A×B): Accession × soil moisture interaction. Dashes (-) indicate missing data due to leaf senescence

Table 8. Effects of accession, soil moisture, and plant organ on biomass and seasonal biochemical yields in bitter melon

Accession (A)	Soil moisture (B, %)	Part of the plant (C)	Total biomass (g plant^{-1})	Seasonal TPC yield (mg GAE plant^{-1})	Seasonal TFC yield (mg QE plant^{-1})
Wild accession	80	Fruit	1737.93a	2862.46abc	1967.73ab
	65		1599.60b	3189.38a	2297.06a
	50		1111.17c	2994.17ab	1749.11bc
	80	Leaf	431.53e	1761.20de	942.87e
	65		426.63e	2328.76cd	1475.58cd
	50		350.57e	1866.40de	1261.56de
Cultivated accession	80	Fruit	1869.47a	2640.59abc	1259.70de
	65		1779.27a	2517.30bc	1673.72bc
	50		834.57d	1389.14e	978.73e
	80	Leaf	167.07f	620.05i	250.46f
	65		113.13f	446.77i	249.66f
	50		140.53f	677.93f	342.18f
Sig. (A)			***	***	***
Sig. (B)			***	*	*
Sig. (C)			***	***	***
Sig. (A×B×C)			**	**	ns

Note: Different letters within columns indicate significant differences ($P<0.05$, Duncan's test). TPC: Total Phenolic Content, TFC: Total Flavonoid Content, Sig. (A): Main effect of accession, Sig. (B): Main effect of soil moisture, Sig. (C): Main effect of plant organ, Sig. (A×B×C): Accession × soil moisture × plant organ interaction. *: $P<0.05$, **: $P<0.01$, ***: $P<0.001$, ns: Not significant. Seasonal leaf TPC and TFC yields were calculated as cumulative sums of per-plant yields across the four sampling dates (60, 80, 100, and 120 DAT). For fruits, biochemical analyses were based on composite seasonal samples prepared from harvests collected throughout the fruiting period

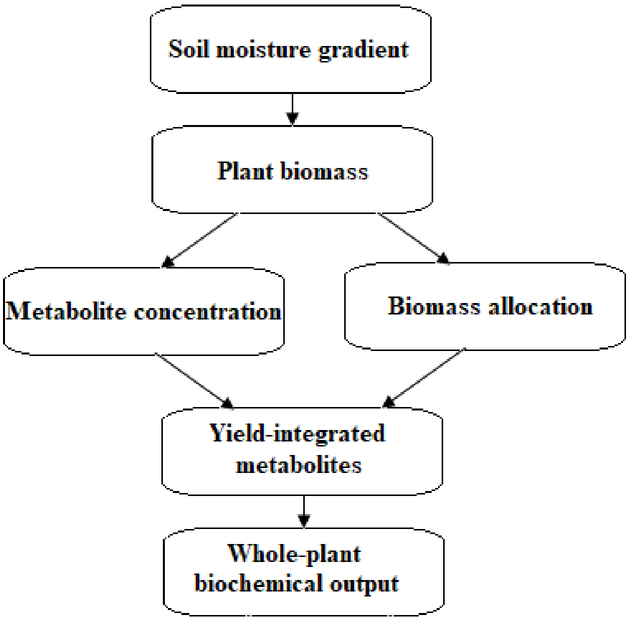

Figure 1. Conceptual framework illustrating the relationships among soil moisture regimes, plant biomass production, metabolite concentration, and yield-integrated biochemical output in bitter melon

Discussion

To facilitate interpretation of these results, a conceptual framework illustrating the relationships among soil moisture regimes, biomass production, metabolite concentration, and yield-integrated biochemical output is presented in Figure 1.

Declining soil moisture resulted in consistent reductions in vegetative biomass in both accessions of *M. charantia*, particularly under severe deficit. Growth inhibition under drought is commonly associated with reduced cell expansion, stomatal limitation, and constrained carbon assimilation (Hasanuzzaman et al. 2020; IPCC 2022). Antioxidant regulation and growth suppression under water limitation have been widely documented across plant species and are closely associated with Reactive Oxygen Species (ROS)-mediated signaling networks that coordinate stress perception and metabolic adjustment (Choudhury et al. 2017; Hasanuzzaman et al. 2020). The present findings align with these general physiological patterns, showing that severe soil moisture reduction was associated with lower vegetative biomass, while moderate moisture deficit often maintained growth levels closer to those observed under well-watered conditions**.** However, the magnitude and timing of biomass responses differed between the two accessions and across developmental stages, indicating that growth sensitivity to soil moisture was not uniform within the species.

Moderate moisture deficit (65% FC) was associated with elevated leaf phenolic and flavonoid concentrations at specific developmental stages. Activation of phenylpropanoid metabolism under moderate stress has been widely linked to ROS-mediated signaling and coordinated antioxidant regulation (Hasanuzzaman et al. 2020), involving complex crosstalk between hormonal and redox signaling pathways (Yaqoob et al. 2022). Phenylpropanoid metabolism itself plays a central role in these responses (Dong and Lin 2021). Enzymatic activation of key phenylpropanoid components, including phenylalanine ammonia-lyase, is frequently reported under drought conditions and contributes to enhanced polyphenol accumulation (Sharma et al. 2019). Experimental evidence from controlled drought studies further indicates that increased phenolic concentration can be accompanied by coordinated modulation of antioxidant enzyme activity and oxidative stress markers (Mohagheghian et al. 2025). Phenolic compounds function not only as antioxidants but also as modulators of plant-environment interactions and developmental processes (Agati et al. 2012; Dong and Lin 2021). Recent syntheses emphasize that phenylpropanoid pathway activity is dynamically regulated in response to environmental cues rather than uniformly upregulated under all stress intensities (Zhang et al. 2024; Ninkuu et al. 2025). The stage-dependent increases observed in the present study, therefore, suggest regulated metabolic adjustment rather than a uniform stress-induced accumulation of phenolic compounds.

In contrast, severe deficit (50% FC) did not consistently enhance phenolic or flavonoid concentrations beyond levels observed at moderate stress. Under intense water limitation, reduced photosynthetic carbon supply, and restricted growth may limit substrate availability for secondary metabolism, resulting in stabilization or decline of metabolite accumulation. Trade-offs between growth and metabolite-mediated stress responses have been described in crop systems subjected to drought (Zhang et al. 2024). Irrigation-dependent reductions in fruit yield and associated biochemical traits have likewise been documented in *M. charantia* under deficit conditions, particularly in interaction with mycorrhizal inoculation and nutrient supply (Dolatmand-Shahri et al. 2024). Additional experimental evidence indicates that drought intensity can alter growth performance and antioxidant-related traits in bitter melon (Hatamian et al. 2026). Importantly, the integrated yield-based indices in this study indicate that increases in metabolite concentration do not necessarily translate into greater biochemical production at the whole-plant level. In several cases, severe moisture deficit reduced total biochemical output primarily through reductions in biomass, even when concentration-based measurements remained relatively stable. These findings underscore the importance of distinguishing between tissue concentration and yield-integrated biochemical production when evaluating stress responses.

Genotype-dependent differences in biochemical modulation and growth response were evident across traits and developmental stages. Although patterns were not uniform, significant genotype × moisture interactions indicate accession-specific regulation under declining soil moisture. Domestication and artificial selection have shaped the genetic architecture of crop species, leading to divergence in adaptive traits between wild progenitors and cultivated forms. Demographic history and selective breeding can influence genomic variation affecting stress-responsive pathways (Gaut et al. 2018), while landrace and wild germplasm frequently retain broader stress-associated trait diversity (Dwivedi et al. 2016). In cucurbit crops, genomic restructuring associated with domestication has been linked to changes in growth-related traits (Ma et al. 2022). Genome-wide population-level studies of bitter melon likewise demonstrate clear differentiation between wild and cultivated forms (Cui et al. 2020; Matsumura et al. 2020). Although the present study evaluated only two accessions, the observed differences in biomass responses and biochemical modulation are consistent with the possibility that domestication history may influence physiological plasticity under moisture limitation.

From a biodiversity perspective, Intraspecific Trait Variation (ITV) represents critical but often underappreciated component of functional diversity (Westerband et al. 2021; Cope et al. 2022). Crop wild relatives are increasingly recognized as reservoirs of adaptive potential under climate change (Cortés and López-Hernández 2021; Bohra et al. 2022), with recent studies further emphasizing their role in stress resilience and breeding strategies (Kapazoglou et al. 2023). The contrasting responses observed between the wild and cultivated accessions under graded moisture regimes highlight the potential importance of wild genetic resources for maintaining biochemical plasticity under environmental stress. Such variation may have implications for breeding strategies and conservation of genetic resources, particularly under increasing climatic variability.

Organ-level analyses further revealed that leaves and fruits responded differently to soil moisture reduction. It should be noted that fruit biochemical measurements were based on seasonal composite samples, whereas leaf traits were assessed at discrete developmental stages. This approach reflects inherent differences in organ longevity and maturity windows, as fruits remain at commercial maturity for a limited period, while mature leaves persist for substantially longer durations. Consequently, fruit biochemical data represent integrated seasonal performance rather than stage-specific responses, and direct temporal comparisons between organs should be interpreted cautiously.

Leaves exhibited stronger concentration-based shifts in phenolic and flavonoid content, whereas fruits contributed substantially to total biochemical output through biomass accumulation. Significant Genotype × Moisture × Organ interactions indicate that allocation patterns between vegetative and reproductive tissues varied depending on accession and irrigation regime. Allocation shifts under drought have been associated with adjustments in source-sink relationships and stress-regulated carbon partitioning (Hasanuzzaman et al. 2020; Dong and Lin 2021). However, because this study did not directly quantify carbon flux, enzyme activity, or gene expression, these mechanisms should be interpreted as plausible explanations rather than direct evidence.

Several limitations should be considered when interpreting these findings. The study evaluated only two accessions, limiting inference regarding species-wide variation. The experiment was conducted during a single growing season, and interannual climatic variability may influence stress responses. Biochemical assessments were based on concentration-based assays and did not include molecular validation of phenylpropanoid pathway regulation. Moreover, field conditions, while enhancing ecological relevance, may introduce environmental heterogeneity that cannot be fully controlled. Future research incorporating multiple genotypes, multi-season trials, and integrative molecular analyses would provide deeper insight into the regulatory basis of accession-dependent moisture responses.

In conclusion, graded soil moisture regimes differentially influenced growth and biochemical traits in wild and cultivated accessions of *M. charantia* under field conditions, with genotype-dependent patterns. Moderate moisture deficit (65% FC) enhanced biochemical traits and antioxidant activity, whereas severe deficit (50% FC) reduced biomass and overall biochemical yield despite occasional increases in metabolite concentration. These findings indicate that yield-integrated biochemical performance is governed by the interaction between metabolite concentration and biomass accumulation, highlighting a trade-off between concentration-based responses and whole-plant productivity under water-limited conditions. Across organs, fruits contributed substantially to total biochemical yield due to their higher biomass, whereas leaves showed greater responsiveness in concentration-based traits. The wild accession generally exhibited higher biochemical plasticity and yield-integrated metabolite production than the cultivated accession under moisture stress. Although limited to two accessions and a single growing season, the study provides empirical evidence that intraspecific variation influences physiological and biochemical responses under water deficit. These findings contribute to understanding how domestication-related divergence and genetic background may shape functional trait variation within cultivated-wild complexes. Future research should incorporate multiple genotypes, multi-season field trials, and integrative molecular approaches (e.g., gene expression and enzyme activity) to elucidate regulatory mechanisms and strengthen breeding strategies for drought adaptation in bitter melon.

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REFERENCES

Agati G, Azzarello E, Pollastri S, Tattini M. 2012. Flavonoids as antioxidants in plants: Location and functional significance. Plant Sci 196: 67-76. https://doi.org/10.1016/j.plantsci.2012.07.014.

Ainsworth EA, Gillespie KM. 2007. Estimation of total phenolic content and other oxidation substrates in plant tissues using Folin-Ciocalteu reagent. Nat Protoc 2: 875-877. https://doi.org/10.1038/nprot.2007.102.

Bohra A, Kilian B, Sivasankar S, Caccamo M, Mba C, McCouch SR, Varshney RK. 2022. Reap the crop wild relatives for breeding future crops. Trends Biotechnol 40 (4): 412-431. https://doi.org/10.1016/j.tibtech.2021.08.009.

Brand-Williams W, Cuvelier ME, Berset C. 1995. Use of a free radical method to evaluate antioxidant activity. LWT Food Sci Technol 28 (1): 25-30. https://doi.org/10.1016/S0023-6438(95)80008-5.

Chang C-C, Yang M-H, Wen H-M, Chern J-C. 2002. Estimation of total flavonoid content in propolis by two complementary colorimetric methods. J Food Drug Anal 10 (3): 3. https://doi.org/10.38212/2224-6614.2748.

Choudhury FK, Rivero RM, Blumwald E, Mittler R. 2017. Reactive oxygen species, abiotic stress, and stress combination. Plant J 90 (5): 856-867. https://doi.org/10.1111/tpj.13299.

Cope OL, Burkle LA, Croy JR, Mooney KA, Yang LH, Wetzel WC. 2022. The role of timing in intraspecific trait ecology. Trends Ecol Evol 37 (11): 997-1005. https://doi.org/10.1016/j.tree.2022.07.003.

Cortés AJ, López-Hernández F. 2021. Harnessing crop wild diversity for climate change adaptation. Genes 12 (5): 783. https://doi.org/10.3390/genes12050783.

Cui J, Yang Y, Luo S et al. 2020. Whole-genome sequencing provides insights into the genetic diversity and domestication of bitter gourd (*Momordica* spp.). Hortic Res 7: 85. https://doi.org/10.1038/s41438-020-0305-5.

Dolatmand-Shahri N, Modarres-Sanavy SAM, Mirjalili MH, Mokhtassi-Bidgoli A. 2024. Study the yield and quality of bitter gourd fruit (*Momordica charantia*) in inoculation with two species of mycorrhizal fungi and phosphorus fertilizer under different irrigation regimes. Plant Physiol Biochem 208: 108479. https://doi.org/10.1016/j.plaphy.2024.108479.

Dong N-Q, Lin H-X. 2021. Contribution of phenylpropanoid metabolism to plant development and plant-environment interactions. J Integr Plant Biol 63 (1): 180-209. https://doi.org/10.1111/jipb.13054.

Dwivedi SL, Ceccarelli S, Blair MW, Upadhyaya HD, Are AK, Ortiz R. 2016. Landrace germplasm for improving yield and abiotic stress adaptation. Trends Plant Sci 21 (1): 31-42. https://doi.org/10.1016/j.tplants.2015.10.012.

FAO [Food and Agriculture Organization]. 2017. The Future of Food and Agriculture - Trends and Challenges. Food and Agriculture Organization of the United Nations, Rome.

FAO [Food and Agriculture Organization]. 2021. The State of the World's Land and Water Resources for Food and Agriculture - Systems at Breaking Point. Food and Agriculture Organization of the United Nations, Rome.

Gaut BS, Seymour DK, Liu Q, Zhou Y. 2018. Demography and its effects on genomic variation in crop domestication. Nat Plants 4: 512-520. https://doi.org/10.1038/s41477-018-0210-1.

Hasanuzzaman M, Bhuyan MHMB, Zulfiqar F, Raza A, Mohsin SM, Al Mahmud J, Fujita M, Fotopoulos V. 2020. Reactive oxygen species and antioxidant defense in plants under abiotic stress. Antioxidants 9 (8): 681. https://doi.org/10.3390/antiox9080681.

Hatamian Z, Roosta HR, Raghami MR, Soroush F, Soufi HR. 2026. Mitigating drought stress in *Momordica charantia* L. through foliar application of potassium, zinc, calcium, and silicon. Sci Rep 16: 7054. https://doi.org/10.1038/s41598-026-38336-7.

IPCC [Intergovernmental Panel on Climate Change]. 2022. Climate Change 2022: Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge.

Kapazoglou A, Gerakari M, Lazaridi E, Kleftogianni K, Sarri E, Tani E, Bebeli PJ. 2023. Crop wild relatives: A valuable source of tolerance to various abiotic stresses. Plants 12 (2): 328. https://doi.org/10.3390/plants12020328.

Ma L, Wang Q, Zheng Y, Guo J, Yuan S, Fu A, Bai C, Zhao X, Zheng S, Wen C, Guo S, Gao L, Grierson D, Zuo J, Xu Y. 2022. Cucurbitaceae genome evolution, gene function, and molecular breeding. Hortic Res 9: uhab057. https://doi.org/10.1093/hr/uhab057.

Matsumura H, Hsiao M-C, Lin Y-P, Toyoda A, Taniai N, Tarora K, Urasaki N, Anand SS, Dhillon NPS, Schafleitner R, Lee C-R. 2020. Long-read bitter gourd (*Momordica charantia*) genome and the genomic architecture of nonclassic domestication. Proc Natl Acad Sci USA 117 (25): 14543-14551. https://doi.org/10.1073/pnas.1921016117.

Mohagheghian B, Saeidi G, Arzani A. 2025. Phenolic compounds, antioxidant enzymes, and oxidative stress in barley (*Hordeum vulgare* L.) genotypes under field drought-stress conditions. BMC Plant Biol 25 (1): 709. https://doi.org/10.1186/s12870-025-06750-0.

Nguyen TV, Kasim M, Anggraini T, Doan LN, Duong NV. 2025. Resilience of wild and cultivated bitter melon (*Momordica charantia*) under deficit irrigation in Vietnam. Biodiversitas 26 (10): 5248-5257. https://doi.org/10.13057/biodiv/d261038.

Ninkuu V, Aluko OO, Yan J, Zeng H, Liu G, Zhao J, Li H, Chen S, Dakora FD. 2025. Phenylpropanoids metabolism: Recent insight into stress tolerance and plant development cues. Front Plant Sci 16: 1571825. https://doi.org/10.3389/fpls.2025.1571825.

Sharma A, Shahzad B, Rehman A, Bhardwaj R, Landi M, Zheng B. 2019. Response of the phenylpropanoid pathway and the role of polyphenols in plants under abiotic stress. Molecules 24 (13): 2452. https://doi.org/10.3390/molecules24132452.

Tan SP, Parks SE, Stathopoulos CE, Roach PD. 2014. Greenhouse-grown bitter melon: Production and quality characteristics. J Sci Food Agric 94 (9): 1896-1903. https://doi.org/10.1002/jsfa.6509.

Westerband AC, Funk JL, Barton KE. 2021. Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. Ann Bot 127 (4): 397-410. https://doi.org/10.1093/aob/mcab011.

Yaqoob U, Jan N, Raman PV, Siddique KHM, John R. 2022. Crosstalk between brassinosteroid signaling, ROS signaling, and phenylpropanoid pathway during abiotic stress in plants: Does it exist? Plant Stress 4: 100075. https://doi.org/10.1016/j.stress.2022.100075.

Zhang F, Rosental L, Ji B, Brotman Y, Dai M. 2024. Metabolite-mediated adaptation of crops to drought and the acquisition of tolerance. Plant J 118 (3): 626-644. https://doi.org/10.1111/tpj.16634.