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Cultivar-by-environment interactions shape strawberry fruit quality: A multi-omics approach across European climates

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ABSTRACT

Flavour inconsistency in *Fragaria x ananassa* remains a challenge, largely due to historical breeding focused on yield over sensory traits. Flavour results from organoleptic and bioactive compounds shaped by cultivar (G), environment (E) and their interaction (GxE). Four strawberry cultivars (Clery, Frida, Gariguette, Sonata) were evaluated across five European environments employing an integrative approach combining metabolomics and transcriptomics. This approach revealed elevated temperatures accelerate the start of the harvest season and shorten fruit development duration. GxE interactions critically influenced flavour compounds accumulation, indicating cooler temperatures during fruit development favor the accumulation of sugars and ɣ-decalactone. Integrative analysis identified cultivar-specific and environmentally stable transcriptional patterns, including promising candidate genes involved in the biosynthesis and degradation of flavour relevant compounds, and revealing starting points for strawberry flavour improvement and stabilization. Our findings highlight the central role of GxE interactions in shaping strawberry flavour profile and emphasize the need for multi-environment trials to support resilient flavour enhancement in future breeding programs.

1. Introduction

The concept of «fruit quality» encompasses a complex array of intrinsic and external attributes that significantly influence both market value and consumer preference (Kyriacou & Rouphael, 2018). Among these, flavour—defined as a composite of taste and aroma—has been identified as one of the critical aspects guiding consumer return buy and product acceptance (Brückner, 2008; Callahan, 2003).

Cultivated strawberry (*Fragaria x ananassa* Duch.), globally one of the most economically important and nutritional valuable fruits, occupies a prominent position in the European market due to its sensory characteristics. The harmonious blend of complex flavours, vibrant pigmentation, succulent texture and rich micronutrient content—such as vitamin C, folate and phenolic compounds—enhances its organoleptic appeal and its health-promoting properties (Colquhoun et al., 2012). In 2022, these attributes contributed to a global production of 9.6 million tonnes, with Europe alone producing 1.8 million tonnes (FAOSTAT, 2023). However, over the past decade, consumer surveys have highlighted growing dissatisfaction with the diminished flavour of commercially available fruits (Barrett et al., 2010; Bruhn et al., 1991;

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Fernqvist & Hunter, 2012; Klee & Tieman, 2018).

In the case of strawberries, it has been suggested that the reduction in sensory quality correlates with a significant decrease —estimated at approximately 35%—in the genetic diversity over the past five decades, leading to consequences for the crop's metabolic and quality profiles (Aharoni et al., 2004; Gil-Ariza et al., 2009). This decline in sensory quality and allelic diversity pose significant challenges for the future of strawberry production, particularly as global food systems increasingly aim to balance productivity with consumer satisfaction (Egea et al., 2022; Lopes et al., 2009; Rodríguez-Burruezo et al., 2011). In this sense, a series of EU initiatives—from COST action 863 (2011–2014) to the EU funded RIBESCO (2007–2011), GenBerry (2008–2012), EUBerry (2011–2014), GoodBerry (Horizon2020–2016–2020) and BreedingValue (Horizon2020–2021–2025) projects—worked to recover the lost genetic diversity of strawberry and other berry crops and maintain crucial genetic resources (Senger et al., 2022).

The sensory profile of fruits is intrinsically linked to the developmental process (Fait et al., 2008). During fruit ripening, gene expression, enzymatic activity and metabolite accumulation are all finely regulated to produce changes in the morphology and composition of the fruit. Throughout the maturation process, the fruit transitions from unripe, green-associated flavours in the early stages to more complex and desirable flavours at full ripeness through biochemical changes (Cherian et al., 2014; Schwieterman et al., 2014; Zhang et al., 2011). This shift facilitates seed dispersal by signaling optimal readiness for consumption by dispersal agents, thereby enhancing the likelihood of successful propagation (Nelson & Whitehead, 2021; Nevo & Ayasse, 2020).

In strawberry fruit, soluble sugars such as sucrose, glucose and fructose are key primary metabolites contributing significantly to the fruit sweetness, along with organic acids, like citric and malic acids, adding fresh and citric notes (Fan et al., 2021). The balance between sugars and acids is commonly used to gauge the optimal quality point, with higher ratios often linked to improved consumer preference (Fait et al., 2008). On the other hand, while more than 360 VOCs have been identified in the aroma of wild strawberries, only 20 are consistently recognized as key contributors to this trait in the commercial varieties (Leonardou et al., 2021; Ulrich et al., 2018). Particularly, methyl and ethyl esters have been described to add fruity notes to the fruits (Dong et al., 2013; Rey-Serra et al., 2022). Linalool and nerolidol constitute two prominent terpenoids known for contributing floral and citrus-like aromas, with linalool particularly showing a positive correlation with flavour intensity and consumer preference (Aharoni et al., 2004). Furans, like mesifurane and furaneol, contribute caramel-like and sweet undertones, while lactones (γ-decalactone, γ-dodecalactone) evoke peachy and fruity perception (Yan et al., 2018). Additionally, fatty acid volatiles (*E*-2hexenal and *Z*-3-hexenal) cause fresh, green aromas that enhance the overall complexity of flavour profiles (Schieberle & Hofmann, 1997). Together, these compounds create the flavour profile that consumer describe as the "ideal" strawberry (Colquhoun et al., 2012; Fan et al., 2021).

The final proportion of this metabolic array depends on the intricate sum and interplay between endogenous and exogenous factors (D'Esposito et al., 2017). The genetic background is a key factor, being the flavour profiles unique to cultivar-type, and yielding a wide spectrum within the same species (Vandendriessche et al., 2013). Likewise, the accumulation of these compounds is intricately regulated by genetic networks, which, in turn, are modulated by multiple environmental cues (Cervantes et al., 2020; Schwieterman et al., 2014; Zorrilla-Fontanesi et al., 2012), underscoring the complexity of flavour and aroma biosynthesis. In this context, maintaining consistent organoleptic properties across different production environments is a challenge exacerbated by the ongoing effects of climate change (Kishor et al., 2023). For instance, rising temperatures, particularly in Southern European regions, frequently exceed the optimal threshold for crop development, leading to reductions in both yield and sensory quality (Mohammadi et al., 2023). Moreover, the impact of these factors is often studied in isolation, which does not adequately reflect the complexity of real-world situations, where multiple factors interact simultaneously (Hardner, 2017). To bridge this gap, multi-environment trials (METs) have become essential for producing reliable data (Prohaska et al., 2024) that support breeding programs aiming to improve fruit organoleptic quality across diverse environmental conditions (Teressa et al., 2021).

Another feature of agronomical interest influencing fruit quality is the duration of development, defined in this context as the period from flowering onset to harvest. This parameter dictates the rhythm of ripening, which in turn impacts the final composition of the fruit (Busatto & Herrera, 2025). As the ripening process occurs at the latest stage of development, incomplete or late ripening can be detrimental to organoleptic properties. Moreover, given the non-climacteric nature of strawberry, early or late picking can be detrimental to quality as the fruit does not continue to ripen after harvested (Błaszczyk et al., 2022). Like fruit composition, this parameter also depends on complex interplay between genetic background, environmental conditions, and their interaction (GxE) (Joine & Sakar, 2025).

Temperature and light availability have been described as substantial factors influencing fruit phenology and final composition in strawberry (Durán-Soria et al., 2021; Pott et al., 2023; Previtali et al., 2021). For instance, elevated temperatures have been described to accelerate fruit development duration (Menzel, 2023) and reduce growth, yield (Kadir et al., 2006) and total carbohydrates in fruit, including glucose and fructose (Wang & Camp, 2000). In contrast, cooler temperatures have been associated to delayed fruit development times and a reduction in anthocyanin accumulation in strawberries resulting in poor coloration (Mao et al., 2022).

In recent years, omics technologies have emerged as powerful tools for elucidating the complex interactions between genetic and environmental factors that influence fruit final quality (Pott, Durán-Soria et al., 2021; Zhang & Hao, 2020). Comparative metabolomics, for instance, enable a detailed characterization of metabolic changes linked to cultivar specificity and environmental adaptation by quantifying metabolic levels (Martínez-Rivas & Fernie, 2024). Likewise, transcriptomics provides insights into the dynamics of gene expression under specific circumstances, allowing e.g. the identification of both upregulated and downregulated genes in response to stimuli (Diao et al., 2023). Traditionally, these methodologies have been applied independently, each offering valuable but often isolated insights into the molecular mechanisms underlying these attributes. However, recent advances have demonstrated that the combined application of multiple omics approaches significantly enhances our understanding of the complexity and regulatory networks governing organoleptic properties in fruit crops (D'Esposito et al., 2017; Pott, Durán-Soria et al., 2021; Umer et al., 2020).

In strawberry such integrative strategies have facilitated the identification of distinct metabolic signatures associated with cultivar variation (Shen et al., 2022) and postharvest practices (Zheng et al., 2022). Nevertheless, despite the advances, studies that fully integrated multiple omics datasets in combination with multi-environment trials remain scarce. A comprehensive, multi-omics approach is still needed to provide a holistic view of the regulatory mechanisms underpinning fruit composition and final quality, which is essential for developing targeted breeding strategies.

In this context, the objective of this research was to: (1) evaluate the effects of cultivar -by-environment (GxE) interactions on the duration of strawberry fruit development, (2) evaluate the stability of key metabolites across different cultivars and their suitability as selection material in breeding programs, and (3) identify promising genes linked to the stable accumulation of quality related metabolites across varying environmental conditions, proposing potential molecular targets for the development of high-quality and climate-tolerant strawberry cultivars.

2. Materials and methods

2.1. Plant materials and field management

Four commercial strawberry cultivars were selected for field experiments based on their diverse genetic backgrounds and adaptability to distinct regional climates: Clery (bred in Italy), Frida (bred in Norway), Gariguette (bred in France), and Sonata (bred in Netherlands). Each cultivar was grown across five geographically and climatically contrasting sites within Europe: Norwegian Institute of Bioeconomy Research (NIBIO) in Norway, National Institute of Horticultural Research (INHORT) in Poland, Hochschule Geisenheim University (HGU) in Germany, Sant'Orsola Società Cooperativa Agricola (SO) in Italy, and Ciref Création Variétale Fraises Fruits Rouges (CIREF) in France (Fig. 1-A). Consistent with local cultivation practices, open field cultivation was employed in Norway, Poland and Germany, with plants being cultivated in single rows directly in the soil. In contrast, plants for the experiments in Italy and France were planted in soilless culture in double rows and protected with polytunnels as soon as plantation occurred.

2.2. Sample preparation and experimental design

Samples from fully ripe fruits (fully red) were taken in three biological replicates per cultivar:environment combinations, consisting of 20 plants per sample. Harvesting occurred at two time points, 10 days apart. From each replicate, 500 g of fruit was frozen in liquid nitrogen and stored at −80 °C. Three replicates were used for metabolomic and transcriptomic analyses, except volatile organic compounds, assessed in two.

2.3. Environmental data

Environmental data, including air temperature (mean, maximum, minimum and thermal amplitude, °C) and global radiation (kWm^{-2}), were recorded at each site (Table S1). Mean and cumulative values were calculated for each cultivar:environment combination. Statistical analyses were conducted in R Studio v.4.3.1, standardizing parameters to zero mean and unit variance. Hierarchical clustering analysis (Ward's linkage, Euclidean distance) classified environments based on climatic similarity during fruit development.

2.4. Phenology data and statistical analysis

For each cultivar:environment combination, flowering and harvesting dates were recorded. Mean fruit development time was calculated as the interval between flowering onset and final harvest. Flowering onset was set to the earliest cultivar's initiation date within each environment. The Kruskal-Wallis rank-sum test assessed the significance of cultivar, environment and GxE interactions effects on this parameter. Dunn's post hoc test (Bonferroni correction) was applied for pairwise comparisons. Pearson correlation coefficients (95% confidence) examined climatic associations with fruit development duration.

2.5. Metabolite extraction and mass spectrometry (MS)

Primary metabolic profiling was performed by using gas chromatography-time of flight-mass spectrometer (GC-TOF-MS), following the protocol previously established by Osorio et al. (2012). Similarly, volatile organic compounds (VOCs) were extracted using solid phase microextraction (SPME) fiber and a gas chromatograph coupled to an ion trap mass spectrometer as described in Pott, Vallarino, and Osorio (2021). Primary metabolites and VOCs were quantified by integrating peak area, employing specific *m/z* ion for each metabolite, from the resulting chromatograms (Pott, Vallarino, and Osorio, 2021). The resultant mass spectra were annotated employing TagFinder and cross-referenced with Golm Metabolome Database (GMD - the Golm Metabolome Database, 2025). Prior to statistical analysis, data was relativised to dry weight and to the control sample, which corresponded to an arbitrary sample prepared with a mixture of all the cultivars involved (Table S2).

2.6. RNA extraction and RNA-Seq analysis

Total RNA was extracted from fruit tissue using the protocol of Manning (1991). Genomic DNA contamination was removed using DNAse I (Fermentas). Quantity and quality of RNA samples were assessed by measuring absorbance ratios at 260/280 and 260/230 nm using NanoDrop spectrophotometer (ND-1000 V3.5, NanoDrop Technologies, Inc.). RNA integrity was further evaluated via agarose gel electrophoresis to confirm the absence of degradation. RNA-Seq libraries were prepared and sequenced on the Illumina HiSeq 2000 platform, generating 300 pb paired-end reads. Raw RNA-Seq reads were processed to remove low-quality nucleotides and aligned to the latest *Fragaria vesca* v4.0.a1 genome assembly (Edger et al., 2019). Reads were assembled into transcripts and classified as known genes, corresponding to annotated genes in *F. ananassa* genome v1.0 (FAN_r1.1, Edger et al. (2019)). Transcript abundance was quantified using Salmon software (Patro et al., 2017) and subsequently imported into R for further statistical analysis.

2.7. Metabolic statistical data analysis

Owing to differences in dimensionality, primary compounds and VOCs were analyzed independently and stratified by cultivation method to reduce system bias, yielding four regional datasets. Zero values were considered biologically absent and replaced with half the minimum detected positive value (Sun & Xia, 2024). Normality was assessed via the Shapiro-Wilk test, with $\log_2$ transformation applied where necessary. All features were standardized (mean-centered, unit variance), missing samples from instrument failure ($n = 4$) were imputed using K-nearest neighbours ($K = 2$) via de *VIM* package in R (Kowarik & Templ, 2016).

Principal component analysis (PCA) was performed and validated using the *ropls* package (v.1.34.0, Thévenot et al., 2015). Hotelling's T^2 ellipse was used to identify outliers. Complementary hierarchical clustering analysis (HCA) employing Euclidean distances on transformed data was visualized using *ComplexHeatmap* package (v.2.20.0). Furthermore, a two-way analysis of variance (ANOVA) was applied to determine significant differences in the mean content of individual metabolites. To complement this, a permutational multivariate analysis of variance (PERMANOVA), based on euclidean distance, was used to assess global compositional differences across the full metabolomic dataset:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the observed metabolite content for cultivar i and environment j and repetition k, μ is the overall mean, α_i is the effect of the cultivar i, β_j the effect of environment j, $(\alpha\beta)_{ij}$ the interaction effect between cultivar i and environment j, and ε_{ijk} is the random error, assumed $\sim N(0, \sigma^2)$.

A supervised multivariate regression analysis using Orthogonal Partial Least Squares Discriminant Analysis (OPLS-DA) in the *ropls* package (Thévenot et al., 2015) identified key metabolites driving group separation. Metabolites were classified as differentially accumulated (DAMs) based on VIP ≥ 1 and $|\text{Log}_2\text{FoldChange}| \geq 1$ (environment) or $|\text{Log}_2\text{FoldChange}| \geq 0.5$ (**cultivar**) (Fig. S1–6).

Fifteen metabolites, comprising sucrose, glucose, fructose, malic acid, citric acid, linalool, terpineol, mesifurane, furaneol, ɣ-decalactone, ɣ-dodecalactone, methyl butyrate, methyl hexanoate, ethyl butyrate and ethyl hexanoate, were selected as they were consistently described as

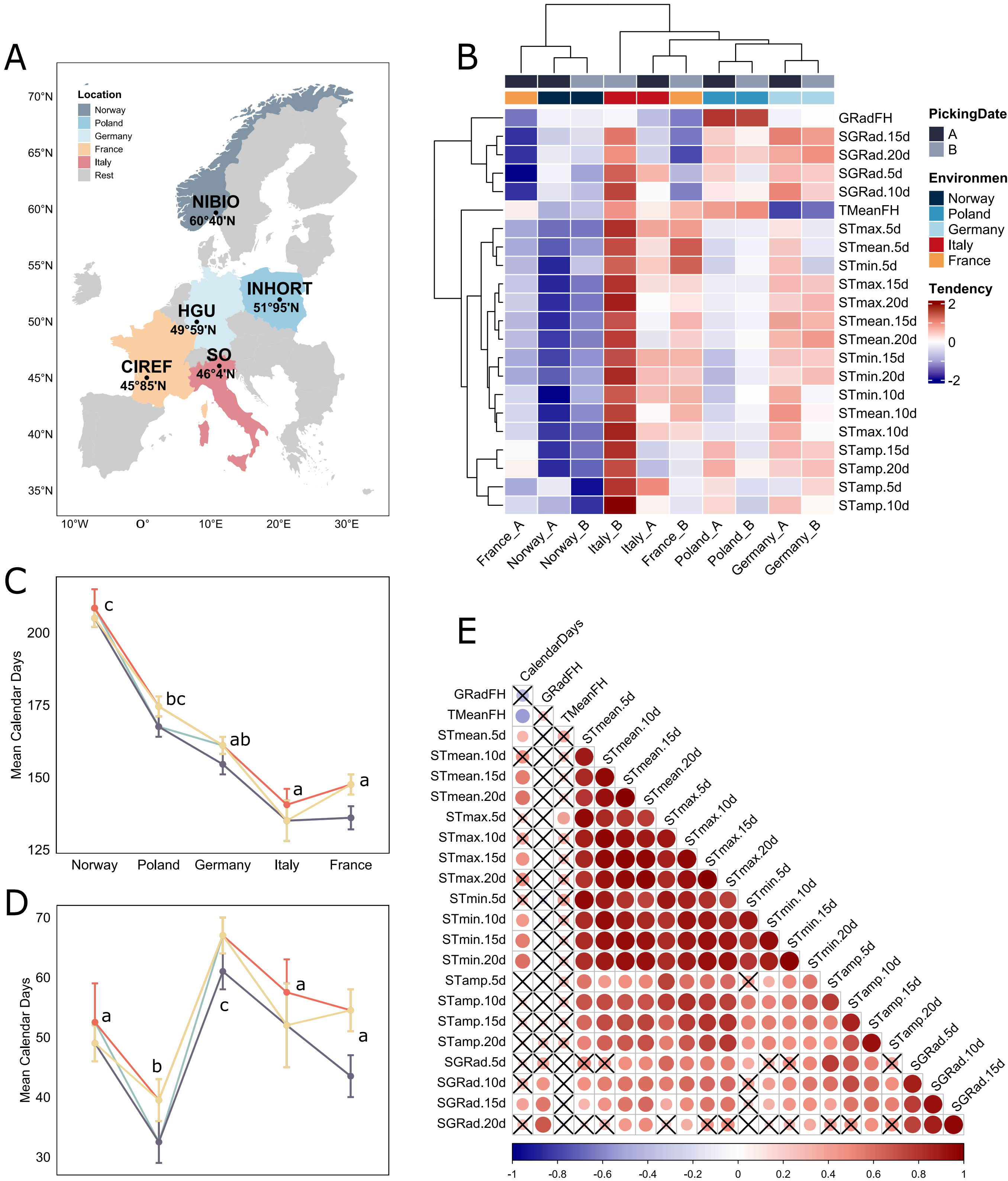

Fig. 1. (A) Geographic locations and latitudes of the experimental sites. (B) Hierarchical Clustering Analysis (HCA) of the environments based on climatic covariates recorded during development time. Colour scale showcases the tendency to be (red) over the mean or (blue) under the mean values across conditions. Line plot showing fruit development time expressed as the mean of the calendar days aggregated by picking dates and G × E combinations (C) from 1 January to harvest and (D) from flowering onset to harvest. (E) Heatmap of Pearson correlation coefficients between environmental covariates and fruit development time (in calendar days) from flowering onset to harvest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

important for strawberry flavour across the literature (Fan et al., 2021; Klee & Tieman, 2018; Ulrich et al., 1997; Yan et al., 2018). Stability and plasticity of these metabolites were evaluated using the *metan* package in R (Olivoto & Lúcio, 2020). Genotype and Genotype-by-Environment (GGE) biplots and the Multi-Trait Stability Index (MTSI) were computed to rank cultivars by integrated performance and stability across selected flavour-associated traits.

2.8. *Transcriptomics statistical data analysis*

Transcript abundance estimates were imported into R using the *tximport* package (Soneson et al., 2015), with transcript-level data aggregated to the gene level to mitigate isoform bias. Normalization factors based on transcript lengths were computed and used to standardize expression values. Log-transformation and z-score normalization were applied to stabilize variance across samples. The resulting data was structured as a *DEGList* object via *edgeR* package (Robinson et al., 2009), containing read counts, library sizes, normalization factors and

Table 1
Functional annotations of genes significantly correlated with metabolite levels.

Correlated Metabolites	Gene ID	Gene name (Phytozome)	Pathway annotation (Phytozome)
Sucrose	maker-Fvb1–1-augustus-gene-9.30-mRNA-1	UDP-glucose pyrophosphorylase	Stachyose degradation, sucrose biosynthesis II, sucrose biosynthesis I (from photosynthesis), UDP-glucose biosynthesis, sucrose degradation II (sucrose synthase)
	maker-Fvb1–4-augustus-gene-17.45-mRNA-1	UDP-glucose-fructose-phosphate glucosyltransferase	sucrose biosynthesis II, sucrose biosynthesis I (from photosynthesis)
	maker-Fvb1–2-augustus-gene-27.46-mRNA-1	Hexokinase type IV (glucokinase)	Homolactic fermentation, sucrose degradation III (sucrose invertase), sucrose biosynthesis II, glucose and glucose-1-phosphate degradation, glycolysis III (from glucose)
	maker-Fvb7–2-augustus-gene-228.60-mRNA-1	Triosephosphate mutase	Calvin-Benson-Bassham cycle, superpathway of cytosolic glycolysis (plants), pyruvate dehydrogenase and TCA cycle, oxygenic photosynthesis, glycolysis III (from glucose), glycolysis IV (plant cytosol), homolactic fermentation, gluconeogenesis III, gluconeogenesis I
	snap_masked-Fvb7–4-processed-gene-57.35-mRNA-1	Triosephosphate mutase	Gluconeogenesis III, gluconeogenesis I, glycolysis IV (plant cytosol), homolactic fermentation, Calvin-Benson-Bassham cycle, superpathway of cytosolic glycolysis (plants), pyruvate dehydrogenase and TCA cycle, glycolysis III (from glucose), oxygenic photosynthesis
Linalool	maker-Fvb7–1-augustus-gene-6.22-mRNA-1	carotenoid cleavage dioxygenase	No pathway annotation
	maker-Fvb3–2-augustus-gene-19.40-mRNA-1	(3S,6E)-nerolidol synthase	(3E)-4,8-dimethylnona-1,3,7-triene biosynthesis I
	maker-Fvb3–2-augustus-gene-294.55-mRNA-1	farnesyl diphosphate synthase (FDPS)	Superpathway of geranylgeranyldiphosphate biosynthesis I (via mevalonate), trans, trans-farnesyl diphosphate biosynthesis
	maker-Fvb3–1-augustus-gene-304.55-mRNA-1	(3S,6E)-nerolidol synthase	(3E)-4,8-dimethylnona-1,3,7-triene biosynthesis I
	maker-Fvb2–2-snap-gene-219.71-mRNA-1	Squalene monooxygenase	Plant sterol biosynthesis, epoxysqualene biosynthesis
Mesifurane	maker-Fvb7–4-augustus-gene-7.44-mRNA-1	6-phosphogluconolactonase	Pentose phosphate pathway (oxidative branch), pentose phosphate pathway
	maker-Fvb5–1-augustus-gene-2.39-mRNA-1	dTDP-6-deoxy-L-mannose dehydrogenase	Calvin-Benson-Bassham cycle, superpathway of cytosolic glycolysis (plants), oxygenic photosynthesis, sucrose biosynthesis I (from photosynthesis), glycolysis IV (plant cytosol), homolactic fermentation, glycolysis III (from glucose), gluconeogenesis I, gluconeogenesis III
	augustus_masked-Fvb4–4-processed-gene-53.9-mRNA-1	Fructose-1,6-bisphosphate triosephosphate-lyase	Calvin-Benson-Bassham cycle, superpathway of cytosolic glycolysis (plants), pyruvate dehydrogenase and TCA cycle, oxygenic photosynthesis, glycolysis III (from glucose), glycolysis IV (plant cytosol), homolactic fermentation, gluconeogenesis III, gluconeogenesis I, sucrose biosynthesis I (from photosynthesis)
	maker-Fvb4–3-augustus-gene-221.50-mRNA-1	D-fructokinase	D-sorbitol degradation I, sucrose degradation II (sucrose synthase), sucrose degradation III (sucrose invertase)
	maker-Fvb4–1-augustus-gene-146.33-mRNA-1	Fructose-1,6-bisphosphate triosephosphate-lyase	gluconeogenesis I, gluconeogenesis III, homolactic fermentation, glycolysis IV (plant cytosol), sucrose biosynthesis I (from photosynthesis), superpathway of cytosolic glycolysis (plants), pyruvate dehydrogenase and TCA cycle, Calvin-Benson-Bassham cycle, oxygenic photosynthesis, glycolysis III (from glucose)
γ-Decalactone	maker-Fvb6–2-snap-gene-40.56-mRNA-1	Pyruvic-malic carboxylase	Gluconeogenesis I, C4 photosynthetic carbon assimilation cycle, PEPCK type, C4 photosynthetic carbon assimilation cycle, NADP-ME type
	maker-Fvb4–2-augustus-gene-86.40-mRNA-1	Citric cleavage enzyme	Acetyl-CoA biosynthesis III (from citrate), superpathway of acetyl-CoA biosynthesis
	maker-Fvb2–3-augustus-gene-54.41-mRNA-1	Pyruvic-malic carboxylase	Gluconeogenesis I, C4 photosynthetic carbon assimilation cycle, PEPCK type, C4 photosynthetic carbon assimilation cycle, NADP-ME type
	snap_masked-Fvb3–1-processed-gene-312.32-mRNA-1	Threonine-specific protein kinase	No pathway annotation
	maker-Fvb4–3-augustus-gene-145.28-mRNA-1	Acyl carrier protein 1, chloroplastic-related	No pathway annotation
	maker-Fvb6–3-snap-gene-224.40-mRNA-1	Enoyl reductase [NADH], Chloroplastic	No pathway annotation
	maker-Fvb6–1-augustus-gene-136.32-mRNA-1	Pyruvic-malic carboxylase	Gluconeogenesis I, C4 photosynthetic carbon assimilation cycle, PEPCK type, C4 photosynthetic carbon assimilation cycle, NADP-ME type
	maker-Fvb4–1-augustus-gene-182.40-mRNA-1	Citric cleavage enzyme	Superpathway of acetyl-CoA biosynthesis, acetyl-CoA biosynthesis III (from citrate)
	augustus_masked-Fvb3–2-processed-gene-26.11-mRNA-1	Malonyl-CoA carboxy-lyase	No pathway annotation

annotations. Gene filtering was conducted using *filterByExpr* function, with default thresholds to retain genes expressed above a cutoff. Genes passing this filter were subjected to differential expression analysis using *DESeq2* within a generalized linear model framework, employing quasi-likelihood dispersion estimation (Love et al., 2014). Transcripts per million (TPM) values were extracted for all retained genes and annotated by cultivar, environment and harvest date (Table S5). Cultivation practice was excluded as a factor, as PERMANOVA indicated it accounted for less than 5% of total variance. Consequently, the full dataset was retained for subsequent analysis. TPM values were Log_2-transformed and z-score normalized. Outliers confirmed via Hotelling's T^2 ellipse were removed prior to final analysis. Pairwise contrasts for cultivar and environmental conditions were constructed from the design matrix. Differentially expressed genes (DEGs) were identified using glmQLFTest, with FDR ≤ 0.05 and LogFoldChange ($|\text{LogFC}|$) threshold >1 (E) and > 2 (G). For GxE interactions, stricter criteria were applied (FDR ≤ 0.05, LogCPM >5), prioritizing abundant and statistically significant transcripts for downstream interpretation.

2.9. Multi-omics data integration and metabolic pathway construction

Weighted gene co-expression network analysis (WGCNA) was conducted on identified DEGs using the *WGCNA* package (v4.4.1), with an optimal soft-thresholding power of 15 (Langfelder & Horvath, 2008; Langfelder & Horvath, 2012). A topological overlap matrix (TOM) and corresponding dissimilarity matrix were computed, followed by hierarchical clustering to classify genes into co-expression modules via dynamic tree cutting (minimum module size: 20). Module eigengenes were calculated, and highly similar modules were merged using a 0.15 threshold. Module-trait correlation analysis examined transcriptomic variation linked to strawberry flavour-related metabolites. Sucrose, linalool, mesifurane and ɣ-decalactone were selected for this analysis as they were consistently annotated as key metabolites in determining strawberry flavour and consumer acceptance (Schwieterman et al., 2014).

Significantly correlated modules ($p < 0.05$) underwent functional analysis, filtering genes associated with key metabolic pathways. Pearson correlation refined the selection of DEGs related to metabolite accumulation. HCA characterized genetic variability and GxE interactions, with line plots illustrating expression dynamics of candidate genes across environmental conditions to identify stable genetic targets for strawberry breeding (Table 1).

3. Results

3.1. Climatic variation across environments

Climatic parameters recorded during the fruit development period separated the five testing locations (Fig. 1-A) into two primary groups (Fig. 1-B), a distinction influenced by latitude and by the cultivation system employed.

The first group, characterized by the lowest cumulative values for temperature and global radiation, comprised Norway (open field) and the first harvest date in France (polytunnel). The extremely low values in Norway underscore the severity of raw open-field conditions at a high latitude, where plants are subjected to direct thermal stress. In contrast, France and Italy, representing the protected cultivation systems (polytunnels), generally exhibited moderate-to-high cumulative climatic values.

These protected environments in the second cluster (France and Italy) modify the microclimate significantly. The polyethylene cladding results in the attenuation of incident solar radiation and an alteration of the light spectral composition (notably filtering UV wavelengths), which directly impacts metabolite biosynthesis. However, due to their Southern and central European locations, Italy still recorded the peak cumulative temperature and global radiation, reflecting significant heat accumulation within the protected structure.

The remaining sites, Poland and Germany (both Open Field), also formed part of the warmer cluster but displayed unique climatic characteristics typical of open field conditions. Poland presented a distinctive climatic profile, marked by moderate-to-low cumulative values but the highest mean temperature and global radiation. This suggests a brief, intense, and exposed open-field developmental phase, allowing for accelerated fruit maturation. Conversely, Germany exhibited moderate cumulative values but notably low mean temperatures. As an open-field site, this profile confirms periods of substantial environmental cooling and greater diurnal temperature fluctuations (low thermal inertia) when compared to the protected systems.

Notably, Italy and France were the only sites to exhibit pronounced intra-seasonal climatic shifts between harvest dates, with early harvests experiencing substantially lower temperatures and radiation than later ones. This highlights the combined influence of seasonal change and the buffering effect of the polytunnel, which can amplify temperature differences between early and late stages more acutely than in open-field sites.

3.2. Phenotypic plasticity of fruit development duration under GxE influences

Kruskal-Wallis test applied to fruit development duration (in calendar days) revealed statistically significant effects of the environment and cultivar-by-environment (GxE) interactions ($p < 0.05$), while cultivar effects alone were not significant. Despite the lack of statistical significance, a considered trend was observed across cultivars: Frida (54.2 days) exhibited a tendency toward prolonged development periods, whereas Gariguette (47.6 days) showed the shortest durations. A similar outcome was observed when assessing the total duration from 1st January to harvest (Fig. 1-C).

Environmental comparisons for the 1st-January-to-harvest interval followed a clear latitudinal gradient, with northern sites exhibiting longer developmental periods. Among these, Italy and France showed no statistically significant differences, both recording the shortest durations within the experimental set (Fig. 1-C). In contrast, when analysing only the actual fruit development period (from flowering to harvest), this spatial pattern shifted. Norway, France and Italy showed comparable intermediate development durations of around 49 days, while Poland exhibited notably shorter periods (36 days) contrary to Germany, which yielded the longest (65.5 days) (Fig. 1-D).

Pearson correlation analysis revealed a significant negative association between fruit development duration and mean daily temperature during this phase, consistent with trends observed in the temporal line plots (Fig. 1-D). Moreover, cumulative mean temperatures at 15- and 20-days pre-harvest, maximum temperatures at 15 days, minimum temperatures at 10, 15 and 20 days, and cumulative global radiation at 15 days pre-harvest were all positively correlated (Rho coefficient > 0) with development duration (Fig. 1-E).

3.3. GxE interactions significantly shaped metabolism groups accumulation patterns

Untargeted metabolomics identified 125 metabolites, encompassing both fifty primary metabolites and seventy-five VOCs (Table S2), pertaining to 11 major classes: straight-chain esters, fatty acid volatiles, amino acids and derivatives, sugars and sugar alcohols, organic acids, methyl ketones, terpenoids, apocarotenoids, furans, lactones and others (Fig. 2).

PERMANOVA test demonstrated environment factor (31.1%) exerted the strongest influence on metabolite groups accumulation, followed by cultivar (19.5%) and GxE interactions (17.8%). Conversely, harvest date effect alone and its interaction with cultivar and environment factors, although statistically significant, contributed less than 5% of total variance. Effect size (η^2) extracted from individual two-way

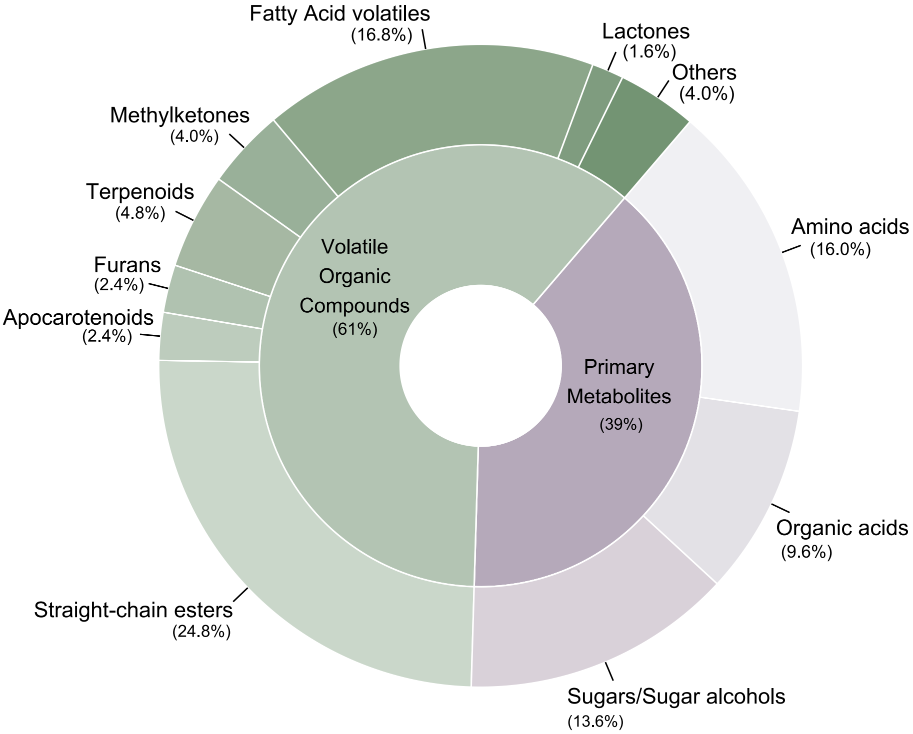

Fig. 2. Pie chart of the proportion of detected metabolic groups across samples.

ANOVA models generated for each metabolic group aligned with previous results and highlighted the individual effects (Table S3). All the metabolic groups were significantly altered by the environment except from terpenoids. Similarly, cultivar factor significantly altered most of the groups, apart from organic acids, fatty acid volatiles and apocarotenoids. Lastly, all primary metabolic groups along with methylketones, apocarotenoids and furans were significantly shaped by GxE interactions. Notably, fatty acid volatiles were only significantly influenced by environmental variations, whereas terpenoids were only significantly shaped by cultivar type. Both cases exhibited high degree of significance ($p < 0.001$; Table S3).

Subsequent analyses were stratified by cultivation practice factor: one group comprised open field cultivation locations (Norway, Germany and Poland) and the other locations where polytunnels were used (Italy and France).

3.4. *Growing location was a key determinant of primary metabolic profiles*

Growing location emerged as the primary driver of variation in primary metabolite profiles of open-field grown fruits, with cultivar effects contributing to secondary stratification (Fig. 3-A, left).

Hierarchical clustering identified two major metabolic trends. Samples from Poland formed a distinct cluster, characterized by elevated levels of key metabolites including sucrose, fructose, glucose, malic and citric acids. Under these conditions, twelve differentially accumulated metabolites (DAMs) were identified (Fig. 3-B). In contrast, samples from Germany and Norway exhibited an overall reduction in primary metabolite abundance. DAM analysis revealed four significantly decreased compounds in Germany (GABA, glutamine, pyroglutamic acid and putrescine), and one (xylose) in Norway. Additionally, minor harvest date effects were detected under German conditions, primary impacting amino acid levels.

Cultivar-specific responses were more evident in Poland, suggesting strong GxE interactions. However, overall cultivar variation in primary metabolism remained limited (Fig. 3-C). DAMs analysis revealed most differences were related to amino acid content. Notably, malic acid was decreased in Clery, whereas sucrose was increased in Sonata. The comparison between Gariguette and Sonata yielded the highest number of DAMs, with most of them decreased in Gariguette.

Under polytunnel cultivation, clustering patterns became more complex, with cultivar emerging as a stronger factor in samples aggregation (Fig. 3-A, right). Clery and Gariguette showed similar responses. In France, these cultivars accumulated higher levels of primary metabolites, whereas the Italian environment resulted in overall decreases, especially in Gariguette. DAM analysis identified amino and organic acids as the principal discriminants (Fig. 3-D). France exhibited increases in five DAMs, including sucrose, whilst Italy induced only galactinol accumulation.

A second cluster revealed strong differentiation between Sonata and Frida. Sonata consistently displayed higher levels of primary metabolites, including malic acid and sucrose, across environments. Environmental modulation of Sonata's metabolome included enhanced amino acid and sucrose accumulation in France, and increased organic acids, notably malic acid, in Italy. Conversely, Frida consistently exhibited lower metabolite levels. Harvest date influenced Frida's soluble sugars content, which peaked at the first harvest date, though amino and organic acids remained low throughout. DAMs calculations corroborated these patterns, with Frida showing extensive reductions. The largest number of DAMs under polytunnel conditions was observed between Clery and Sonata, indicating marked differences in their metabolomic responses to controlled environments (Fig. 3-D).

3.5. *Cultivar factor gained weight in determining volatile organic compounds accumulation*

Volatile organic compounds (VOCs) profiles exhibited higher heterogeneity than primary metabolites. In open-field grown fruits, samples clustering primarily reflected growing location, with cultivar-specific responses contributing to further stratification (Fig. 4-A, left). Notably, Frida displayed a distinct metabolic signature, forming a separate cluster and exhibiting elevated accumulation of multiple VOCs under Polish

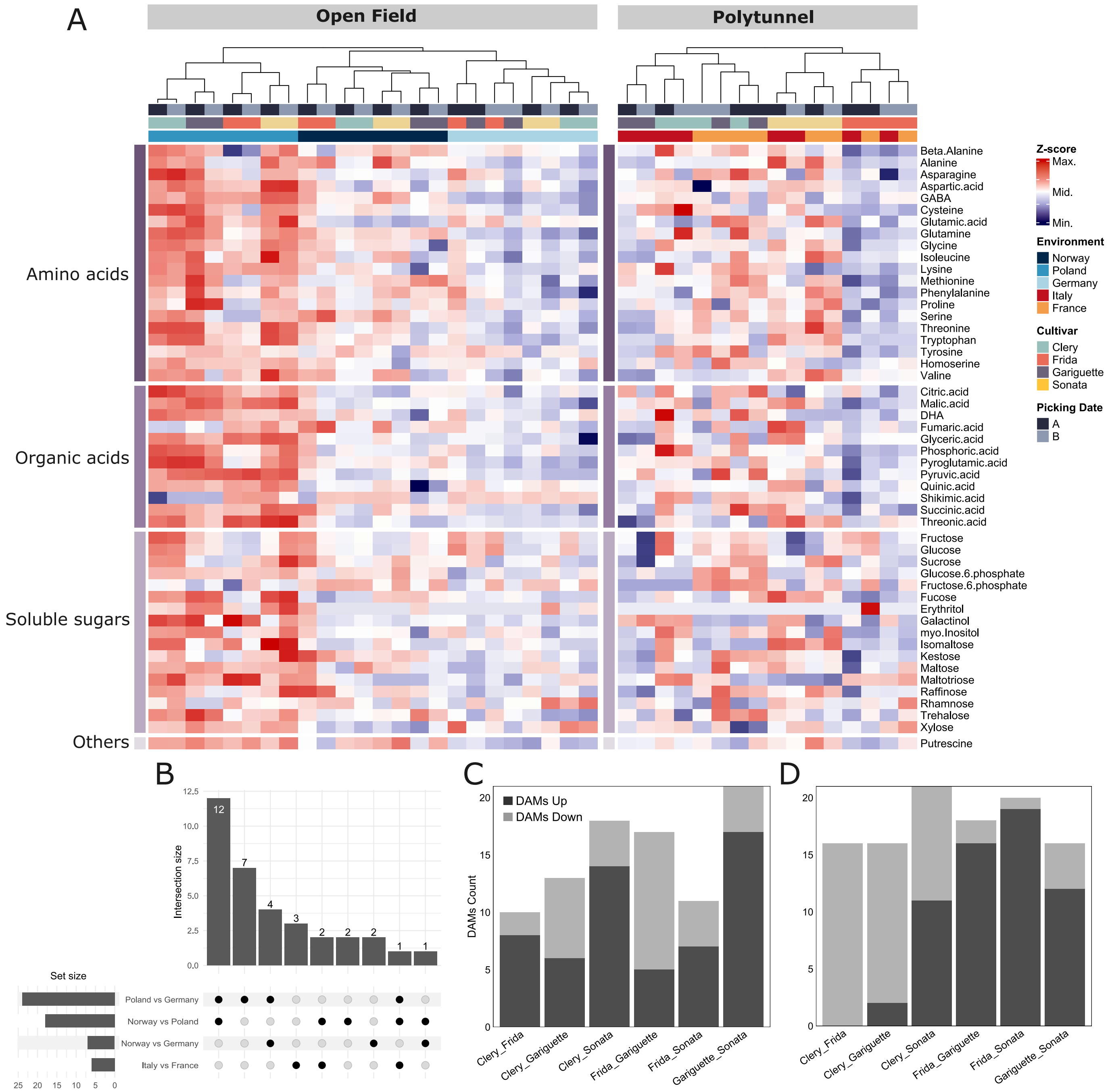

Fig. 3. (A) Accumulation patterns of the primary metabolites for four strawberry cultivars grown in open fields in Norway, Poland, and Germany (left) and under polytunnels in Italy and France (right). Each heatmap displays the clustering of samples based on Pearson correlation of normalized mean intensities of three biological replicates. The normalization step was done individually to each dataset. Red and blue colours indicate high and low metabolite abundance, respectively. Sample group discrimination is indicated by colour labelling. (B) Upset plot for differentially accumulated metabolites (DAMs) across environments. Bar plots for the DAMs counts across cultivars pairwise comparisons for open field (C) and polytunnel regions (D). Light grey denotes increased metabolites, whereas dark grey denotes decreased metabolites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

conditions.

Norwegian-grown samples were clearly separated from other locations, showing a trend toward increased accumulation of fatty acid-derived volatiles and methylketones although only three DAMs from these classes were identified (Fig. 4-B). Polish samples shared a similar VOC profile to norwegian samples. German samples exhibited the most pronounced reduction in volatile content, with twelve decreased DAMs predominantly comprising straight-chain esters and fatty acid volatiles. Clery was the only cultivar to deviate from this trend in Germany, displaying enhanced accumulation of VOCs under these conditions.

Cultivar-specific DAM calculations highlighted distinct metabolic signatures related to aroma-relevant compounds. Frida exhibited the highest number of VOCs-related DAMs (eleven), mostly decreased straight-chain esters and methylketones (Fig. 4-C). Clery followed with eight decreased volatiles, including methyl hexanoate. Gariguette showed a distinct increase in four terpenoids, including linalool. Sonata presented reduced levels of two esters and increased accumulation of γ-decalactone.

VOC profiles under polytunnel cultivation showed GxE interactions markedly influencing sample grouping (Fig. 4-A, right). Frida again

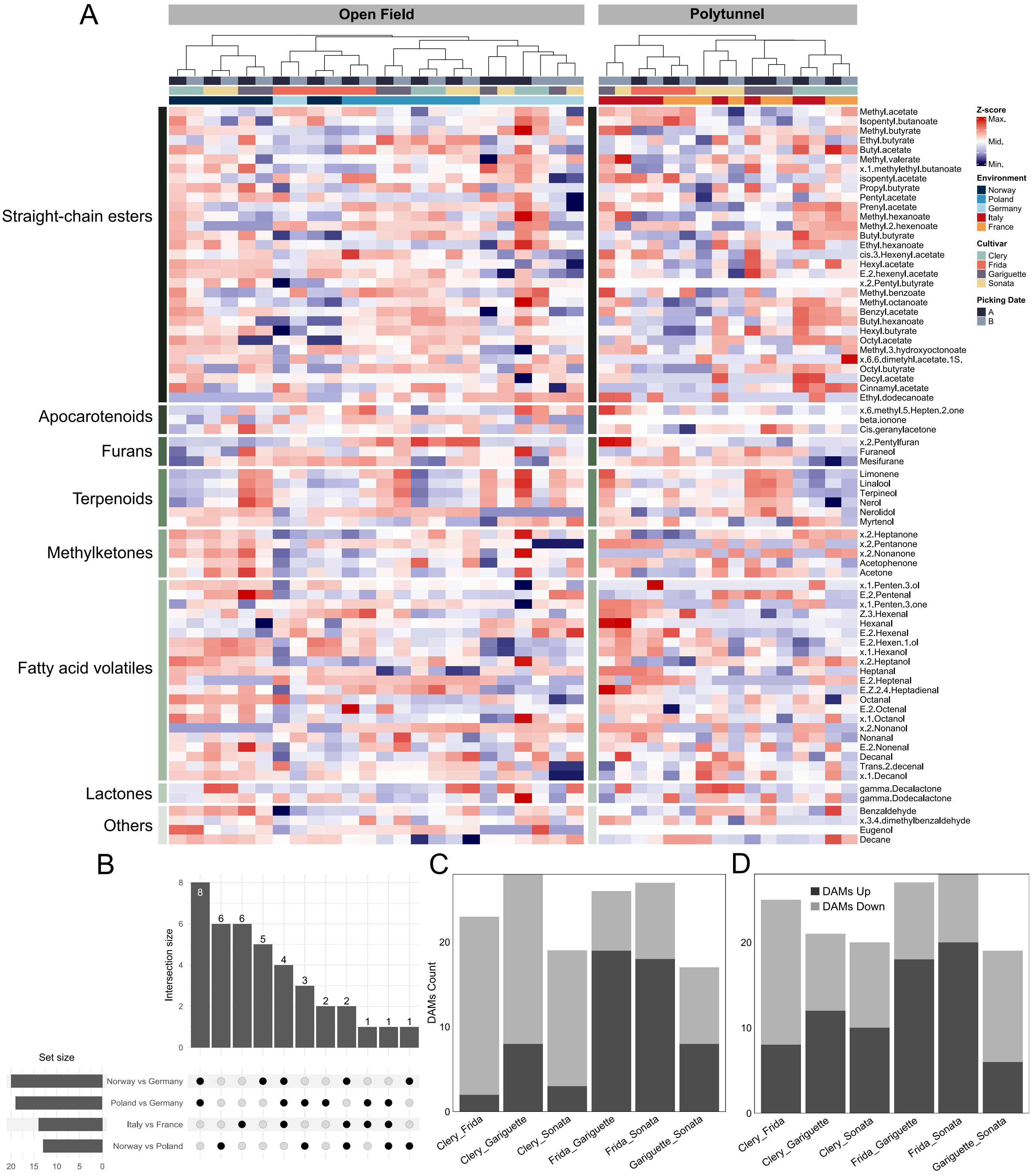

Fig. 4. (A) Accumulation patterns of the volatile organic compounds (VOCs) for four strawberry cultivars grown in open fields in Norway, Poland, and Germany (left) and under polytunnels in Italy and France (right). Each heatmap displays the clustering of samples based on Pearson correlation coefficients of normalized mean intensities of three biological replicates. The normalization step was done individually to each dataset. Red and blue colours indicate high and low metabolite abundance, respectively. Sample group discrimination is indicated by colour labelling. (B) Upset plot for differentially accumulated metabolites (DAMs) across environments. Bar plots for the DAMs counts across cultivars pairwise comparisons for open field (C) and polytunnel regions (D). Light grey denotes increased metabolites, whereas dark grey denotes decreased metabolites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

formed a separate group, clustering with second-harvest Sonata and Gariguette samples. These cultivars accumulated higher levels of VOCs under Italian environmental conditions, while a general reduction was observed under French conditions. DAMs calculations confirmed these trends, identifying thirteen increased volatiles in Italy—mainly esters and methylketones—and only one in France.

The remaining cultivars—Clery, Sonata and Gariguette—clustered together and further stratified by location and, for Sonata and Gariguette, also by harvest date. DAMs calculations for these samples revealed cultivar-specific metabolic footprints (Fig. 4-D). Frida consistently exhibited reduced straight-chain esters and methylketones. Sonata showed elevated ɣ-decalactone levels, Clery accumulated distinct straight-chain esters, and Gariguette demonstrated a consistent increase in terpenoids, particularly linalool. These results were consistent with what was observed for the open-field regions.

3.6. *GxE interactions is a strong factor determining flavour-relevant compounds*

Effect sizes of the evaluated factors were quantified for key flavour-related compounds consistently reported in the literature (Fan et al., 2021; Yan et al., 2018). Notably, the magnitude of these effects varied considerably between the two cultivation systems (Table S4). Under polytunnel conditions, environmental effects were substantially reduced, while cultivar contributions to variance became more pronounced.

The selected sugars (glucose, fructose, and sucrose - main sugars in fruit) were influenced significantly by different factors, inconsistent between cultivation methods. In open-field conditions, the accumulation of sucrose, glucose and fructose were moderately influenced by GxE interactions, accounting for approximately 20% of the variance. In contrast, under polytunnel cultivation, these sugars were significantly influenced solely by the cultivar, with a comparable effect size. Notably, sucrose was the only sugar displaying a significant environmental effect under polytunnel cultivation, contributing to 26% of the total variance (Table S4).

Among the selected organic acids, malic and citric acids exhibited strong significant effects on both cultivar and environment, with environmental factors dominating in open-field conditions. However, in polytunnel trials, the environment effect was not significant, with cultivar being the predominant factor, contributing around 20% to the variation in malic and citric acid accumulation. Additionally, for malic acid, a significant GxE interaction effect was detected within polytunnel environments, accounting for 17.6% of the variance (Table S4).

Regarding the selected VOCs, most compounds exhibited consistent effect influence comparing both cultivation methods, and most of them were predominantly determined by the cultivar, with mesifurane and ɣ-decalactone showing the strongest cultivar effects among the selected compounds. Interestingly, furaneol did not show any significant effects, and ɣ-dodecalactone was affected significantly by only GxE interactions under open-field conditions (Table S4).

To further delineate the environmental determinants of fruit metabolic composition, correlation analysis uncovered a robust and consistent negative association between cumulative temperature during the previous days to harvest and the accumulation of all three major sugars (Fig. S7). In contrast, mean global radiation exhibited a significant positive correlation with sugar content. Organic acids responded differently, both malic and citric acids content positively correlated with mean daily temperature throughout the fruit development phase, contrary to ɣ-decalactone which consistently showed a negative correlation with these covariates. Furans compounds did not display any statistically significant relationship with the environmental covariates assessed. Furthermore, methyl butyrate levels were inversely associated with mean global radiation, whereas both ethyl esters exhibited positive correlations with cumulative radiation exposure during the previous days to harvest. Particularly, ethyl butyrate showed a pronounced positive correlation with mean daily global radiation during the fruit development period.

3.7. *Stability and plasticity analysis of metabolites contributing to organoleptic quality*

GGE biplots along with norm plots enabled the assessment of specific metabolites plasticity across cultivar:environment combinations, revealing numerous cross-over interactions (Fig. 5-A and Fig. S8).

Main soluble sugars (sucrose, fructose and glucose) displayed similar behaviors with high plasticity across environment and strong GxE effects. Open field cultivation regions yielded higher content of these metabolites than polytunnel cultivation regions. Best performing cultivar (accounting stability and mean performance) for sucrose was Sonata, whereas Frida cultivar exhibited the best performance for fructose and glucose.

Organic acids displayed low GxE but high environmental sensitivity. Both citric and malic acid reached peak levels in Poland and minimum levels in Germany. Clery exhibited the highest and most stable malic acid content, while both Clery and Gariguette showed strong and consistent performance for citric acid across environments. Line plots for terpenoids (linalool and terpineol) revealed major cultivar determination, with limited GxE. An exception was Clery, which showed a pronounced increase in Germany compared to the other regions. Notably, Gariguette demonstrated that highest mean levels and overall stability for both volatiles.

Furans derivatives exhibited divergent patterns. Mesifurane displayed minimal plasticity, with cultivar effects predominating and Frida cultivar being the best performing for this compound. In contrast, furaneol was highly plastic and GxE-dependent, peaking in Germany and with Gariguette cultivar obtaining the best performance. Like furans, lactones exhibited different behaviors: ɣ-decalactone was largely stable across environments and mostly cultivar-driven, while ɣ-dodecalactone exhibited higher phenotypic plasticity. In this case, Sonata and Frida presented the highest mean levels for ɣ-decalactone and ɣ-dodecalactone, respectively.

Methyl esters revealed high GxE influences whereas ethyl esters displayed patterns mainly based on growing location. Methyl esters peaked in Germany, with Clery performing best. Ethyl esters varied by compound: ethyl butyrate decreased from north to south following a latitude gradient, with Gariguette showing highest means and Frida the greatest stability; ethyl hexanoate peaked in Germany and France environments, with Clery demonstrating both high performance and stability.

Genotype plus GxE effects heatmap (Fig. 5-B) and “Mean Vs. Stability” plot (Fig. 5-C) indicated that Clery performed optimally in Poland, Frida in Norway, Gariguette in Germany and France. Lastly, Sonata showed consistent high performance across all environments, indicating it was the top-performing cultivar for the selected metabolites in terms of stability and performance (Fig. 5-D).

3.8. *Cultivar type overrides environment in shaping gene expression*

RNA-Seq analysis of 120 strawberry fruits yielded a total of 107,054 transcripts, out of which 56,055 passed the minimum expression threshold. PERMANOVA analysis revealed that the cultivar factor accounted for approximately 12% of the total transcriptional variance, followed by the environmental factor, which accounted for 8.9%. GxE interactions were not statistically significant, and cultivar system effects contributed less than 5% to the observed variance, thus, this factor was excluded from subsequent analyses.

PCA model of gene expression matrix clearly separated samples by cultivar (Fig. 6-A), along with correlation between samples (Fig. 6-B). The first four principal components explained 51.1% of the total variance, with PC2 and PC4 effectively distinguishing cultivars (Fig. S9). Notably, Frida and Gariguette formed distinct clusters, while Clery and

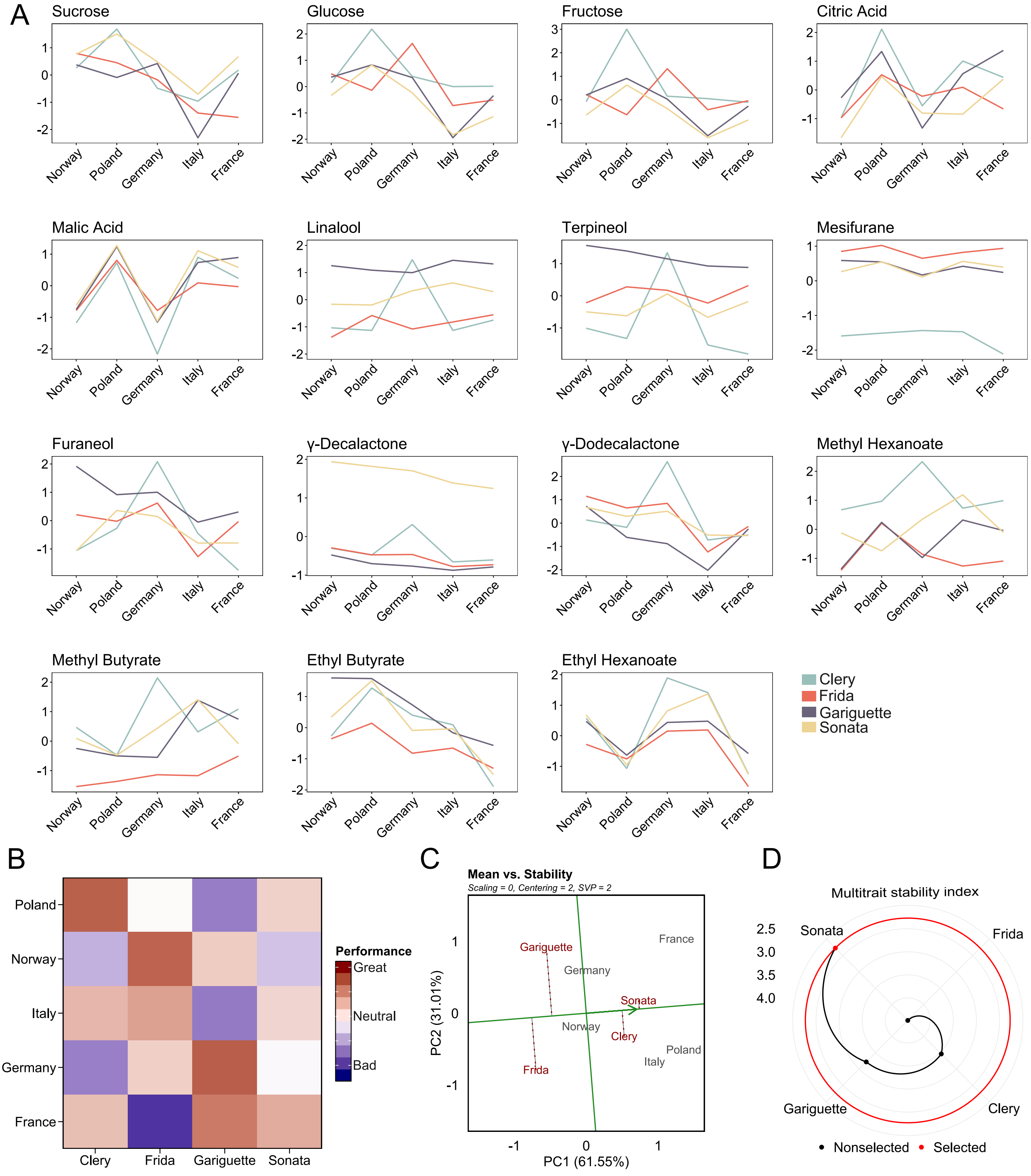

Fig. 5. (A) Line plots of the mean normalized relative contents (z-score) of the selected flavour-relevant metabolites. The metabolites were selected based on the literature consistency about relevant metabolites for strawberry flavour. (B) Ranking of the residual effects from the genotype and genotype-by-environment interaction (GGE) additive model across different environments. Positive values (red) indicate positive performance of the cultivar within the environment, whereas negative values (blue) indicate deficient performance. (C) "Mean versus Stability" GGE biplot representing the mean performance (abscissa) and stability (ordinate) of cultivars across environments. (D) Radial plot for the multi-trait stability index, which integrates mean performance and stability information for identifying superior cultivars for the traits studied. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

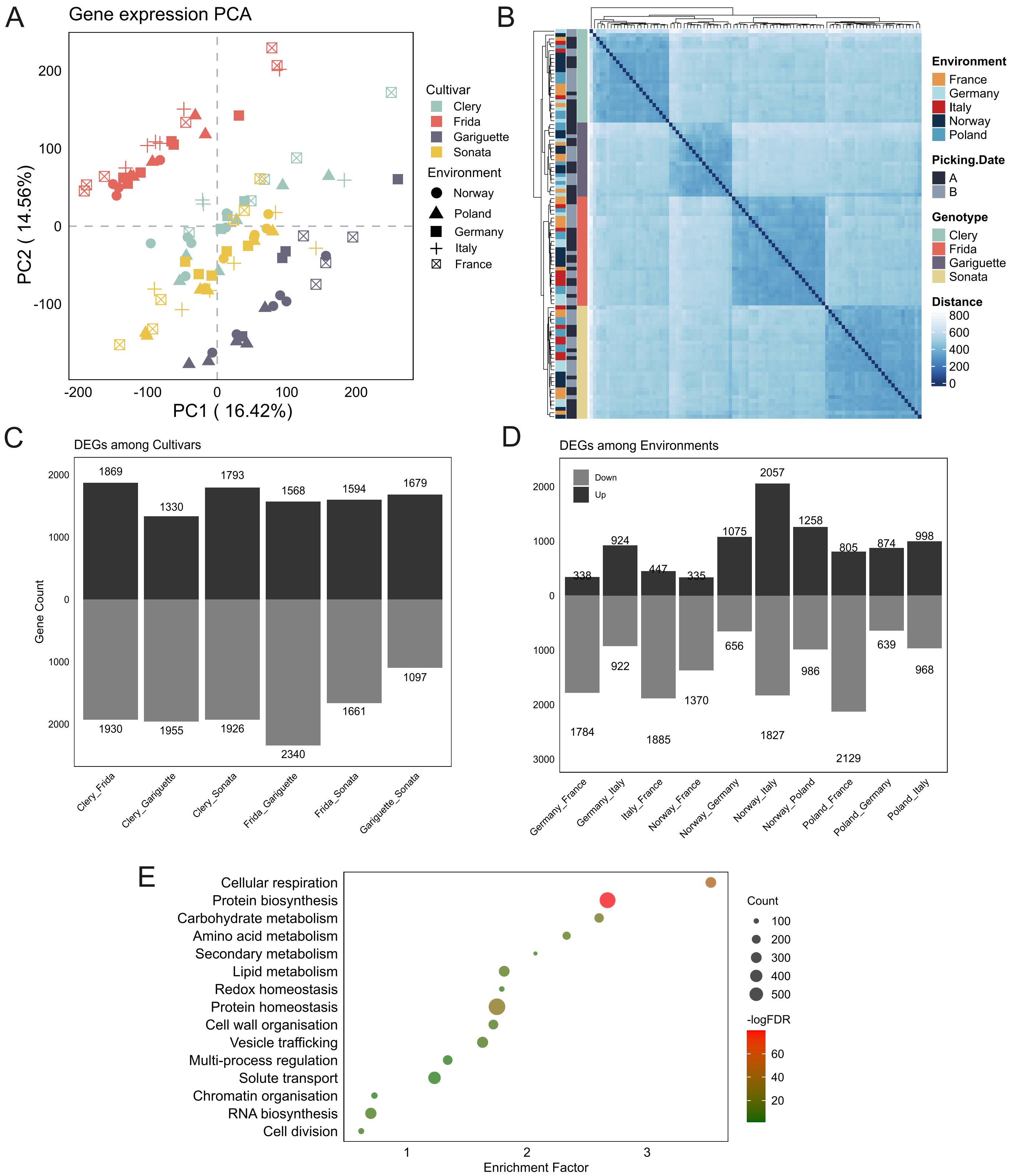

Fig. 6. (A) PCA of z-scores using Log$_2$TPM normalized values of the collected samples. (B) Euclidean distance heatmap of the z-scores using Log$_2$TPM normalized values. (C and D) Bar plots for the number of differentially expressed genes (DEGs) for the sample pair comparisons among (C) cultivars and (D) environments. (E) Bubble plot of the pathway enrichment analysis of the DEGs among G × E combinations.

Sonata exhibited partial overlap. PC3 further separated Clery samples, suggesting a unique transcriptional signature.

Cultivar-specific differential expression analysis identified distinct transcriptional patterns (Fig. 6-C). Clery presented 1011 differential expressed genes (DEGs), including 10 acyltransferases involved in ester biosynthesis. Frida exhibited 866 DEGs, with notable representation of genes involved in carbohydrate metabolism and bZIP transcription factors. Gariguette displayed 742 DEGs, seven of which were linked to terpenoids and carotenoid biosynthesis through the mevalonate pathway (MVA). Sonata showed 808 DEGs, including nine related to fatty acid metabolism.

Environmental pairwise comparisons highlighted underlying strong transcriptional specificity by location (Fig. 6-D). None DEGs were consistently shared across all contrasts. The largest transcriptional divergence was observed between Norway and Italy (2949), with light-responsive genes predominantly upregulated in Norway and temperature-responsive genes in Italy. Moreover, Poland-France contrast yielded 436 DEGs, with differential regulation of heat and cold-responsive genes consistent with regional temperature profiles.

Finally, DEGs calculation across all cultivar:environment combinations simultaneously identified 5895 common DEGs (Fig. 6-E and Fig. S10). Gene function enrichment (Mercator4) revealed 15 significantly overrepresented functional categories (FDR $\leq$ 0.05). The most enriched categories included cellular respiration (243 genes) and protein biosynthesis (573 genes), alongside four flavour-related pathways: carbohydrate (189), amino acid (147), secondary (89) and lipid metabolism (244), indicating their potential role in metabolic adaptation of flavour compounds under varying environmental contexts.

3.9. *Integrative analysis of metabolomic and transcriptomic profiles*

Weighted Gene Co-expression Network Analysis (WGCNA) of the gene expression matrix identified 40 co-expression modules (Fig. S11-A, B). Correlation analysis between these modules and selected key flavour metabolites (sucrose, linalool, mesifurane and ɣ-decalactone), revealed potential regulatory networks specific to cultivar type (Fig. S11—C). Pathway-specific filtering of significantly correlated ($p \leq 0.05$) modules refined candidate genes strongly associated with metabolite accumulation.

3.9.1. *Sucrose related co-expression modules analysis*

Co-expression module analysis linked to sucrose accumulation identified 187 carbohydrate metabolism related genes, including 40 genes directly annotated within sucrose metabolic pathways. Hierarchical clustering of gene expression patterns revealed two major cultivar groupings: Clery-Gariguette and Frida-Sonata, each displaying distinct transcriptional footprints (Fig. 7-A). Clery and Gariguette showed reduced expression of sucrose biosynthesis alongside elevated expression of degradation-associated genes. In contrast, Frida and Sonata

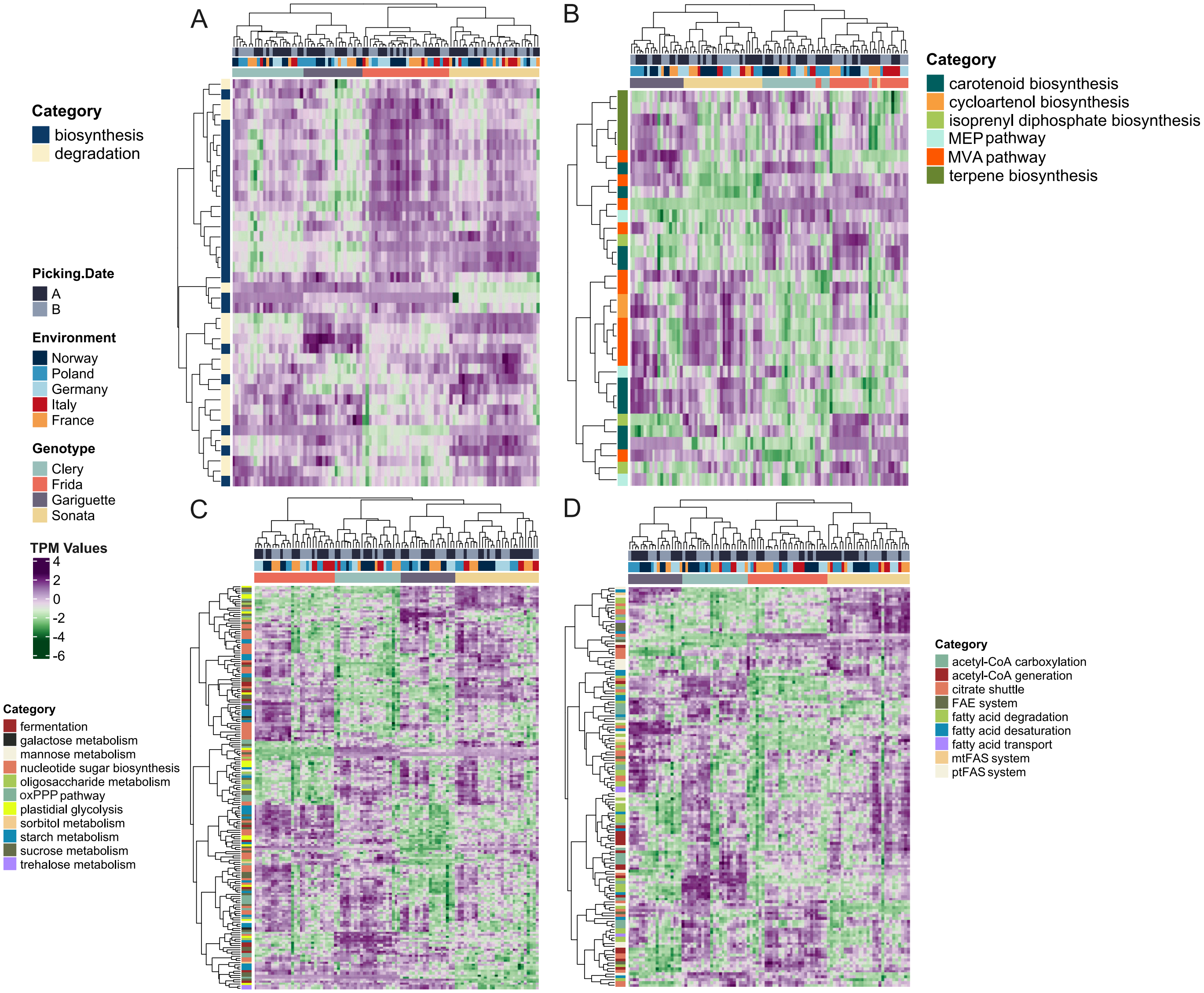

Fig. 7. Heatmaps showing the Log^2-normalized z-scores of expression levels for relevant differentially expressed genes (DEGs) associated with metabolite content. (A) DEGs involved in sucrose metabolism in relation to sucrose levels. (B) DEGs linked to terpenoid metabolism in relation to linalool levels. (C) DEGs associated with carbohydrate metabolism in relation to mesifurane levels. (D) DEGs related to fatty acid metabolism in relation to γ-decalactone levels. Each heatmap includes colour annotations representing the corresponding biological process categories.

exhibited higher expression of biosynthetic genes, with Sonata also showing partial upregulation of sucrose degradation genes.

Pearson correlation analysis between gene expression and sucrose content identified five genes significantly associated with sucrose levels ($p < 0.05$), including cytosolic UDP-glucose pyrophosphorylase, sucrose-phosphate synthase, hexokinase and two cytosolic triose-phosphate isomerases.

Line plots across cultivar:environment combinations demonstrated a strong cultivar-specific transcriptional regulation of these genes, with minimal environmental influence (Fig. S12-A). UDP-glucose pyrophosphorylase was upregulated in Clery and Frida but downregulated in Gariguette and Sonata. Conversely, sucrose-phosphate synthase showed higher expression in Gariguette and Sonata. The two triose-phosphate isomerases displayed divergent expression: one was upregulated in Clery, Frida and Gariguette, but repressed in Sonata; the other was downregulated in Gariguette and upregulated in the remaining cultivars.

3.9.2. *Linalool related co-expression modules analysis*

Gene expression analysis related to linalool accumulation identified 89 genes associated with secondary metabolism, including 33 specifically annotated within terpenoid biosynthetic pathways (Fig. 7-B). Hierarchical clustering of these genes predominantly separated samples by cultivar, revealing distinct expression patterns. Gariguette and Sonata grouped together, while Clery and Frida formed a separate cluster. An upper gene cluster, enriched in terpenoid biosynthesis genes, exhibited strong upregulation in Gariguette, Clery and Frida, but was markedly downregulated in Sonata. Conversely, a lower gene cluster, primarily composed of genes involved in mevalonate pathway (MVA) and carotenoid biosynthesis pathways, showed higher expression in Gariguette and Sonata, and lower expression in Clery and Frida.

Correlation analysis identified five genes potentially associated with linalool accumulation: cleave dioxygenase 1, two nerolidol synthases, farnesyl diphosphate synthase and squalene monooxygenase (Fig. S12—B). These genes demonstrated cultivar-dependent expression patterns with minimal environmental modulation.

Notably, both nerolidol synthases were consistently upregulated in Gariguette, exhibiting negligible expression plasticity across environments. The identified squalene monooxygenase also displayed higher expression levels in Gariguette, with low environmental variation. In contrast, carotenoid cleave dioxygenase and farnesyl diphosphate synthase were downregulated in Gariguette and upregulated in other cultivars, which showed greater transcriptional plasticity across locations. Overall, Gariguette showed remarkably stable expression across environments for the proposed genes.

3.9.3. *Mesifurane related co-expression modules analysis*

Co-expression modules significantly correlated with mesifurane content were filtered by carbohydrate metabolism, given the established role of fructose as its primary precursor in strawberry fruit (Roscher et al., 1998). The hierarchical clustering analysis revealed a predominant stratification of samples by cultivar, suggesting cultivar-specific gene expression patterns (Fig. 7-C).

DEGs associated with multiple metabolic processes were identified, including plastidial glycolysis, the oxidative pentose phosphate pathway and sucrose metabolism, among others. The genes were organized into two principal clusters exhibiting distinct expression patterns. The first cluster demonstrated in Gariguette and Sonata. Conversely, the second major cluster exhibited the opposite trend, with upregulation in Gariguette and Sonata and partial downregulation in Frida and Clery.

Further correlation analysis identified four genes exhibiting statistically significant associations with mesifurane accumulation across samples (Fig. S13-A). These included a triose-phosphate isomerase, a dTDP-4-dehydroharmnose reductase, two fructose-biphosphate aldolases, and a D-fructokinase. All genes, except for the fructokinase, exhibited their highest expression levels and lowest plasticity in the Frida cultivar, followed by Sonata.

3.9.4. *ɣ-Decalactone related co-expression modules analysis*

In the case of this compound, the filtering process led to the identification of 244 DEGs in relation to lipid metabolism. These genes were implicated in phytosterol metabolism, glycerolipid metabolism and fatty acid metabolism—pathways intimately linked to ɣ-decalactone biosynthesis. Genes from fatty acid metabolism were filtered yielding 144 DEGs. Subsequent hierarchical clustering of expression profiles revealed a strong cultivar-dependent stratification of samples (Fig. 7-D).

Within the identified DEGs, key functional categories included genes involved in fatty acid degradation and desaturation as well as the plastidial fatty acid synthase system. Correlation analysis further identified nine genes exhibiting statistically significant relationships with ɣ-decalactone accumulation across samples (Fig. S13—B). These included three NADP-dependent malic enzymes, two malonyl-CoA decarboxylases, two ATP-citrate synthases, one enoyl-[acyl-carrier-protein] reductase [NADH] 1, and one acyl carried protein 1.

Expression patterns varied across cultivars, reflecting distinct transcriptional regulation. Among the three NADP-dependent malic enzymes, only one was significantly upregulated in Sonata, whereas the remaining two exhibited higher expression in Gariguette. Both malonyl-CoA synthases displayed consistently high and stable expression levels in Sonata, contrasting with more variable expression patterns across other cultivars and environments. Furthermore, Sonata exhibited the highest and most stable expression of the enoyl-[acyl-carrier-protein] reductase [NADH] 1, an enzyme catalyzing the terminal step of fatty acid biosynthesis.

4. Discussion

Under the current scenario, where climatic change poses a significant challenge to fruit development and quality, studying cultivar-by-environment (GxE) interactions through multi-environment trials helps to understand the effects of these factors and to develop strategies for mitigating and/or avoiding negative impacts on important traits (Adunola et al., 2024). Unlike climacteric fruits, strawberries—non-climacteric—do not undergo significant ripening post-harvest, thereby necessitating harvest at peak maturity (Li et al., 2022; Pedrozo et al., 2023; Perotti et al., 2023). This biological constraint is further compounded by commercial imperatives, where producers are pressured to ensure rapid fruit turnover to maximize profitability (Kouloumprouka Zacharaki et al., 2024). Accelerating or delaying the development and ripening processes in fruits can alter their metabolic profiles and, thus, their organoleptic quality (Castellarin et al., 2007; Orisa & Usoroh, 2020; Maduwanthi & Marapana, 2019). Within this framework, the ability to dissect the effects of cultivar, environment and their interaction on fruit development duration becomes a powerful tool to improve the quality of the fruits and their environmental resilience (Krüger et al., 2012).

Our findings confirmed that harvest season and fruit development duration was significantly modulated by temperature and global radiation, with higher latitudes delaying harvest season and higher mean daily temperatures form flowering onset to harvest accelerating the fruit development duration, such as in Poland. It has been described that high temperatures accelerate flower development in strawberry fruits, aligning with the acceleration of fruit development that we observed (Menzel, 2023). Specifically, temperature-dependent regulation of gibberellins and auxins plays a central role in cell expansion and fruit maturation, with higher temperatures leading to increased metabolic flux through carbohydrate metabolism, thereby shortening fruit development times (Kurokura et al., 2013).

Elevated mean daily temperatures and global radiation during fruit development in Poland environment yielded higher accumulation of primary metabolites and great accumulation of volatile compounds in comparison to the other regions, suggesting this phenomenon could be due to the reduction in fruit size observed in fruits grown under high temperatures (Menzel, 2021; Menzel, 2023). This reduction could have caused the concentration of metabolites within the fruit explaining the observed patterns. Conversely, regions like Germany, characterized by lower mean daily temperatures and reduced global radiation, exhibited prolonged development times. Such observations are consistent with prior research demonstrating that suboptimal temperatures can delay physiological processes such as anthesis-to-ripening transition, starch hydrolysis and pigmentation biosynthesis, ultimately prolonging the ripening phase (Kadir et al., 2006). This also align with the thermal accumulation hypothesis, which posits that lower temperatures slow metabolic rates by downregulating key enzymes involved in glycolysis and cell division, thereby prolonging fruit development (Brizzolara et al., 2020; Mao et al., 2022).

Light availability has also emerged as co-determinant of development timing, reinforcing the central role of photothermal regimes in regulating phenological events (Cervantes et al., 2019; Jiang et al., 2023). Variations in cumulative global radiation were mirrored by changes in fruit development duration, highlighting the synergistic impact of temperature and light on ripening. Given projections of increasingly erratic weather patterns and altered light regimes (Orlowsky & Seneviratne, 2012), these results raise important concerns regarding the future synchronization of ripening dynamics and market supply chains (Jiang et al., 2023; Twitchen et al., 2021).

Environmental modulation of key flavour compounds was particularly pronounced. Sugars, especially sucrose, fructose and glucose, showed a consistent negative correlation with temperature, which aligned with higher sugar rates within cooler environments. This phenomenon has been described in literature before and has been associated to changes in the transcription of genes related to carbohydrate metabolism in conjunction to hormonal signaling that leads to increased soluble sugar contents (Wang & Camp, 2000). Additionally, some sugars such as sucrose serve as protective compounds, osmolytes, maintaining membrane integrity under cold stress (Pirzadah et al., 2014). In contrast elevated temperatures before harvest favoured the accumulation of malic and citric acids. However, conflicting literature on these organic acids suggests that the metabolic responses are complex and potentially cultivar-dependent, reinforcing the need for more granular, cultivar-specific analyses (Uleberg et al., 2012; Wang & Camp, 2000). For instance, in grapefruit elevated temperatures reduced malic acid in a genotype-dependent manner (Wang et al., 2025).

Volatile profiles were also influenced by climatic conditions. Temperature and global radiation modulated the accumulation of several VOCs, including ɣ-decalactone and ethyl esters, central to peachy and fruity aromatic notes of strawberry (Klee & Tieman, 2018; Yan et al., 2018). Yet, literature remains inconsistent regarding specific effects of climate on VOCs, underscoring the importance of conducting further multi-environment trials to establish robust, reproducible associations under real-world conditions. Our findings, particularly, indicated that elevated cumulative temperatures before harvest can reduce ɣ-decalactone content. Similarly, high cumulative global radiation values before harvest can increase ethyl butyrate and ethyl hexanoate content in strawberry fruits.

Stability and performance analysis further demonstrated the breeding potential of specific cultivars. Gariguette showed high and stable accumulation of linalool, a key terpene linked to desirable floral aromas and consumer liking (Klee & Tieman, 2018). Sonata performed consistently well for ɣ-decalactone, contributing peach-like notes to the aroma, while Frida emerged as a strong candidate for mesifurane accumulation, associated with caramel-like nuances. Notably, Clery exhibited potential for enhancing esters profile, which contributes to fruity aromas (Klee & Tieman, 2018). Importantly, the metabolite stability of these key volatiles across environments suggests their robustness as breeding resources, capable of supporting flavour-oriented cultivar development even under varying climatic pressures. However, the current scarcity of studies assessing the impact of G × E interactions on flavour-related metabolites in non-climacteric fruits underscores an urgent need for comprehensive, multi-environment investigations. Such efforts are essential to elucidate complex regulatory networks underlying flavour resilience and to guide the development of new cultivars capable of maintaining the high sensory quality demanded by consumers under increasingly variable climatic conditions.

The integration of transcriptomic data indicated genetic background plays a dominant role in shaping metabolic pathways underpinning strawberry flavour, with strong cultivar-specific transcriptional responses modulated by environmental context. A dynamic interplay between cultivar and environment was observed in the regulation of genes involved in carbohydrate metabolism, secondary metabolism and lipid biosynthesis—pathways directly associated with the accumulation of key flavour compounds such as sugars, terpenoids, furans, lactones and esters (Bood & Zabetakis, 2002; Yan et al., 2018). These findings underscore the existence of distinct, cultivar-dependent regulatory mechanisms, which can be strategically exploited in targeted breeding programs to improve flavour profiles under specific environmental conditions (Urrutia et al., 2017; Vallarino et al., 2018).

Crucially, transcriptomic variation influenced by local adaptation, supporting the hypothesis that fine-tuning cultivation environments to match specific cultivars could substantially enhance fruit quality (Gao et al., 2023). This reinforces earlier findings in other horticultural crops that demonstrate the efficacy of environmental optimization in improving metabolite accumulation (Hu et al., 2022).

By integrating transcriptomic and metabolomic data, we identified promising genetic targets associated with the accumulation of sucrose, linalool, ɣ-decalactone and mesifurane—metabolites with key roles in defining strawberry flavour (Table 1) (Schwieterman et al., 2014). UDP-glucose phosphorylases and hexokinases emerged as candidates for enhancing sucrose accumulation, particularly under environmental variability. These enzymes are key to sugar metabolism, and their regulatory roles extend beyond carbohydrate processing, linking metabolic flux with developmental control (Wang et al., 2014; Wenqi, 2025). Their upregulation in Sonata—the top performing cultivar for sucrose content—further highlights the value of this cultivar for breeding programs focused on sweetness enhancement.

Similarly, the identification of DEGs within the mevalonate pathway (MVA) and methylerythritol phosphate (MEP) pathways, along with terpene synthase (TPS) activity, confirms the known linalool biosynthesis in strawberry (Aharoni et al., 2004; Barbey et al., 2021; Chambers et al., 2012; Nagegowda et al., 2008). The stability of these genes across environmental conditions was particularly pronounced in Gariguette, a cultivar widely recognized for its strong strawberry aroma and optimal organoleptic qualities (Aubert et al., 2021). Given its superior performance and stability for linalool accumulation, Gariguette represents an excellent candidate for breeding programs aiming to enhance terpene-derived aroma compounds in commercial cultivars. Previous studies have demonstrated the role of MEP and MVA pathways regulation in the biosynthesis of volatiles contributing to fruit flavour (Aharoni et al., 2004; Chambers et al., 2012; Hampel et al., 2006) and can be used to improve further sensory characteristics attributed to terpenoids. The potential for metabolic engineering or marker-assisted selection to optimize linalool production in strawberry cultivars should thus be explored further.

Correlation analysis further identified promising candidate genes associated with the biosynthesis of ɣ-decalactone and mesifurane, two key volatiles responsible for peach-like and caramel-like aroma notes, respectively. These genes were predominantly involved in carbohydrate and fatty acid metabolisms, both known to drive the synthesis and accumulation of these aroma compounds by providing precursors (Barbey et al., 2021; Oh et al., 2021; Sánchez-Sevilla et al., 2014; Zorrilla-Fontanesi et al., 2012). Notably, cultivar Frida exhibited the highest mean performance and phenotypic stability for mesifurane accumulation, whilst Sonata excelled in ɣ-decalactone content, indicating their potential as valuable genetic resources for improving the production and stabilization of these metabolites in strawberry breeding. A consolidated summary of the key findings characterizing the specific profile of each cultivar is presented in Table 2.

Collectively, these findings underscore the transformative potential of multi-omics integration in pinpointing robust molecular targets for strawberry flavour improvement, with particular emphasis on the influence of genotype-by-environment interactions at both metabolic and transcriptional levels (Vallarino et al., 2019). However, it will be essential to move beyond association-based inferences and systematically assess the functional contribution of the candidate genes. This should include targeted analyses of gene expression dynamics across contrasting environments, as well as functional interrogation of selected loci using reverse-genetic approaches that perturb their activity in a controlled manner. Such efforts would enable the confirmation of causal links between specific transcriptional regulators, metabolic shifts, and flavour-related phenotypes, thereby overcoming the current limitation that the proposed targets remain supported primarily by correlative evidence. Establishing this mechanistic validation pipeline will be a necessary step to translate the multi-omics predictions into actionable markers and tools for breeding programs aimed at stabilizing strawberry flavour under variable climatic conditions.

Moreover, integrating additional omics layers will unravel deeper regulatory intricacies underlying fruit quality, accelerating the development of strawberry cultivars that combine superior sensory attributes with resilience to variable climates. It is also important to recognize that the present study, by centering on European-bred cultivars, provides critical insight into regional adaptation but imposes inherent geographical limitations on the broader applicability of the molecular findings. To transcend these constraints, future research must include cultivars from diverse breeding backgrounds, as for example from major strawberry-producing regions in Asia and the Americas. Such an expansion will be pivotal for determining the universality of the identified regulatory modules and for translating these discoveries into globally applicable, flavour-oriented breeding strategies.

5. Conclusion

These findings underscore the critical influence of cultivar-by-environment (GxE) interactions on strawberry fruit quality, demonstrating that both, phenological traits and flavour-related metabolites, are highly sensitive to climatic variation and cultivar specification. The divergent responses of primary and specialized metabolism highlight intrinsic differences in their evolutionary plasticity, underscoring the imperative for cultivar-tailored strategies in flavour optimization.

Our identification of cultivar-specific transcriptional regulation for key compounds—such as sucrose, linalool, γ-decalactone and mesifurane—reveals untapped potential for precision breeding. Notably, the discovery of robust and environmentally stable genetic targets provides a tangible framework for the development of elite cultivars with enhanced and consistent flavour profiles across diverse agroclimatic conditions, maintaining environmental resilience.

In the face of ongoing climate change and its impact on photothermal regimes, exploiting the predictive power of GxE-responsive genes emerges as a critical path forward. Our results advocate for the development of integrative, environmentally aware breeding pipelines that prioritize metabolite stability and sensory quality. Moreover, these findings call for the expansion of multi-environment, multi-omics trials to establish robust models capable of guiding cultivar deployment under diverse agroclimatic scenarios.

CRediT authorship contribution statement

Patricia Pacheco-Ruiz: Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis. **Elisa Senger:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Formal analysis. **Delphine M. Pott:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Freya M.R. Ziegler:** Resources, Methodology, Formal analysis. **Lidia Jiménez:** Methodology, Investigation. **Anita Sønsteby:** Writing – review & editing, Resources, Investigation. **Erika Krüger:** Writing – review & editing, Resources, Investigation. **Philippe Chartier:** Resources. **Agnieszka Masny:** Resources. **Daniela Mott:** Resources.

Table 2

Summary of key metabolic and transcriptomic findings for the studied strawberry cultivars, highlighting performance across environments and Genotype x Environment (GxE) interactions.

Cultivar	Metabolic signatures in comparison to the other cultivars	Transcriptomic signatures in comparison to the other cultivars	Top performance location	Worst performance location	Plasticity (GxE effects)
Clery	High: Glucose, fructose, citric acid, and methyl/ethyl esters. Low: Malic acid, terpenes (linalool, terpineol), and mesifurane.	Pronounced upregulation of acyltransferases (AATs) involved in ester biosynthesis and key enzymes in carbohydrate metabolism (specifically sucrose degradation DEGs).	Poland	Germany	Trait-dependent plasticity - High environmental sensitivity observed for the accumulation of most key flavour compounds, with the exception of mesifurane and γ-decalactone, which displayed consistent accumulation patterns.
Gariguette	High: Malic acid, terpenes (linalool, terpineol), furanones (mesifurane, furaneol), and ethyl butyrate. Low: Sucrose, fructose, and glucose.	Strong upregulation of MVA pathway DEGs, including terpenoid biosynthesis genes (e. g., terpene synthases).	Germany & France	Poland & Italy	Trait-dependent plasticity - High plasticity observed for most flavour-relevant metabolites. Conversely, linalool, terpineol, mesifurane, and γ-decalactone showed stable accumulation across conditions.
Sonata	High: Sucrose, malic acid, mesifurane, and γ-decalactone. Low: Fructose, glucose, citric acid, and furaneol.	Upregulation of DEGs related to sucrose biosynthesis and degradation (including hexokinase). Distinct differential expression of fatty acid biosynthesis and degradation genes.	All environments, excelling in France	Norway	Global stability - Ranked as the top-performing cultivar based on the Multi-Trait Stability Index (MTSI). Demonstrates consistent high accumulation and stability across environments for the majority of key strawberry flavour compounds.
Frida	High: Mesifurane. Low: Consistent low profile for all other metabolites across conditions.	Strongest upregulation of DEGs corresponding to sucrose biosynthesis. Notably, inverse expression patterns were identified for genes related to linalool, mesifurane, and γ-decalactone in comparison to the other cultivars.	Norway	France	Trait-dependent plasticity - High stability observed for linalool, terpineol, mesifurane, γ-decalactone, and γ-dodecalactone. High plasticity observed for the remaining metabolites.

Aurélie Petit: Writing – review & editing, Resources. **Gianluca Savini:** Resources. **Björn Usadel:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis. **Sonia Osorio:** Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **José G. Vallarino:** Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodchem.2026.148161.

Data availability

Data will be made available on request.

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