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Flavor-Related Precursors and Other Compounds in Raw Organic Dry Pea (*Pisum sativum* L.) for Plant Breeding

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ABSTRACT

Dry pea (*Pisum sativum* L.) is a cold-season food legume widely used as a source of plant-based protein. Improving flavor-related traits through conventional plant breeding, rather than food additives, is vital to creating desired outcomes for consumers. This study aimed to identify precursor molecules associated with flavors in organically grown dry pea. The experiment was conducted with 44 genotypes (25 dry pea cultivars and 19 dry pea breeding lines) in a randomized complete block design in two locations with two replicates per location ($n = 176$). Unsaturated fatty acid esters, organic acids, terpenoids, and phytosterols were identified. Among unsaturated fatty acid esters, linoleic acid esters had the highest concentration (1518.52 ± 59.4 mg/100 g) while linolenic acid esters had the lowest (295.58 ± 9.20 mg/100 g). Citric acid (27.58 ± 2.60 mg/100 g) was the most abundant organic acid in dry pea. Concentrations of phytosterols (γ-sitosterol: 4.25 ± 0.06 mg/100 g and stigmasterol: 1.07 ± 0.004 mg/100 g) were higher than those of terpenoids (β-amyrin: 0.65 ± 0.011 mg/100 g and γ-tocopherol: 0.56 ± 0.01 mg/100 g). Of the identified traits, tartaric acid, citric acid, β-amyrin and γ-sitosterol demonstrated significant genotype effects at $p < 0.05$ and $p < 0.001$. The remainder of the traits evaluated did not significantly vary with genotype, environment, or genotype by environment effects. Identification of these flavor-related precursors provides foundational insights for targeted breeding approaches aimed at improving the flavor towards consumer acceptance of dry pea.

1 | Introduction

Dry pea is a cool-season legume that belongs to the Fabaceae family. The crops are harvested as dry seeds, known as pulses, and consumed as whole food. Dry pea is rich in low-digestible carbohydrates (12%–15%), proteins (20%–25%), fats (< 1%), vitamins (such as A, B, and E), and various minerals (~1%)(Thavarajah et al. 2023). Dry pea is rich in high-quality protein and possesses an in vitro protein digestibility of >87% (Thavarajah et al. 2023). Dry pea is a primary ingredient in plant-based proteins, especially vegan burgers (Cohen 2023). The plant-based protein market is currently worth USD 14.3 billion, with growth anticipated to reach USD 20.5 billion by 2029 (Mehra 2025). Organically grown dry pea is an environmentally friendly, sustainable option for this multibillion-dollar industry, which is one of the fastest-evolving segments in the US market (Reganold and Wachter 2016). High-yielding and nutritionally high-quality dry pea varieties under organic farming conditions have been reported (Thavarajah et al. 2022, 2023). Understanding the flavor-related traits associated with such varieties is important to ensure further consumer acceptance of plant-based proteins.

Flavor is the combined perception of aroma and taste, while the aroma is primarily driven by odor-active volatile compounds that stimulate the human olfactory system (Roland et al. 2017).

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Tastes arise from the chemical interactions between nonvolatile molecules and sensitive tongue receptors (Roland et al. 2017; Trindler et al. 2022). Not all volatile compounds are odor-active, and the calculated odor-active values (OAVs) estimate their contribution towards the overall aroma (Bi et al. 2020; Trindler et al. 2022). Dry pea has a blend of beany, earthy, and green (grass-like) aromas extending from volatile aldehydes, ketones, and alcohols (i.e., hexanal, 1-octen-3-one, hexanol, etc.). In dry pea, hexanal (OAV = 280) and 3-methyl butanoic acid (OAV = 382) are strong contributors to aroma with high OAVs (Bi et al. 2020). Dry pea sweetness is attributed to simple sugars (such as glucose, fructose, and sucrose) and sugar alcohols (such as sorbitol and mannitol), while organic acids contribute slightly by imparting tartness (Thavarajah et al. 2022). Dry pea genotypes include bitter tastes mainly derived from nonvolatile saponins, such as saponin B and 2,3-dihydro-2,5-dihydroxy-6-methyl-4H-pyran-4-one (DDMP) saponin (Heng et al. 2006; Roland et al. 2017). Saponins are also associated with bitter, astringent, and metallic tastes in dry pea (Price et al. 1985). Besides sweetness, beany, earthy, green aromas, bitter, astringent, and metallic tastes contribute to off flavors in dry pea, adversely affecting its palatability (Roland et al. 2017).

Aligned with optimal nutritional quality, dry pea breeding should target flavor traits (taste and aroma) to mitigate off-flavors and enhance consumer acceptance. Unlike nutritional traits, off-flavors arise from the enzymatic and nonenzymatic degradation of several unsaturated fatty acid esters (Fischer et al. 2022). These compounds are precursors to forming aldehydes, ketones, and alcohols, associated with beany, earthy, green off-flavors (Bi et al. 2020; Fischer et al. 2022). These byproducts are produced during preharvesting and postharvesting storage (Roland et al. 2017). Contrastingly, organic acids and saponins are primary and secondary metabolites. Organic acids are primarily synthesized in central metabolic pathways (i.e., tricarboxylic acid and shikimic acid pathways). In contrast, dry pea saponins are synthesized from the isoprenoid biosynthetic pathways via β-amyrin as a molecular precursor (Hodgins et al. 2024).

Identifying and quantifying precursor compounds and primary metabolites (i.e., organic acids) linked to dry pea off-flavors can offer valuable insights to strengthen sensory evaluations and make them more acceptable for consumers. Therefore, dry pea genotypes combined with palatability and high protein quality can be selectively bred to meet the demands of the plant-based protein market. The present study aimed to identify and analyze such compounds in organically grown raw dry pea seeds. This study was conducted with 44 genotypes (25 dry pea cultivars and 19 dry pea breeding lines) organically grown in two locations in South Carolina, USA, with two replicates per location ($n = 176$). The effects of genotype and environment on these traits were also assessed to provide insights into future breeding strategies.

2 | Materials and Methods

2.1 | Materials

All chemical standards, solvents, and eluents were high-purity HPLC grade (assay ~97–99%), purchased from Fisher Scientific (Waltham, Massachusetts, USA). Nano-pure water (resistance: 18–20 MΩ) generated by a Milli-Q water system (PURELAB flex 2 system, ELGA Lab Water North America, Woodridge, Illinois, USA) was used to prepare standard solutions, samples, and eluents required for chromatography analyses.

2.2 | Experimental Design and Seed Samples

The field design of this experiment was a randomized complete block design (RCBD) with a total of 44 accessions, including 25 cultivars and 19 breeding lines. Each accession was replicated twice in two locations (Clemson and Pelion, South Carolina) in 2019 ($n = 176$; Table 1) (Thavarajah et al. 2022). All the seeds analyzed in the study were round and smooth with white testa and primarily with a blend of green and yellow colors in the cotyledon.

2.3 | Land Preparation and Seeds

All seeds for this study were sown at USDA-certified organic farms located at WP Rawls and Sons (Pelion, South Carolina, USA) and Calhoun Fields Laboratory (Clemson University, South Carolina, USA) (Thavarajah et al. 2022). In May 2019, the Pelion area had warmer temperatures (25.6°C) and higher rainfall (68.6 mm) than the Clemson area. However, between January and May, the Clemson area received more precipitation (111.6 mm) than the Pelion area (75.7 mm). At the time of the field study, soils at the Clemson site had low pH (6.3) soil with higher concentrations of nitrate nitrogen ($N\text{-}NO_3$; 48 ppm), potassium (K; 284 lbs/ac), and organic matter (4.3%) than soils at the Pelion site, which had more phosphorus (P; 727 lbs/ac) (Thavarajah et al. 2022).

TABLE 1 | The experimental design for the dry pea trials conducted in 2019 at Clemson and Pelion, South Carolina, USA.

Year (location)	2019 (Clemson; Pelion)
Location	Clemson, SC; Pelion, SC
Replicates (Year)	2 (2019)
Cultivars	**Cultivars (25):** AAC Carver, AAC Comfort, AC Agassiz, AC Earlystar, Banjo, CDC Amarillo, CDC Gwater, CDC Inca, CDC Saffron, CDC Spectrum, CDC Striker, Delta, DS Admiral, Durwood, Fiddle, Flute, Hampton, Jetset, Korando, LG Koda, Matrix, Mystique, Nette 2010, SW Arcadia, SW Midas **Breeding lines (19)**: PS01100925, PS03101445, PS05100735, PS08100582, PS08101004, PS08101022, PS12100047, PS14100079, PS1410B0003, PS1410B0006, PS1410B0065, PS1410B0073, PS1514B0002, PS16100003, PS16100038, PS16100085, PS16100086, PS16100096, PS16100127
Total	176

2.4 | Fatty Acid Ester Analysis

The fat extraction procedure was based on Christie (1982) and Shantha et al. (1992) with modifications. Briefly, 200 ± 0.1 mg flour samples from seeds were weighed, transferred into glass bottles, and mixed with 5 mL of hexane. The samples were defatted through sonication for 10 min, and the hexane supernatants (4 mL) were then carefully transferred into glass tubes. Ten milliliters (mL) of freshly prepared 2 M potassium hydroxide (KOH) in methanol were mixed with the content in each glass tube and vortexed. Fatty acid esters in hexane were derivatized into volatile fatty acid methyl esters (FAMEs) through transesterification. The vortexed mixtures were allowed to stand for 10 min, allowing phase separation. One-milliliter portions from the top hexane layer were diluted four times and analyzed for FAMES. The analysis was performed with an 8860-gas chromatography (GC) system coupled to a 5977B mass spectrometry detector (MSD) (Agilent Technologies, Santa Clara, California, USA). All the separations were performed with an HP-5 ms ultra inert (UI) column (30 m × 0.250 mm × 0.25 μm) (Agilent Technologies, Santa Clara, California, USA) using Helium (He) gas (99.9995%) as the carrier gas. The FAMES were quantified in selective ion monitoring (SIM) mode. The temperature program of the GC analysis and the relevant mass to charge (m/z) ratios of the ionic fragments, along with retention times, are indicated in the supplementary information section 1 (Tables S1 and S2). The selected m/z ratios were based on Thurnhofer and Vetter (2005). The chromatogram of the analysis is indicated in the supplementary information section 1 (Figure S1).

2.5 | Organic Acid Analysis

Flour samples from seeds (200 ± 0.1 mg) were weighed and mixed thoroughly with 5 mL of water and then vortexed for 1 min. The samples were left to stand overnight in the dark. The following day, samples were mixed thoroughly and centrifuged (1500 rpm for 10 min) to separate particulate matter in the aqueous phase. The supernatants (25 μL) were immediately analyzed for simple organic and phenolic acids. Simple organic acids were analyzed using a Dionex ICS-5000$^+$ system (Thermo Scientific, Waltham, Massachusetts, USA) following modifications to an earlier method described by Talamond et al. 2000 and Thavarajah et al. 2009. Briefly, the device was connected to a Dionex OmniPac PAX-100 (4 (id) mm × 250 mm) (Thermo Scientific, Waltham, Massachusetts, USA) column and equipped with an anion dynamically regenerated suppressor (ADRS 60, 4 mm; set-current: 300 mA and set-voltage: 10 V) (Thermo Scientific, Waltham, Massachusetts, USA) attached to a conductivity detector (Thermo Scientific, Waltham, Massachusetts, USA). Solvents A (150 mM KOH), B (acetonitrile (15%), methanol (17%), ethanol (18%), and deionized water (50%) w/w mixture), and C (deionized water) were the eluents of this analysis. The gradient elution and the retention times are indicated in the supplementary information section 2 (Tables S3 and S4). The chromatograms of the analysis are indicated in the supplementary information section 2 (Figure S2). Gallic acid was analyzed using Agilent's 1100 series reverse-phase high-performance liquid chromatography (RP-HPLC) system with a G1315B diode array detector (Agilent Technologies, Santa Clara, California, USA). This analysis was conducted with the method described by Berry and Henderson (2010) without further modifications. Briefly, this separation was conducted with an Agilent Zorbax RRHD SB-C18 (2.1 (id) mm × 100 mm) column with the eluents A (water +0.1% formic acid) and B (acetonitrile +0.1% formic acid). The gradient elution is in the supplementary information section 2 (Table S5). The chromatograms associated with the analysis are indicated in the supplementary information section 2 (Figure S3).

2.6 | Terpenoid and Phytosterol Analysis

Flour samples (5.0 ± 0.001 g) were weighed and loaded into syringes. Samples were mixed with 2 mL of isopropyl alcohol (IPA) and agitated by shaking for 10 min (inside the syringes) to ensure sufficient mixing. The supernatants were filtered through a nylon syringe filter (13 mm × 0.45 μm) and diluted by a factor of 1000 before analysis. The analysis was performed with an 8860-gas chromatography (GC) system coupled to a 5977B mass spectrometry detector (MSD) (Agilent Technologies, Santa Clara, California, USA). All the separations were carried out with an HP-5 ms UI (30 m × 0.250 mm × 0.25 μm) (Agilent Technologies, Santa Clara, California, USA) column using He gas (99.9995%) as the eluent. The compounds were analyzed in the scan mode (window: 50–550 m/z) and confirmed with standards using the National Institute of Standards and Technology (NIST) library for mass spectra, built into Agilent's Mass Hunter Workstation Qualitative Analysis for GC–MS and LC–MS (version 10.1) software. All identified phytosterols and terpenoids (Table 2) were quantified using Selected Ion Monitoring (SIM) mode based on targeted m/z values from the NIST Library (NIST 2025). The temperature program of the chromatography analysis, the relevant m/z ratios of the ionic fragments, and retention times are indicated in the supplementary information section 3 (Tables S6 and S7). The chromatogram associated with this study is in supplementary information section 3 (Figure S4).

2.7 | Statistical Analysis

Genotypes, replicates, and locations were included as class variables. Data from both locations were combined and analyzed with a generalized linear mixed model approach (PROC GLM). Mean separation was performed with Fisher's least significant difference (LSD) at ≤ 0.05. Pearson correlation coefficients were calculated among unsaturated fatty acid esters and phenolic compounds identified in dry pea. Analysis of variance (ANOVA) was applied to evaluate the significance of genotype, location, and genotype × location effects. In this approach, genotype and location were considered fixed effects, while the interaction between genotype and location was treated as a random effect. Principal component analysis (PCA) was performed using the means of all genotypes for all flavor-related traits. Three major clusters of genotypes were observed in the PCA. According to the scree plot, the first eight principal components (PCs) accounted for 80% of the variance. However, the first three PCs were mainly considered as they accounted for 56.4% (more than half) of the overall variance. The eigenvalues of PC1, PC2, and PC3 were 3.69, 2.88, and 1.88, respectively.

This study considered co-eluting organic acids as acid groups (i.e., malic + succinic acids and lactic + quinic + shikimic acids). JMP Pro 18.0.0 was used to perform all statistical analyses.

3 | Results

Fatty acid esters, organic acids, terpenoids, and phytosterols were quantified in this organically grown dry pea panel. Genotype was significant for tartaric acid ($p < 0.05$), citric acid ($p < 0.001$), β-amyrin ($p < 0.001$), and γ-sitosterol ($p < 0.001$) (Table 2). Location was significant for linoleic acid esters ($p < 0.05$), oleic acid esters ($p < 0.01$), tartaric acid ($p < 0.001$), β-amyrin ($p < 0.001$), stigmasterol ($p < 0.05$), and γ-tocopherol ($p < 0.001$) (Table 2). The genotype × location interaction was significant for malic + succinic acids ($p < 0.05$), β-amyrin ($p < 0.001$), and γ-sitosterol ($p < 0.001$) (Table 2). Therefore, citric acid was only affected by genotype; linoleic acid esters, oleic acid esters, and stigmasterol were only affected by location, and malic + succinic acids were only affected by the genotype × location interaction. Tartaric acid was affected by both genotype and location effects, while β-amyrin and γ-sitosterol were affected by genotype, location, and genotype × location effects.

TABLE 2 | Analysis of variance for the compounds related to the flavor in dry pea accessions grown in South Carolina, USA, in 2019.

Variable	Genotype	Location	Genotype × location
Fatty acid esters			
Linoleic acid esters	NS	*	NS
Oleic acid esters	NS	**	NS
Linolenic acid esters	NS	NS	NS
Palmitic acid esters	NS	NS	NS
Stearic acid esters	NS	NS	NS
Organic acids			
Lactic + shikimic + quinic acids	NS	NS	NS
Mallic + succinic acids	NS	NS	*
Tartaric acid	*	***	NS
Citric acid	***	NS	NS
Gallic acid	NS	NS	NS
Terpenoids and phytosterols			
β-Amyrin^{T}	***	***	**
γ-Tocopherol ^{T}	NS	NS	NS
Stigmasterol ^{P}	NS	*	NS
γ-Sitosterol ^{P}	***	***	***

*, **, and *** denote significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. Abbreviations: NS = not significant at $\alpha = 0.05$, ^{P} = phytosterol, ^{T} = terpenoid, total unsaturated fatty acids = oleic acid + linoleic acid + linolenic acid.

Among fatty acid esters, linoleic acid esters (1518.52 ± 59.34 mg/100 g) had the highest genotype mean followed by oleic (1137.62 ± 39.31 mg/100 g), palmitic (585.03 ± 16.76 mg/100 g), linolenic (295.58 ± 9.20 mg/100 g), and stearic (259.63 ± 89.18 mg/100 g) acid esters (Table 3). The genotype mean of total unsaturated fatty acid (TUSFA) esters (2951.72 ± 72.84 mg/100 g) was higher than that of overall saturated fatty acid ester concentration in dry pea, as this value represented almost 80% of the total fatty acid concentration of 3731.88 ± 56.79 mg/100 g (Table 3). Of all the genotypes, linoleic acid esters exhibited the largest range in values (1400.67–1636.38 mg/100 g) among all fatty acid esters (Figure 1).

Of the identified organic acids, citric acid exhibited the highest genotype mean (27.58 ± 2.60 mg/100 g) (Table 3) and the largest range across dry pea genotypes (Figure 2), while tartaric acid had the lowest genotype mean (5.47 ± 0.81 mg/100 g) (Table 3). Gallic acid was the only phenolic organic acid detected at quantitative concentrations with a genotype mean of 9.01 ± 0.39 mg/100 g (Table 3). The genotype means of malic + succinic acids (15.98 ± 1.05 mg/100 g) were higher than those of lactic + shikimic + quinic acids (13.59 ± 0.94 mg/100 g) (Table 3). Throughout this study, lactic +shikimic + quinic acids and malic + succinic acids were observed to co-elute at times 2.18 and 2.89, respectively (supplementary information section 2: Table S4).

β-amyrin and γ-tocopherol were two major terpenoids quantified in these organic dry pea cultivars, while stigmasterol and γ-sitosterol were predominant phytosterols. The genotype mean of β-amyrin was higher (0.65 ± 0.011 mg/100 g) than that of γ-tocopherol (0.56 ± 0.01 mg/100 g), whereas γ-sitosterol (4.25 ± 0.06 mg/100 g) was more abundant than stigmasterol (1.07 ± 0.004 mg/100 g). Overall, the genotype mean of total phytosterols was higher than that of total terpenoids identified in this panel (Table 3).

According to the PCA, the highest proportion of variance was observed in PC1 (24.7%), followed by PC2 (19.2%) and PC3 (12.6%) (Figure 3). The variables with the highest weightage to PC1 were TUSFA, γ-tocopherol, linoleic acid, gallic acid, and oleic acid with loading values 0.950, 0.869, 0.714, 0.749, and 0.591, respectively. For PC2, β-amyrin, malic + succinic acids, sitosterol, stearic acid, and citric acid had the highest weightages with loading values 0.759, 0.615, 0.594, −0.692, and −0.594, respectively. The highest weightage to PC3 was observed from linolenic acid with a loading value of 0.813 (Figure 3A–D and supplementary information section 4: Table S8). The red cluster (mostly extending in the positive direction of PC1) in PCA represents genotypes with the highest influence on traits loading strongly with PC1 (Figure 3A,C). The blue cluster represents genotypes strongly influenced by malic + succinic, tartaric, and palmitic acids (Figure 3A,B). The green cluster represents genotypes strongly influenced by stearic and citric acids (Figure 3A,B). The red cluster's dispersion along PC1 and PC3 suggests that most cultivars are primarily influenced by the concentrations of unsaturated fatty acid esters and phenolic

TABLE 3 | Range, mean, and genotypic effects of the compounds related to flavors identified in dry pea accessions grown in South Carolina, USA.

Variable	Range (mg/100 g)	Mean ± SE (mg/100 g)	Genotype effects
Fatty acid esters			
Linoleic acid esters	1400.67–1636.38	1518.52 ± 59.34	NS
Oleic acid esters	1059.53–1215.69	1137.62 ± 39.31	NS
Linolenic acid esters	277.30–313.86	295.58 ± 9.20	NS
Palmitic acid esters	551.94–618.13	585.03 ± 16.76	NS
Stearic acid esters	246.36–272.90	259.63 ± 89.18	NS
TUSFA	2807.06–3096.38	2951.72 ± 72.84	—
Total fatty acid esters	3619.79–3843.97	3731.88 ± 56.79	—
Organic acids			
Lactic + shikimic + quinic acids	11.72–15.47	13.59 ± 0.94	NS
Mallic + succinic acids	13.89–18.08	15.98 ± 1.05	NS
Tartaric acid	3.86–7.08	5.47 ± 0.81	*
Citric acid	22.40–32.76	27.58 ± 2.60	***
Gallic acid	8.22–9.79	9.01 ± 0.39	NS
Total organic acids	69.56–78.93	74.24 ± 2.37	—
Terpenoids and phytosterols			
β-Amyrin [T]	0.632–0.677	0.65 ± 0.011	***
γ-Tocopherol [T]	0.54–0.58	0.56 ± 0.01	NS
Stigmasterol [P]	1.06–1.08	1.07 ± 0.004	NS
γ-Sitosterol [P]	4.12–4.38	4.25 ± 0.06	***
Total terpenoids and phytosterols	5.99–6.22	6.11 ± 0.06	—

*, **, and *** denote significance at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.
Abbreviations: NS = not significant at $\alpha = 0.05$, [P] = phytosterol, SE = standard error of the mean, [T] = terpenoid, TUSFA = total unsaturated fatty acids (oleic acid + linoleic acid + linolenic acid).

compounds, particularly gallic acid and γ-tocopherol, among the compounds analyzed (Figure 3C,D). In PC1, strong positive correlations were observed between total unsaturated fatty acids (TUSFA) and the identified phenolic compounds, including gallic acid and γ-tocopherol. A similar relationship is observed for linoleic and oleic acids with the identified phenolic compounds (Figure 3B,D). Based on Pearson's correlation coefficients, the positive correlations are significant between unsaturated fatty acid esters (linoleic, linolenic, and oleic acid esters) versus gallic acid and γ-tocopherol at $p < 0.001$, $p < 0.01$, and $p < 0.05$ (supplementary information section 4: Table S9).

4 | Discussion

This study identified precursor compounds and key metabolites linked to off-flavors in a selected panel of recombinant inbred dry pea genotypes grown across two environments. Genotypes and locations were considered as fixed effects, whereas the environmental interaction was treated as a random effect to account for variability in genotypic responses to environmental conditions, providing unbiased estimates of the main effects (Henderson 1975; Malosetti et al. 2013). Off-flavor and undesirable taste attributes in dry pea are known to arise from a diverse range of chemical compounds, spanning from small volatile molecules such as alkanals, alkenals, and alcohols to larger nonvolatile metabolites, including saponins and polyphenols (Bi et al. 2020; Roland et al. 2017; Trindler et al. 2022). Targeting a single or class of volatile molecules for conventional breeding is often ineffective, as dry pea off-flavor is a combined effect of the volatile compounds (i.e., alkanals, alkenals, and alcohol) at empirical concentration ratios (Pavagadhi and Swarup 2020). Quantitative profiling of biochemical precursors linked to these metabolites provides more certainty in selective breeding aimed at mitigating off-flavor intensity and improving overall flavor quality (Trindler et al. 2022).

Unsaturated fatty acid esters were known as precursors to most of the volatile compounds associated with the characteristic dry pea beany flavor. Based on this study, both unsaturated and saturated fatty acid esters were identified in the panel of dry pea advanced breeding lines. The unsaturated fatty acids constituted linoleic, linolenic, and oleic acid structures, while palmitic and stearic acid structures were among the identified saturated fatty acid esters. The linolenic acid, oleic acid, and linolenic acid concentrations in the present study were lower than reported

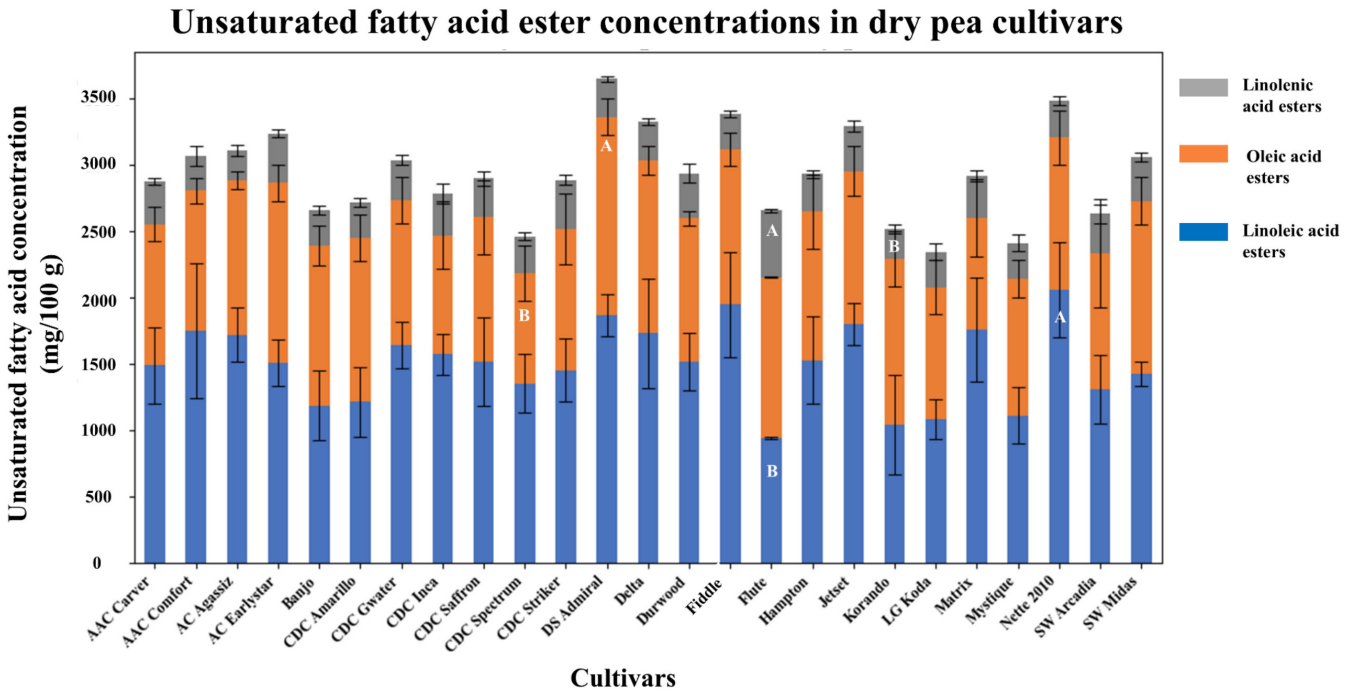


FIGURE 1 | Fatty acid esters identified in dry pea cultivars. The letters indicate the significantly high and low cultivars for a given trait based on the LSD analysis.

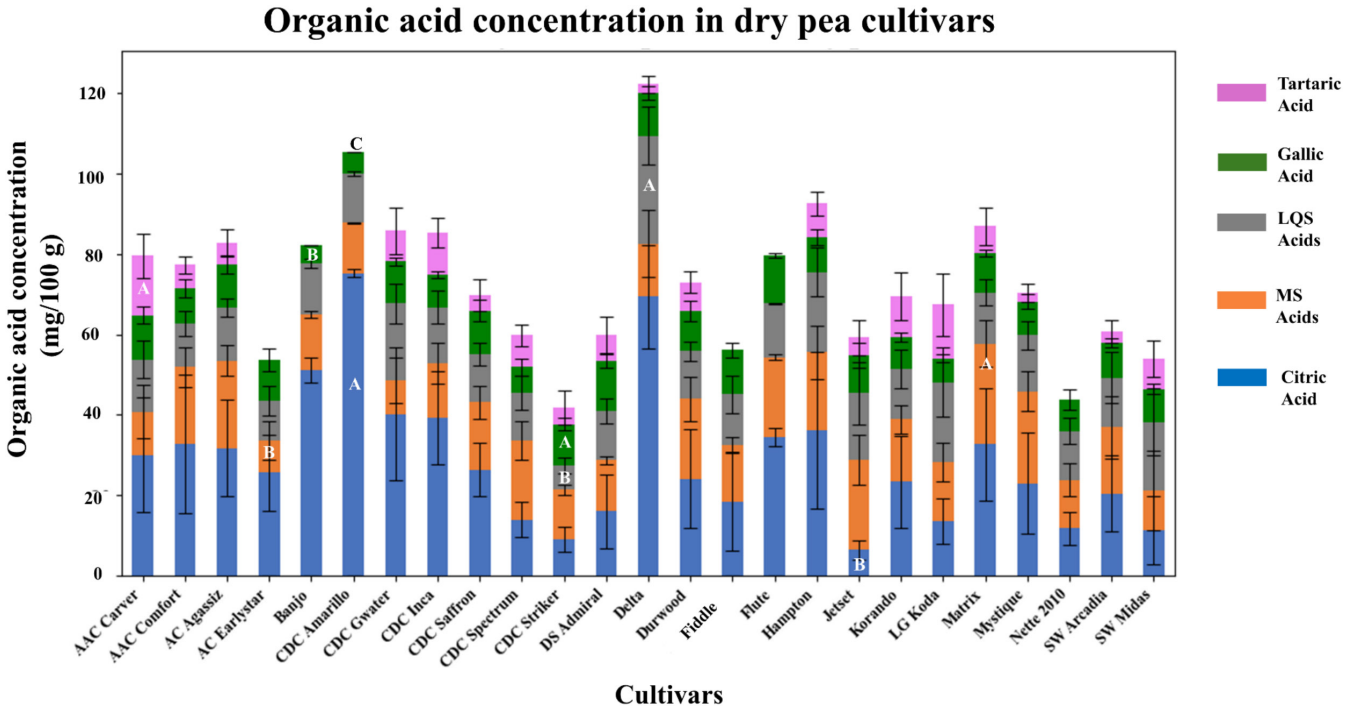


FIGURE 2 | Organic acids identified in dry pea cultivars. The letters indicate the significantly high and low cultivars for a given trait based on the LSD analysis.

for chickpea (Roland et al. 2017; Salaria et al. 2023) but higher than reported for the vegetable pea (USDA 2025). The results indicate that the dry pea genotypes had no significant effect on the concentration of unsaturated fatty acid esters. In contrast, location had a significant influence on the concentrations of linoleic acid and oleic acid esters. Linoleic and oleic acid esters are biosynthetic precursors to heptanal, octanal, and nonanal, mostly in the presence of lipoxygenase enzymes, which impart beany and grassy notes in dry pea (Baysal and Demirdöven 2007). It can be observed that the environment has a key role in the off-flavor associated with these compounds. Neither genotype nor environment had a significant role in dry pea linolenic acid ester concentration, which is a biosynthetic precursor to hexanal contributing to be any notes in dry pea. In this study,

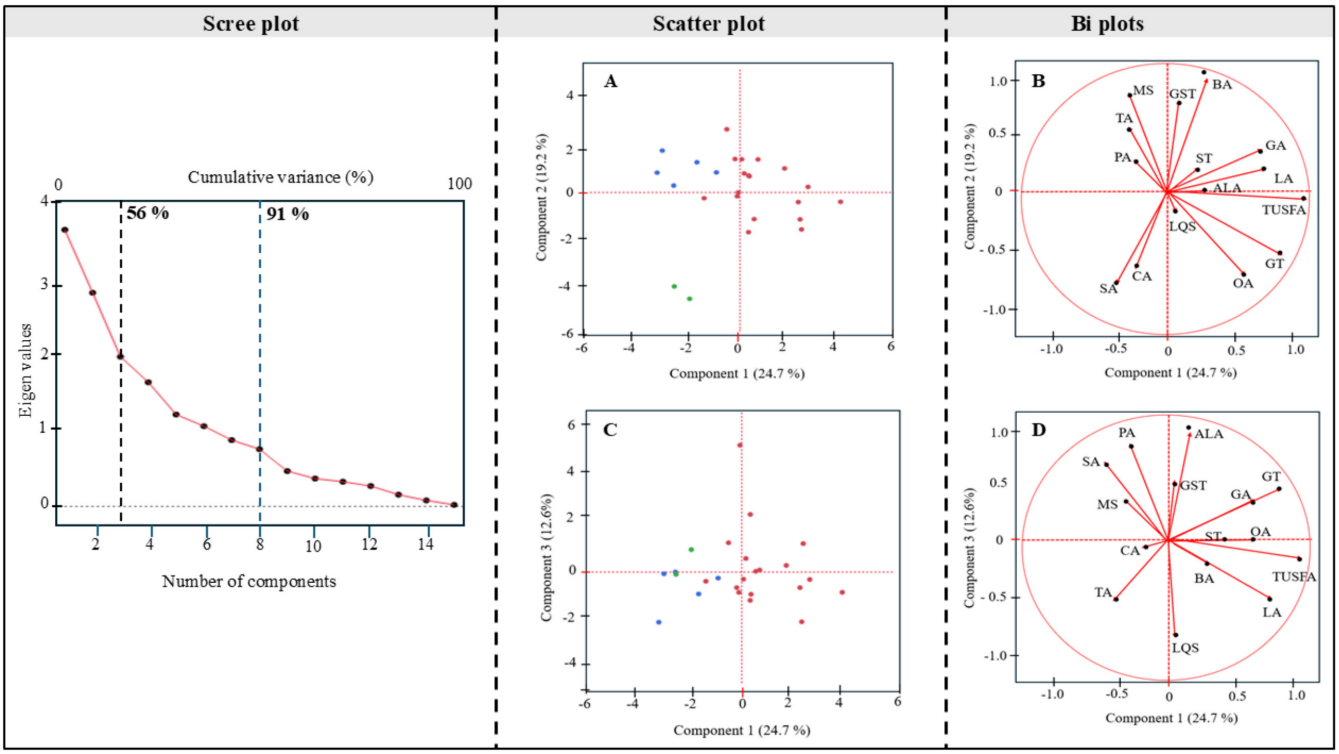


FIGURE 3 | Principal component analysis on all traits associated with the 25 cultivars. (A) The scatter plot of PC1 versus PC2. (B) The biplot indicating the correlations between traits (mostly phenolic compounds and unsaturated fatty acid esters) based on the variations of PC1 versus PC2. (C) The scatter plot of PC1 versus PC3. (D) The biplot indicating the correlations between traits (i.e., phenolic compounds and unsaturated fatty acid esters) based on the variations of PC1 and PC3. The red cluster represent cultivars that are strongly influenced by the concentrations of unsaturated fatty acid esters and phenolic compounds, the blue cluster represents cultivars influenced by malic + succinic, tartaric, and palmitic acids and the green cluster represents genotypes strongly influenced by stearic and citric acids.

Nette 2010, DS Admiral, and Flute cultivars exhibited significantly higher concentrations of linoleic acid, oleic acid, and linolenic acid esters, respectively, while Flute, CDC Spectrum, and Korando constituted significantly lower concentrations of these esters, respectively (Figure 1). The identified saturated fatty acid esters (palmitic and stearic acid esters) are also indirect contributors to dry pea off-flavors. These compounds promote oleic acid ester biosynthesis through elongation and desaturation processes in dry pea (Ohlrogge and Browse 1995), which leads to heptanal, nonanal, and any associated derivatives (Baysal and Demirdöven 2007).

Organic acids were known to influence the taste and color of cooked food while enhancing the flavor perception (Shi et al. 2022). Typically, these compounds are popular for sourness, tartness, and sweetness in certain foods (Yılmaz Tuncel et al. 2025), while certain organic acids (i.e., phytic acid and gallic acid) are antinutrients affecting the bioavailability of certain minerals (i.e., iron) (Brune et al. 1989; Thavarajah et al. 2009). The organic acids identified in this organically grown dry pea were comparable to those reported in commercial vegetable pea, including citric acid (52.5–67.3 mg/100 g), malic acid (7.4–15.56 mg/100 g), and succinic acid (1.73–4.2 mg/100 g) (Mabesa et al. 1979) (Table 3). Citric acid had the highest abundance in dry pea and vegetable pea (Mabesa et al. 1979). Vegetable pea had a higher concentration of citric acid than that measured in organic dry pea. Given its significance on genotype effects (Table 2), citric acid may represent a candidate trait for the selective breeding of organic dry pea. However, its validity should be further tested on a more diverse panel, such as the USDA pea single plant plus collection (PSPPC) (Holdsworth et al. 2017). Of the organic cultivars, CDC Amarillo and Banjo had a high concentration of citric acid (green cluster in PCA; Figure 3A), while Jetset had the lowest (Figure 2). The measured malic + succinic acid concentrations were higher in dry pea cultivars than in vegetable pea. Shikimic, quinic, tartaric, and gallic acids were only identified and measured in dry pea (Table 3; Figure 2). Citric acid enhances the perception of sweetness from sucrose (Veldhuizen et al. 2018). Therefore, optimizing this trait through breeding could potentially enhance the sweetness profile of dry pea. The roles of malic, succinic, shikimic, quinic, and tartaric acids in pea flavor are not well characterized (Mabesa et al. 1979). However, shikimic acid is a part of the shikimic acid pathway leading to the formation of phenolic compounds (i.e., gallic acid) responsible for astringency and bitterness at high concentrations (Kougan et al. 2013). Throughout this study, the only phenolic compounds identified among these cultivars were gallic acid and γ-tocopherol, suggesting a minimal possibility of bitterness and astringency, given that γ-tocopherol lacks a characteristic flavor. Previous studies have demonstrated additional phenolic compounds, such as anthocyanins and proanthocyanidins, in addition to the phenolic compounds identified in the present study (Dueholm et al. 2025). Most dry pea accessions consisting of many phenolic compounds were characterized by

light brown to black seed coats (testas) (Dueholm et al. 2025; Hradilová et al. 2017). This observation was consistent with the present study, which detected a limited number of phenolic compounds, as these organic dry pea cultivars exhibited a transparent seed coat, indicating minimal accumulation of complex phenolic compounds.

β-amyrin and γ-tocopherol were the most abundant terpenoids identified in this panel of organic dry pea. β-amyrin is also not known to impart any flavor to dry pea (Lagarda et al. 2006), and it is a molecular precursor to saponin B and DDMP saponin (Vernoud et al. 2021). Although saponin B (~2.6–4.2 mg/100 g) and DDMP saponins (~96–300 mg/100 g) had been reported (Dueholm et al. 2025; Vernoud et al. 2021), these compounds were not detected in the cultivars of the present study (supplementary information section 5). The reported β-amyrin concentrations (0.632–0.677 mg/100 g) in these cultivars were significantly lower than the reported saponin concentrations in previous studies. This should potentially indicate the low concentrations of saponins in these cultivars. However, no research on the correlations of β-amyrin and saponin concentrations had been performed on dry pea to validate the trends of saponin concentrations in terms of identified β-amyrin concentrations. The measured β-amyrin concentration was significantly

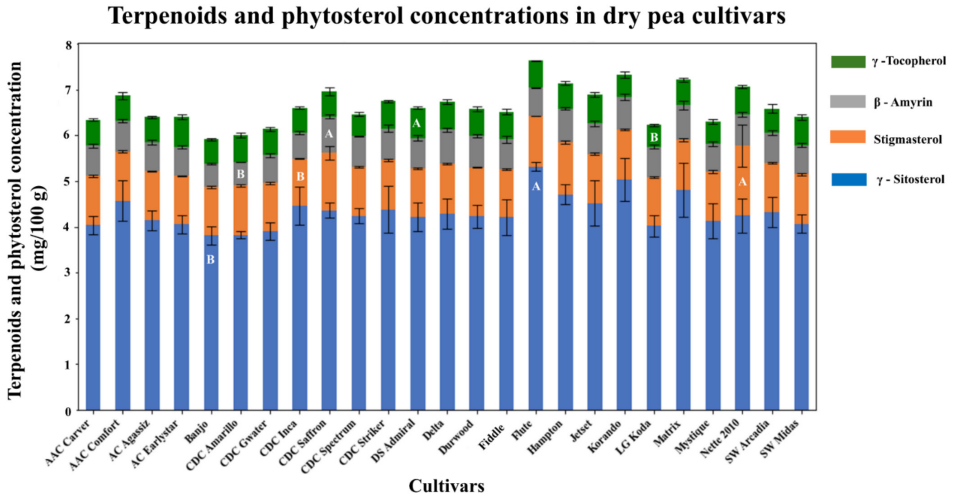


FIGURE 4 | Terpenoids and phytosterols identified in dry pea cultivars. The letters indicate the significantly high and low cultivars for a given trait based on the LSD analysis.

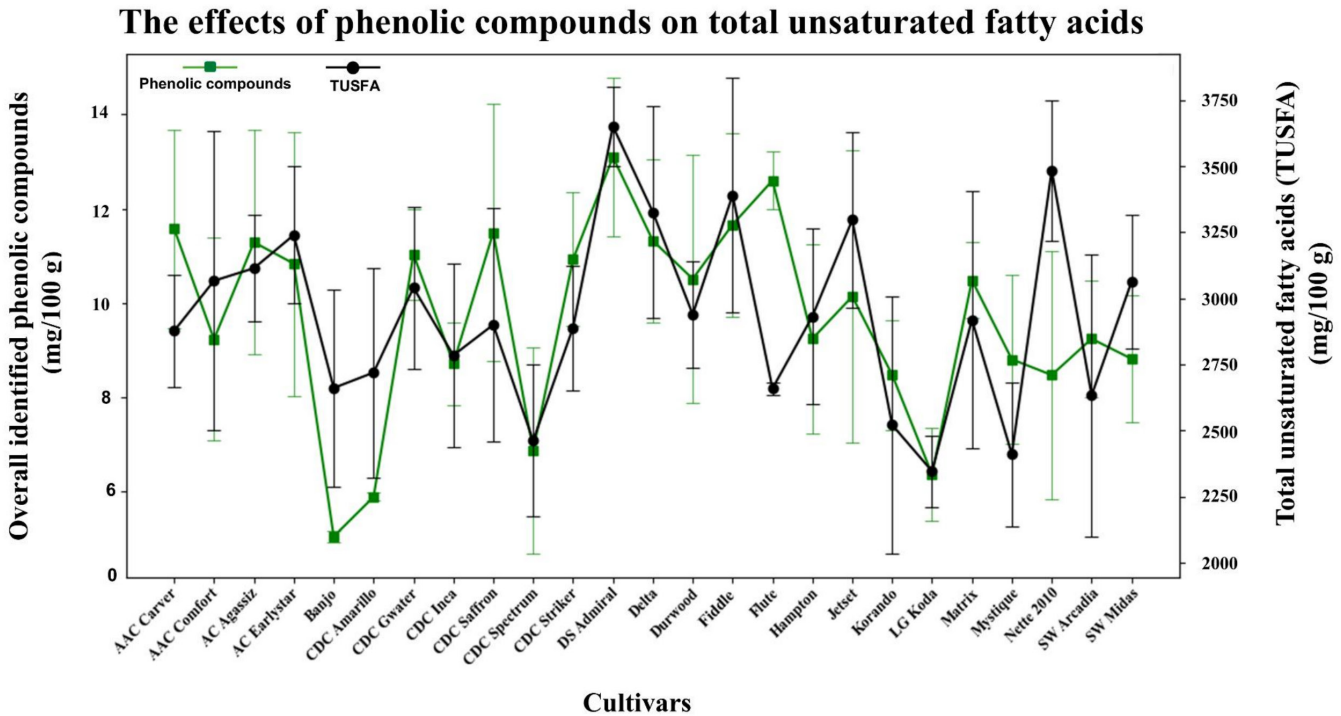


FIGURE 5 | The trend of the effects of the overall phenolic compounds on TUSFA. Here, the TUSFA concentrations are high in cultivars with high concentrations of phenolic compounds (γ-tocopherol + gallic acid) and vice versa. This supports the observation of positive correlations between those traits as predicted by the PCA.

higher in CDC Saffron and lower in CDC Amarillo (Figure 4). Because mutagenesis of β-amyrin synthase is known to generate saponin-free dry pea genotypes (Hodgins et al. 2024) with respect to its significance on genotypes even among these cultivars (Table 2), β-amyrin in diverse populations can potentially support genome-wide association mapping of single-nucleotide polymorphism markers associated with β-amyrin synthase, facilitating marker-assisted selections to mitigate bitterness (Hodgins et al. 2024; Holdsworth et al. 2017). However, sensory profiling (i.e., based on CDC Saffron and CDC Amarillo) is necessary to validate bitterness as a function of β-amyrin concentrations, primarily related to seed saponin accumulation as indicated above. The other identified terpenoid, γ-tocopherol, is a biosynthetic precursor for vitamin E (Niu et al. 2022) and is observed at approximately one-tenth (0.54–0.58 mg/100 g; Table 3) of other recently reported concentrations (4.6–5.4 mg/100 g) (Wu et al. 2023). The concentration was highest at DS Admiral and lowest in LG Koda. γ-Tocopherol is also known as a flavor antioxidant and is known to alter the flavor of foods (Parshall et al. 2007).

Stigmasterol and γ-sitosterol are among the identified phytosterols. Like the above terpenoids, the characteristic influences of these compounds on dry pea flavor are unclear. Concentrations of phytosterols measured in the current study (stigmasterol: 1.07 mg/100 g; γ-sitosterol: ~4.25 mg/100 g; Table 3) are lower than those previously reported (stigmasterol: ~200 mg/100 g; γ-sitosterol: ~25 mg/100 g) (Zia-Ul-Haq et al. 2013). With cholesterol-like structures, these compounds are known to influence the mechanical properties of certain foods (i.e., hardness, gumminess, and chewiness) (Matheson et al. 2018). Therefore, under the minimal influence of amylose and amylopectin, these compounds should potentially affect the mouth feel of dry pea-based food (i.e., protein extracts) (Beck et al. 2018; Matheson et al. 2018). However, a complete assessment of the effects of these traits on the dry pea or other leguminous crops' food matrix has not been evaluated in detail. Findings from this study indicate high concentrations of stigmasterol and γ-sitosterol in Flute and Nette 2010 and low concentrations in Banjo and CDC Inca, respectively (Figure 4).

Most genotypes (cultivars) in this study were predominantly influenced by the concentrations of unsaturated fatty acid esters and the identified phenolic compounds (red cluster of PCA; Figures 3A–D). Given that high OAV compounds are derived mainly from the oxidative degradation of these unsaturated fatty acid esters (Roland et al. 2017), it is evident that these off-flavor (beany, earthy, and green) volatiles play an important role in shaping the sensory profiles in most of these cultivars. Consequently, such compounds may suppress or mask the sensory contributions of minor constituents, including organic acids (Mabesa et al. 1979). Based on this study, location has a significant role in these off-flavors due to the environmental effects observed for unsaturated fatty acid esters (Table 2), which act as precursors to these volatile compounds. These variations are due to the significant environmental effects observed for those traits (Table 2).

The biosynthesis of unsaturated fatty acid esters is also known to have been significantly affected by upregulation and downregulation of fatty acid desaturase genes 2 and 3 in dry pea with respect to genotype effects and cold stress (i.e., colder temperatures at the Clemson site than the Pelion site) (Saini et al. 2019; Thavarajah et al. 2023). Cold-induced stress upregulates the genes associated with shikimic acid and phenylpropanoid pathways, especially intensifying the activity of key enzymes (i.e., 3-deoxy-D-arabino-heptulosonate 7-phosphate synthase) (Yokoyama et al. 2022; Zhang et al. 2015). This intensifies the demand for the biosynthesis of phenolic compounds (i.e., gallic acid and γ-tocopherol) (Wu et al. 2022). By quenching reactive oxygen species, phenolic compounds suppress the oxidation of unsaturated fatty acid esters, reducing the formation of volatile degradation products and contributing to their antioxidant functionality (Maqsood et al. 2014). These antioxidant effects on flavor-associated compounds were observed through significant positive correlations between total unsaturated fatty acids and individual unsaturated fatty acid esters versus gallic acid and γ-tocopherol (supplementary information section 4: Table S9). This observation is further supported by large loading factors associated with these compounds in PC1 (supplementary information section 4: Table S8) and relatively proportional variation of total unsaturated fatty acids and total phenolic compositions across most cultivars, as depicted in Figure 5. Many cultivars with high gallic acid and γ-tocopherol concentrations have been observed to possess significant antioxidant activity against the degradation of unsaturated fatty acid esters (Maqsood et al. 2014). With this trend, the perception of beany, earthy, and grassy off-flavors in dry pea flour could be influenced by the antioxidant activity in the seed matrics potentially yielding low concentrations of volatiles (i.e., alkanals, alkenals, and alkanols) (Trindler et al. 2022).

5 | Conclusions

This study aimed to evaluate the chemical composition of raw dry pea seeds, which is potentially known to influence the flavor associated with dry pea-based food products. Dry pea fatty acid esters had the highest concentration, followed by organic acids, terpenoids, and phytosterols. Among these traits, unsaturated fatty acid esters were observed to influence the chemical composition of most cultivars, while citric and stearic acids influenced the minority. The presence of unsaturated fatty acid esters was significantly affected by location, while traits like citric acid, tartaric acid, and β-amyrin were significantly affected by genotype. Phenolic compound concentration strongly correlated with the composition of unsaturated fatty acid esters. This indicated the quenching effects of antioxidants towards the oxidation of unsaturated fatty acid esters, potentially minimizing the formation of OAV compounds responsible for beany, earthy, and grassy off-flavors. These findings suggest the need for sensory evaluations with a trained panel to validate the identified compounds on flavor to assist with developing cultivars with better flavor for consumer acceptance.

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Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** The temperature program for fatty acid ester analysis. **Table S2:** The temperature program for fatty acid ester analysis. **Figure S1:** Chromatograms of derivatized fatty acid methyl esters in dry pea from GC–MS analysis. **Table S3:**: The gradient elution for the organic acid analysis. **Table S4:** The temperature program for organic acids (LSQ = co-eluting lactic, shikimic, and quinic acids and MS = co-eluting malic and succinic acids). **Figure S2:** Chromatograms of organic acids as identified with ion exchange chromatography. (LQS = co-eluting lactic, quinic, and shikimic acids and MS = co-eluting malic and succinic acids considered in groups). **Table S5:** The temperature program for phenolic acids. **Figure S3:** Chromatograms for phenolic acids. Only gallic acid was observed in the panel of analyzed samples. The absence of other phenolic acids for this panel was further confirmed by comparing the chromatogram for the standard mixture with that of the sample.. **Table S6:** The temperature program for fatty acid ester analysis. **Table S7:** The temperature program for terpenoids and phytosterols. **Figure S4:**: Chromatograms of terpenoids and phytosterols identified in dry pea with GC–MS. These chromatograms are provided with specific colors for clarity. **Table S8:** Principal components and respective traits with significant contributions. **Table S9:**: Correlation matrix for the chemical species identified in organically grown dry pea accessions. **Table S10:** The gradient elusion for saponin B and DDMP saponins (Hu et al., 2002) Injection volume: 5 micro liters and the volume flow rate: 0.623 mL/min. **Figure S5:**: Chromatograms for saponin B and DDMP saponin standards. Those saponins were not detected in any sample of the present analysis.