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► To cite this version:

Ahlem Azri, Mohamed Debouba, Jalloul Bouajila, Mekonnen Yeshitila, Muriel Cerny, et al.. Lipids composition, Fatty Acid and Squalene contents in a wide Amaranth collection. *Journal of Food Composition and Analysis*, 2025, 148 (2), pp.108305. <10.1016/j.jfca.2025.108305>. <hal-05272717>

HAL Id: hal-05272717

<https://hal.science/hal-05272717v1>

Submitted on 22 Sep 2025

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Lipids composition, fatty acid and squalene contents in a wide Amaranth collection

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ARTICLE INFO

Keywords:

Amaranthus spp.
Lipids
Acylglycerols
Fatty acid
Squalene
Nutritional indices

ABSTRACT

Vegetables contribute significantly to human health. Amaranth is considered as a promising species that could provide significant unsaturated fats, proteins and other beneficial ingredients. The present investigation focused on a comprehensive analysis of the lipid content and composition in 128 accessions belonging to ten *Amaranthus* species. Squalene (SQ) yield, acylglycerols (AG) content and fatty acid (FA) profiles were determined by Gas chromatography with a flame ionization detector analysis. Oil content varied significantly among accessions, ranging from 4.4 % in *Amaranthus* sp. to 9.4 % in *A. palmeri*. The SQ yield ranged from 1.8 % to 6.9 %, with *Amaranthus hybridus* L. subsp. *hybridus* exhibiting the highest yield. Data showed an interspecific variation. *Amaranthus palmeri* had significantly ($P < 0.05$) the highest oil content, while *Amaranthus hybridus* L. subsp. *hybridus* and *Amaranthus hypochondriacus* had the highest SQ yield. Linoleic, oleic, palmitic and stearic acids are the predominant FA in amaranth oils. AG represented the major lipid constituent. A multivariate analysis also elucidated the taxonomic relationship of ten species, revealing three classes based on their lipid composition. This variation enables the use of amaranth oils according to the target molecules, as a renewable source of various essential compounds for food, pharmaceuticals and cosmetics.

1. Introduction

Amaranth is a leafy vegetable belonging to the *Amaranthaceae* family. It is grown worldwide for its seeds and leaves and used for human consumption (Habtemariam and Dana, 2025, Zhu, 2020)). It holds considerable promise for enhancing food security and could provide a

solution to malnutrition in the future (Jimoh et al., 2019). Numerous studies have highlighted the diverse applications of *Amaranthus* across various sectors... Aderibigbe et al. (2022) have reported that the leaves and stems are an excellent source of protein, which are commonly used for food preparation, particularly in African regions such as Southern Africa (Baraniak & Kania-Dobrowolska, 2022; Martínez-Núñez et al.,

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<https://doi.org/10.1016/j.jfca.2025.108305>

Received 23 June 2025; Received in revised form 29 August 2025; Accepted 10 September 2025

Available online 12 September 2025

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2019). Recently, Hebtariam and Dana (2025) have reported the nutritional benefits of *Amaranthus caudatus* leaves as a balanced diet. They have revealed a significant accumulation of protein (12.9–18.4 %), carbohydrate (38.8–57.9 %), and fiber (9.8–11.6 %) contents, and a high energy value up to 319.1 Kcal/100 g. Notably, the seeds are the most typically consumed after cooking (Mota et al., 2016). Seeds are a source of vegetable oil, SQ, minerals, and proteins, and are the primary ingredient of flour used in the baking industry (Sots et al., 2024). *Amaranthus* seeds are a rich source of starch. It plays a crucial role in the functional and technological properties of the food industry (Sindhu and Khatkar, 2016). The *Amaranthus* plant is recognized as a "superfood" and is ideally suited for inclusion in nutrient, low-calorie diets (Waisundara, 2020). Squalene (SQ) (C₃₀H₅₀) is a linear triterpene hydrocarbon that refers to the genus *Squalus* spp., from which it was isolated. It accumulates in the liver of the *Squalidae* family (sharks). It provides numerous skin benefits, functioning as an emollient, antioxidant, moisturizer, photoprotective, and anti-tumour agent (Lozano-Grande et al., 2018; Melguizo-Rodríguez et al., 2022; Singh et al., 2023). Amaranth is among the richest sources of vegetable derived SQ (Kraujalis and Venskutonis, 2013). Its content ranged from 2.4 % to 8.0 % (Nandan et al., 2024) and reaches 12 % in the wild type (Hussain et al., 2023), compared to other oilseeds. Amaranth is recognized as a biopharmaceutical plant due to its SQ concentrations, which regulates lipid metabolism when combined with tocopherols (Azri et al., 2025). Its antioxidant and hypocholesterolemic properties are attributed to several active ingredients. An amaranth plant can be a valuable source of antioxidants. Li et al. (2015) have recorded antioxidant activity in seeds, stalks, flowers, sprouts, and mainly in the leaves owing to the presence of betacyanin, rutin, amaranthine, and other antioxidants (Li et al., 2015). In particular, its ability to reduce serum cholesterol levels is largely attributed to its high SQ content (Caselato-Sousa and Amaya-Farfán, 2012). In the food process, Longato et al. (2017) have studied the effect of amaranth seed supplementation on the diet of broiler chickens. They have reported a positive effect on growth performance and meat production in terms of quality and sensory properties, with balanced FA profiles. Besides their nutritional value, the lipid fractions used for various applications. For cosmetic purposes, Korabel et al. (2022) have developed a comprehensive scheme for the purification of some bioactive substances such as FA, the sum of triterpenoids, SQ, and lecithin from the seeds of *A. caudatus* L. Moreover, amaranth oil has been used to prepare W/O formulations enriched with 2 % amaranth oil, and with 1 % oil and 1 % squalene (Sayed-Ahmad et al., 2022). They produced an effective moisturizing cream (Sayed-Ahmad, 2018; Sayed-Ahmad et al., 2022). Likewise, Patil et al. (2021) have prepared a moisturizing cream with 3 % *A. cruentus* seed oil. The performed formulation provided good cosmetic and moisturizing properties on human skin compared to the simple cream base. Recent studies have reported the use of amaranth oil in other fields. Hu et al. (2020) have assayed the incorporation of amaranth oils into quaternary ammonium chitosan (QC)/fish gelatin (FG) blend films. The mixture was used as an antioxidant, antimicrobial agent, and smart packaging in the food industry. Among the other applications the processing of *Amaranthus* stems after splitting them into two parts (bark and pith) to produce biomaterials. Evon et al. (2021) have successfully produced insulating blocks and low-density hardboards from these fractions, which can serve as a starting point for designing building materials. Researches have mainly focused on the nutritional properties, such as the high content of proteins, amino acids, and dietary fiber, as well as bioactive components (Bojórquez-Velázquez et al., 2018; Kachiguma et al., 2015; Manyelo et al., 2022; Mérida-López et al., 2023).

Amaranth is classified as a C4 plant, allowing the plants to produce ample biomass and adapt rapidly to harsh environmental conditions, in different types of soil, and temperatures range (Tsutsumi et al., 2017; Tyrus et al., 2023; Azri et al., 2025). Overall, Peru and Mexico are the leading producers of amaranth seed, producing from 4600 to 7200 kg/ha of seed yield. In Mediterranean regions of Europe, seed

yields range from 1200 to 6700 kg/ha (Alemayehu et al., 2015; Azri et al., 2025). Various factors can significantly influence the yield of amaranth seed crops, particularly the genetic and environmental factors (Szabóová et al., 2020; Azri et al., 2025).

Several studies have been conducted to understand adaptation to different environments, agronomic potential, and domestication (Das, 2012; Raiyemo et al., 2023; Segun and Ja, 2022; Thapa et al., 2021). Yeshitila et al. (2024) have investigated the physio-morphological traits and growth composition of a broad amaranth collection to identify their relevant agronomic traits, and contribute to the conservation and improvement of the amaranth genetic resources.

Fatty acids (FA) are organic acids with at least one carboxyl (–C(=O)OH, –COOH, or –CO₂H) group and a long carbon chain whose links can be double bonds, as in unsaturated fatty acids (UFA), or single bonds, as in saturated fatty acids (SFA). *Amaranthus* oils are dominated by linoleic and oleic acids, which play a crucial role in human health (Tarhan, 2021; Zhang et al., 2019; Arkhipov et al., 2024; Azri et al., 2025). There are high demands of long chain polyunsaturated fatty acids (PUFA) due to their numerous benefits, particularly their ability to meet the nutritional needs of general or target populations (Meynier & Genot, 2017). These compounds serve as crucial markers for assessing the purity, quality, and authenticity of edible oils. They play a key role in quality control and help to detect possible adulteration (Tarhan, 2021). The number of research papers on chemical composition, cultivation process, pharmaceutical and functional food applications has been steadily increasing. Several review articles have summarized findings from these fields (Aderibigbe et al., 2022; Baraniak & Kania-Dobrowolska, 2022; Venskutonis & Kraujalis, 2013). However, few studies have been conducted to investigate lipid composition in a large collection of *Amaranthus*. He et al. (2003) have investigated the lipid composition of both leaves and seeds in a collection of 104 genotypes from 30 *Amaranthus* species in China. Recently, Mérida-López et al. (2023) have assessed the macro and micro-mineral, oil contents, and FA profiles of six Andean varieties of *A. caudatus*. Hussain et al. (2023) have studied the lipid composition of six wild amaranth species collected in Italy. Oteri et al. (2021) have recorded the lipid composition of four *A. hypochondriacus* in southern Italy. Kachiguma et al. (2015) have studied the mineral (calcium, iron, magnesium, etc.) and the proximate composition (crude protein, ash, etc.) of twenty accessions of *A. cruentus*, *A. hypochondriacus*, and *A. hybridus* in Central Malawi, Africa, without measuring the lipid composition of these genotypes. These studies identify genotypes with desirable traits for crop improvement and biodiversity conservation and highlight amaranth's value as a renewable source of bioactive molecules. However, none of these studies showed the concentrations of the acylglycerols. AG are esters formed from a glycerol backbone linked to one or more FA chains, mainly composed of mono-, di-, and triacylglycerols (TAG). A few studies have examined TAG profiles of *Amaranthus* seed collection (Bozorov et al., 2018; León-Camacho et al., 2001; Zhang et al., 2019). TAG are lipids composed of a glycerol backbone esterified with three FA chains. They are the main form of fat stored in plants and animals and are a major source of energy. In addition, no more than two studies have indicated the nutritional indices of amaranth seeds using the FA profiles (Gresta et al., 2020; Oteri et al., 2021). Hence, studying the lipid composition of a wide seed collection from different *Amaranthus* species and different geographical regions enables the exploitation of renewable resources such as SQ and AG, and underscores their importance for cosmetic, food, and pharmaceutical industries. The aim of this study is therefore to investigate the oil, SQ, free fatty acid (FFA), and AG contents as well as the FA composition of 128 *Amaranthus* accessions belonging to ten different amaranth species.

2. Materials and methods

2.1. Reagents

The reagents were purchased from several providers. Below, we list the reagents, the provider (city and country), CAS number, and purity (if applicable).

Cyclohexane, Sigma Aldrich (St Quentin Fallavier, France), CAS 110–82–7, purity $\geq 99\%$.

N-trimethylsilyl-N-methylheptafluorobutyramide (MSHFBA), Sigma-Aldrich (Macherey-Nagel, Hoerd, France), CAS 53296–64–3, purity $\geq 90\%$.

Tert-butyl methyl ether (TBME), Sigma Aldrich (St Quentin Fallavier, France), CAS 1634–04–4, purity $\geq 99.99\%$.

Trimethylsulphonium hydroxide (TMSH), Merck (Macherey-Nagel, Hoerd, France), CAS 701520.110.

Supelco 37 Component FAME Mix, Sigma-Aldrich (St. Quentin Fallavier, France), CAS 200–838–9.

Squalane, Merck (Darmstadt, Germany), CAS 8.14605, Pharmaceutical Secondary Standard, purity 96% .

Sodium sulfate (Na_2SO_4), Sigma Aldrich (St Quentin Fallavier, France), CAS 7757–82–6, purity $\geq 96\%$.

Acylglycerols standards (C18, MG, DAG, TAG, and TAG), Sigma-Aldrich (Saint Louis, USA).

2.2. Plant material

The research study was carried out on a collection of 128 genotypes belonging to ten species collected from various sources. A collection of 120 accessions, belonging to seven *Amaranthus* species, provided by the Hawassa University Agricultural Research Site (Ethiopia) (Yeshitila et al., 2024), five genotypes supplied by Ovalie innovation (France) with one genotype of *A. cruentus* (Panam), and four genotypes belonging to *A. hypochondriacus* (Lera, Kharkiv, Ultra, and ultra), two other species of *A. cruentus* bought from an African supermarket in Congo, and one genotype from biocoop.

2.3. Lipid extraction and oil content determination

At the First step, we crushed *Amaranthus* seeds using a mortar and pestle. The extraction process was conducted using a cold extraction method (Azri et al., 2025). Briefly, we performed three successive extractions with cyclohexane (Sigma Aldrich, St Quentin Fallavier, France), by adding 200 mg of ground amaranth seeds with 5 mL of cyclohexane in a plastic flask. Then, we centrifuged the mixture for 6 min at $12,000\text{ g}$ at 14°C by a refrigerated centrifuge (Sigma 6K15 Fisher Bioblock Scientific, Illkirch, France). After centrifugation, we filtrated the supernatant through a Whatman TM paper (5 mm) and a small amount of sodium sulfate (Na_2SO_4 ; Sigma Aldrich, St Quentin Fallavier, France). The extract was recovered in a glass bottle of 15 mL. Finally, we dried the extracts using a flux of nitrogen gas (N_2) to remove traces of solvent. The lipid content is expressed in mg per 100 mg of seeds.

2.4. Determination of squalene, free fatty acid, and acylglycerols contents

The SQ, FFA, and AG contents were determined using a Varian 3900 gas chromatographer coupled to a flame ionization detector using a PerkinElmer apparatus (Norwalk, Connecticut, USA) (Azri et al., 2025). We prepared 10 mg of the extracted oil in 10 mL of cyclohexane (Sigma Aldrich, St Quentin Fallavier, France). We added 100 μL of squalane solution (Merck, Darmstadt, Germany) at 5 mg/mL to the mixture, which served to quantify SQ content. Then we added 160 μL of each sample solution with 40 μL of N-trimethylsilyl-N-methylheptafluorobutyramide (MSHFBA; Macherey-Nagel, Hoerd, France) in a vial. We performed an initial calibration before analyzing the samples. This step serves to determine the AG and FFA contents by mixing FA, mono,

di-, and triacylglycerols components. These compounds serve as to calculate the AG and FFA amounts. The data were analyzed on a DB5HT Agilent column (15 m, 0.32 mm i.d., 0.25 μm film thickness). The carrier gas was helium. The oven temperature was initially set at 55°C for 0.5 min, then increased to 80°C at a rate of $45^\circ\text{C}/\text{min}$, then increased to 360°C at rate of $10^\circ\text{C}/\text{min}$ and maintained at 360°C for 16 min. The temperature of the flame ionization detector (FID) was set at 365°C . Acylglycerols and squalene were identified by comparing retention times with reference standards and quantified by internal calibration with the squalane. The standard solution used is a mixture of oleic acid, monoolein, diolein, triolein, and tripalmitin, purchased from Sigma-Aldrich (Saint Louis, USA).

2.5. Fatty acids analysis and nutritional indices determination

The FA were determined after transesterification (norm ISO, 5509:2000) by a gas chromatographic method (GC-FID) described by Gravé et al. (2023). Firstly, the vegetable oils have been methylated and converted into fatty acid methyl esters (FAMES). We prepared 12 mg/mL of sample extracts in the tert-butyl methyl ether (TBME), provided by Sigma Aldrich (St Quentin Fallavier, France). The mixture was stirred using a vortex. Into an insert, we transferred 100 μL of each sample extract and 50 μL of trimethylsulphonium hydroxide (TMSH) solution, purchased from Macherey-Nagel (Hoerd, France), based on AFNOR Method NF EN ISO 12966–3 (ISO 5983–1, 2005). A capillary column CP-Select CB (fused silica WCOT, 50 m $\times$ 0.25 mm; film thickness was 0.25 μm) has been used for the FAMES analysis in the GC-FID (Agilent, Les Ulis, France). FAMES were compared with a commercial standard mixture, the Supelco 37 Component FAME Mix (Sigma-Aldrich, St. Quentin Fallavier, France). This mixture contains 37 different FAMES, which allows the retention time of each methylated fatty acid peak to be directly matched with that of the corresponding standard. The retention time data from the Supelco 37 Component FAME Mix were used for the calibration, quantification, and identification of individual peaks in the amaranth oil samples.

2.5.1. Nutritional indices

Various Nutritional indices have been calculated from the identified FA using different equations. The atherogenicity index (AI) characterized the atherogenic potential of FA and indicated the relationship between the sum of saturated fatty acids (SFA) without the C18:0. The thrombogenicity index (TI) characterized the thrombogenic potential of FA. We calculated both AI and TI indices using the equations developed by Ulbricht and Southgate (1991).

$$AI = [C12 : 0 + (4 \times C14 : 0) + C16 : 0] / \left[\sum n6 - PUFA + \sum n3 - PUFA + \sum MUFA \right] \quad (1)$$

$$TI = (C14 : 0 + C16 : 0 + C18 : 0) / \left[0.5 \times \sum MUFA + (0.5 \times \sum n6 - PUFA) + (3 \times \sum n3 - PUFA) + \left(\sum n3 - PUFA / \sum n6 - PUFA \right) \right] \quad (2)$$

The hypocholesterolemic and hypercholesterolemic ratio (H/H) has been used to assess the balance between FA that lower blood cholesterol (hypocholesterolemic) and those that raise it (hypercholesterolemic). We calculated the H/H ratio using the Santos-Silva et al. (2002) equation.

$$HH = (C18 : 1n - 9 + C18 : 2n - 6 + C20 : 4n - 6 + C18 : 3n - 3 + C20 : 5n - 3 + C22 : 5n - 3 + C22 : 6n - 3) / (C14 : 0 + C16 : 0) \quad (3)$$

Moreover, the health-promoting index (HPI) has been used to assess the nutritional value of dietary fats. We calculated the HPI using the formula cited by Chen et al. (2020):

$$HPI = \Sigma UFA / [C12 : 0 + (4 \times C14 : 0) + C16 : 0] \quad (4)$$

Furthermore, the peroxidation index (PI) is used to estimate the susceptibility of FA to oxidative degradation. We calculated the PI index using the formula proposed by Luciano et al. (2013) below:

$$PI = (\%dienoic \times 1) + (\%trienoic \times 2) + (\%tetraenoic \times 3) + (\%pentaenoic \times 4) + (\%hexaenoic \times 5) \quad (5)$$

2.6. Statistical analysis

All data were expressed as means $\pm$ standard deviations ($\pm$ SD) of triplicate measurements. The confidence limits were set at $P \leq 0.05$ determined by the ANOVA using Tukey's test, with 95 % of confidence intervals. Principal components analysis (PCA) and Hierarchical Ascending Classification (HAC) were also carried out using XLSTAT (version 2019).

3. Results

The 128 accessions of ten *Amaranthus* species are listed in Table S1 (Supplementary material) with plant inventory code.

3.1. Chemical composition

3.1.1. Oil content

A total of 120 accessions from the Hawassa University collection (Ethiopia) and 8 genotypes of *Amaranthus* seeds from 10 species have been investigated for oil content, SQ concentration, FFA content, and AG content, as listed in Table S1. The crude oil content varied even twice and ranged from 4.4 % in *A. hybridus* L. subsp. *hybridus* to 9.4 % in *A. palmeri* S. Wats (Table S1). Fig. 1 presented the average oil content of all genotypes within the same species. *A. palmeri* S. Wats genotypes significantly ($P < 0.05$) exhibited the highest average oil content, reaching 7.6 %, while *A. sp* genotypes had the lowest value (5.0 %). The other species showed similar average oil content ranging from 5.3 % to 5.6 % (Fig. 1).

3.1.2. Squalene yield

Fig. 1 and Table S1 presented the mean and specific values of SQ yield for the collection. The obtained data exhibited a specific variability

in SQ yield between both amaranth species and genotypes (Fig. 1 and Table S1). The SQ yielded a high variation among the accessions ranging from 1.8 % in *A. palmeri* S. Wats to 6.9 % in *A. hybridus* L. subsp. *hybridus* (Table S1). Fig. 1 showed the average SQ yield of all genotypes within the same species. *A. hypochondriacus* had the highest average SQ yield (5.5 %), followed by Biocoop (5.3 %), *A. viridis* L. (5.1 %), *A. cruentus* (5.1 %), *A. hybridus* L. subsp. *cruentus* (L.) Theil. (5.4 %) (Fig. 1). For the three species of *A. hybridus* L. subsp. *hybridus*, *A. sp.*, and *A. caudatus* L., the average of SQ yield ranged from 4.3 % to 4.7 % (Fig. 1). However, these species recorded no significant ($P > 0.05$) differences (Fig. 1). However, *A. spinosus* L. and *A. palmeri* S. Wats exhibited the lowest average SQ yield in the range of 2.7 % for both species.

3.1.3. Free fatty acid and acylglycerol contents

Table S1 recorded a high variability of FFA in the studied collection. The amounts of FFA presented 0.3 % for *A. palmeri* S. Wats and 6.2 % for the ultra-genotype belonging to *A. hypochondriacus* (Table S1). The average FFA content varied five times from 0.6 % to 5.0 % between the ten species (Fig. 2). *A. hypochondriacus*, Biocoop, and *A. palmeri* S. Wats genotypes had significantly ($P < 0.05$) the highest FFA content, ranging from 2.2 % to 5.0 %. The remaining species had a low average FFA level, ranging from 0.6 % to 0.8 %.

The AG content greatly varied in the collection and within the same species, allowing three times between the accessions of the studied collection (Table S1). The AG content ranged from 32.9 % to 97.2 % for the two genotypes of *A. hybridus* L. subsp. *hybridus* (Table S1). Based on interspecific analysis, *A. cruentus*, *A. palmeri* S. Wats, and *A. sp* had significantly ($P < 0.05$) the highest AG values ranging from 64.6 % to 65.6 % (Fig. 2). The average of AG in *A. hypochondriacus*, *A. hybridus* L. subsp. *hybridus*, *A. spinosus* L., *A. caudatus* L., *A. hybridus* L. subsp. *cruentus* (L.) Theil., Biocoop, and *A. viridis* L. ranged from 55.1 % to 65.2 % (Fig. 2). Hence, among the ten species, the average AG content recorded no significant ($P > 0.05$) difference (Fig. 2).

The FFA and AG exhibited a great intraspecific and interspecific variability (Fig. 2). The high standard deviations shown in the histograms (Fig. 2) can be explained by the significant diversity among genotypes belonging to the same species.

3.1.4. Fatty acids composition and nutritional indices

Table 1 presented the average percentages of FA for the ten species.

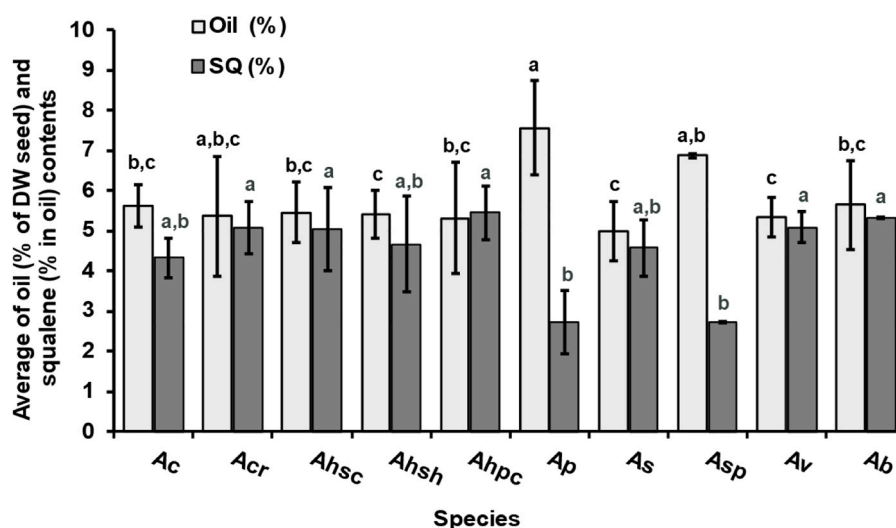


Fig. 1. Average of oil and squalene contents of ten *Amaranthus* species (representing 128 accessions); oil content: the percentage of oil in percentage of dry seed weight: % of DW seed Oil (%); squalene content SQ (% in oil); *A. caudatus* L. (Ac); *A. cruentus* (Acr); *A. hybridus* L. subsp. *cruentus* (L.) Theil. (Ahsc); *A. hybridus* L. subsp. *hybridus* (Ahsh); *A. hypochondriacus* (Ahpc); *A. palmeri* S. Wats (Ap); *A. sp* (As); *A. spinosus* L. (Asp); *A. viridis* L. (Av), and Biocoop (Ab). Different letters indicate significant differences (within each row) based on Tukey's test ($P \leq 0.05$) with a confidence interval of 95 %. Results are the means ($\pm$ SD; standard deviation) for two independent biological replicates.

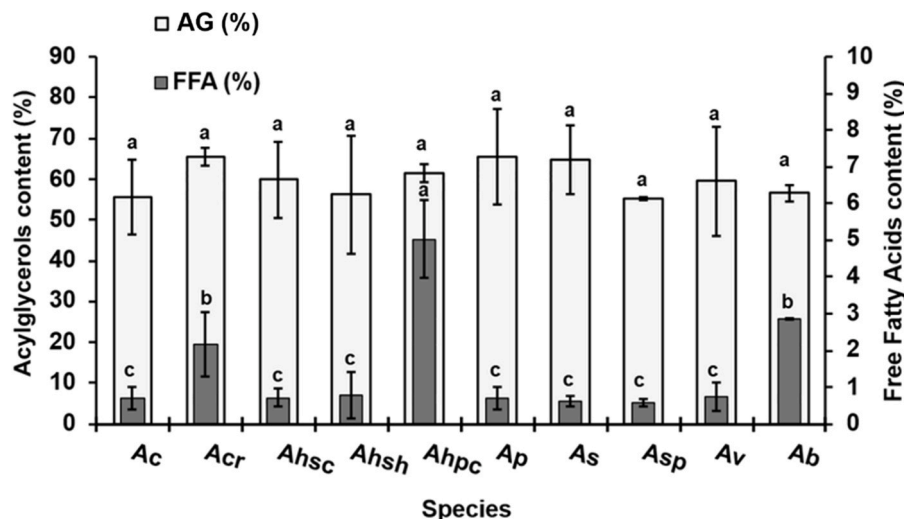


Fig. 2. Average of free fatty acids: FFA (%) and acylglycerols contents: AG (%) in oil. *A. caudatus* L. (Ac); *A. cruentus* (Acr); *A. hybridus* L. subsp. *cruentus* (L.) Theil. (Ahsc); *A. hybridus* L. subsp. *hybridus* (Ahsh); *A. hypochondriacus* (Ahpc); *A. palmeri* S. Wats (Ap); *A. sp* (As); *A. spinosus* L. (Asp); *A. viridis* L. (Av), and Biocoop (Ab). Different letters (a–c) indicate significant differences (within each row) based on Tukey's test ($P \leq 0.05$) with a confidence interval of 95 %. Results are the means ($\pm$ SD; standard deviation) for two independent biological replicates.

Our data revealed five SFA: palmitic acid (C16:0), stearic acid (C18:0), myristic acid (C14:0), eicosanoic or arachidic acid (C20:0) and docosanoic or behenic acid (C22:0); four UFA: two monounsaturated fatty acids (MUFA) oleic acid (C18:1n-9), cis vaccenic acid or cis 11

octadecanoic acid (C18:1n-7), which contain only one double bond (C=C); is, and two polyunsaturated fatty acids (PUFA): linoleic acid (C18:2n-6) and linolenic acid (C18:3n-3), which contain more than one double bond (C=C). The C16:0 and C18:1n-9 presented no significant

Table 1

The average percentage of fatty acid composition and contents of *Amaranthus* species seeds.

A. species	Ac	Acr	Ahsc	Ahsh	Ahpc	Ap	As	As	Av	Ab
C14:0	0.30 $\pm 0.03^a$	0.20 $\pm 0.01^{a,b,c}$	0.22 $\pm 0.03^b$	0.20 $\pm 0.02^{b,c,d}$	0.24 $\pm 0.02^b$	0.17 $\pm 0.04^{c,d}$	0.20 $\pm 0.02^{b,c,d}$	0.16 $\pm 0.01^d$	0.22 $\pm 0.02^{b,c}$	0.25 $\pm 0.00^{a,b}$
C16:0	19.80 $\pm 0.41^a$	19.83 $\pm 0.43^a$	20.35 $\pm 0.66^a$	20.28 $\pm 1.01^a$	20.16 $\pm 0.30^a$	17.92 $\pm 0.88^b$	19.74 $\pm 0.32^a$	20.47 $\pm 0.00^a$	20.56 $\pm 0.37^a$	19.94 $\pm 0.02^a$
C18:0	2.94 $\pm 0.24^e$	4.52 $\pm 0.07^a$	3.72 $\pm 0.31^{b,c,d}$	3.52 $\pm 0.25^{c,d}$	4.14 $\pm 0.25^{a,b}$	3.46 $\pm 0.55^d$	3.85 $\pm 0.17^{a,b,c,d}$	4.03 $\pm 0.02^{a,b,c}$	3.66 $\pm 0.11^{b,c,d}$	4.18 $\pm 0.01^{a,b}$
C18:1n-9	23.75 $\pm 1.10^{a,b}$	27.64 $\pm 5.06^a$	24.39 $\pm 3.16^{a,b}$	22.96 $\pm 4.87^{a,b}$	28.27 $\pm 6.13^a$	18.80 $\pm 2.23^b$	21.12 $\pm 1.55^{a,b}$	21.55 $\pm 0.00^{a,b}$	25.27 $\pm 4.22^{a,b}$	23.96 $\pm 0.11^{a,b}$
C18:1n-7	1.70 $\pm 0.12^a$	1.02 $\pm 0.09^{b,c,d}$	1.33 $\pm 0.15^{b,c,d}$	1.39 $\pm 0.11^{b,c}$	1.18 $\pm 0.07^{c,d,e}$	1.44 $\pm 0.17^b$	1.11 $\pm 0.09^{d,e}$	1.42 $\pm 0.01^{b,c}$	1.37 $\pm 0.13^{b,c}$	1.00 $\pm 0.01^e$
C18:2n-6	49.60 $\pm 1.23^b$	43.89 $\pm 5.03^b$	48.00 $\pm 3.19^b$	49.76 $\pm 5.34^b$	43.22 $\pm 6.57^b$	56.63 $\pm 2.85^a$	51.98 $\pm 1.29^{a,b}$	50.65 $\pm 0.01^{a,b}$	47.06 $\pm 4.67^b$	48.60 $\pm 0.12^b$
C20:0	0.73 $\pm 0.03^c$	0.96 $\pm 0.07^a$	0.77 $\pm 0.06^{b,c,d,e}$	0.81 $\pm 0.06^{b,c,d,e}$	0.85 $\pm 0.06^{a,b,c,d}$	0.74 $\pm 0.08^{d,e}$	0.79 $\pm 0.04^{b,c,d,e}$	0.85 $\pm 0.00^{a,b,c}$	0.75 $\pm 0.02^{c,d,e}$	0.86 $\pm 0.01^{a,b}$
C18:3n-3	0.86 $\pm 0.05^{a,b}$	0.66 $\pm 0.11^{b,c}$	0.87 $\pm 0.14^a$	0.77 $\pm 0.10^{a,b}$	0.85 $\pm 0.26^{a,b}$	0.55 $\pm 0.08^c$	0.88 $\pm 0.09^a$	0.55 $\pm 0.02^c$	0.83 $\pm 0.17^{a,b}$	0.86 $\pm 0.00^{a,b}$
C22:0	0.31 $\pm 0.07^b$	1.30 $\pm 0.24^a$	0.32 $\pm 0.07^b$	0.32 $\pm 0.09^b$	1.41 $\pm 0.52^a$	0.32 $\pm 0.11^b$	0.32 $\pm 0.02^b$	0.34 $\pm 0.03^b$	0.29 $\pm 0.06^b$	0.35 $\pm 0.01^b$
SFA	24.07	26.80	25.39	25.13	26.79	22.60	24.90	25.84	25.48	25.58
UFA	75.90	73.21	74.60	74.87	73.53	77.41	75.1	74.16	74.52	74.42
SFA/UFA	0.32	0.37	0.34	0.34	0.36	0.29	0.33	0.35	0.34	0.34
MUFA	25.44	28.66	25.73	24.35	29.46	20.23	22.24	22.96	26.64	24.96
PUFA	50.46	44.55	48.88	50.52	44.07	57.17	52.86	51.19	47.89	49.47
SFA/MUFA	0.95	0.94	0.99	1.03	0.91	1.12	1.12	1.13	0.96	1.02
SFA/PUFA	0.48	0.60	0.52	0.50	0.61	0.40	0.47	0.50	0.53	0.52
$\omega 3/\omega 6$	0.02	0.02	0.02	0.02	0.02	0.01	0.02	0.01	0.02	0.02
AI	0.28	0.28	0.28	0.28	0.29	0.24	0.27	0.28	0.29	0.28
TI	0.57	0.64	0.61	0.61	0.63	0.54	0.60	0.64	0.62	0.62
HH	3.69	3.60	3.56	3.59	3.55	4.20	3.71	3.53	3.52	3.64
HPI	3.62	3.55	3.51	3.55	3.48	4.16	3.66	3.51	3.48	3.56
PI	51.32	45.21	49.75	51.29	44.93	57.72	53.74	51.74	48.72	50.33

A. caudatus L. (Ac); *A. cruentus* (Acr); *A. hybridus* L. subsp. *cruentus* (L.) Theil. (Ahsc); *A. hybridus* L. subsp. *hybridus* (Ahsh); *A. hypochondriacus* (Ahpc); *A. palmeri* S. Wats (Ap); *A. sp* (As); *A. spinosus* L. (Asp); *A. viridis* L. (Av), and Biocoop (Ab). Myristic acid (C14:0); palmitic acid (C16:0); stearic acid (C18:0); oleic acid (C18:1n-9); vaccenic acid (C18:1n-7); linoleic acid (C18:2n-6); arachidic acid (C20:0); linolenic acid (C18:3n-3); behenic acid (C22:0); saturated fatty acids (SFA); unsaturated fatty acids (UFAs); monounsaturated fatty acids (MUFAs); poly-unsaturated fatty acids (PUFAs); ratio saturated/unsaturated fatty acids (SFA/UFA); ratio linolenic acid/linoleic acid ($\omega 3/\omega 6$), index of atherogenicity (AI), index of thrombogenicity (TI), hypocholesterolemic/hypercholesterolemia ratio (HH), health-promoting index (HPI), peroxidation index (PI). Different letters (a–e) indicate significant differences (within each row) by Tukey's test ($p \leq 0.05$) with a confidence interval of 95 %. Results are the means ($\pm$ SD; standard deviation) for two independent biological replicates.

($P > 0.05$) differences between the species, except for *A. palmeri* S. Wats, which had the lowest values. However, it presented significantly ($P > 0.05$) the highest C18:2n-6 content. C18:0, C14:0, C20:0, and C22:0 were lower than 2 % in all the samples. *A. sp* presented significantly ($P < 0.05$) the highest of C18:3n-3 (Table 1).

As regards the nutritional indices, the AI, the TI, the H/H, the HPI, and PI indices, strictly related to the FA composition. The AI ranged from 0.24 to 0.28, the TI ranged from 0.54 to 0.64, the H/H ratio ranged from 3.52 to 4.20, the HPI ranged from 3.48 to 4.16, and the PI value ranged from 44.9 to 57.7 for the studied species (Table 1). *A. palmeri* S. Wats had the highest H/H, HPI and PI and the lowest AI. *A. hypochondriacus* and *A. viridis* L. had the highest AI, while *A. sp* had the highest TI (Table 1).

3.2. Statistical analysis

3.2.1. Principal Components Analysis (PCA)

The PCA analysis of the obtained results revealed that the PC1 and PC2 components accounted for 77.6 % of the total variation of 26 variables, with 61.3 and 16.3 %, respectively (Fig. 3). The lengths of the dashes reflect the variance of the variables, while the angles between the corresponding variables indicate the degree of their correlations (Fig. 3). The small angles are related to high correlations, and the opposite sides of the plot refer to negative correlations. PC1 positively correlated with oil content, C18:1n-7, C18:2n-6, PUFA (%), UFA (%), SFA/MUFA, HH, HPI, and PI with 0.7, 0.6, 1.0, 0.7, 0.8, 0.8, and 0.9, respectively. However, it negatively correlated with SQ yield and the remaining variables. PC2 positively correlated with the SQ yield, C14:0, C16:0, C18:1n-9, C18:1n-7, C18:3n-3, UFA (%), $\omega 3/\omega 6$, AI with 0.4, 0.7, 0.1, 0.7, 0.2, 0.5, and 0.3, respectively (Fig. 3 and Table 2). Fig. 3 indicated three classes based on the lipid composition and nutritional value of different amaranth species. The classes called A, B and C, respectively, for the group of distinct species (Fig. 3). Group A regrouped *A. hybridus* L. subsp. *cruentus* (L.) Thell.; *A. hybridus* L. subsp. *hybridus*; *A. caudatus* L.; *A. viridis* L., and Biocoop, group B regrouped *A. cruentus* and

A. hypochondriacus, and group C regrouped *A. palmeri* S. Wats and *A. sp* (Fig. 3).

Fig. 4 displayed the correlation matrix graphic. This analysis has been conducted using the coefficient of correlation to determine the direction and intensity of the relationship between the variables. Among variables, SQ yield, C18:1n-9, C18:3n-3, and MUFA (%) exhibited a positive correlation about 0.8. FFA (%) and SFA positively correlated with SQ yield. However, there was no correlation between SQ and oil contents (Fig. 4).

3.2.2. Single linkage dendrogram for ten *Amaranthus* species on some seed composition of oilseed chemical composition

The scatter diagram of studied *Amaranthus* species has been based on the first two principal components PC1 and PC2 (Fig. 3). Fig. 5 indicated distinct species groupings based on lipid composition, (oil, SQ, FA and AG contents). Notably, it displayed the dendrogram of the distance relationships between the ten species. The relative positions of the points indicated the similarities and differences between their chemical traits. Three classes of *Amaranthus* species were presented in Fig. 5. C1 regrouped six species, such as *A. hybridus* L. subsp. *cruentus* (L.) Thell.; *A. hybridus* L. subsp. *hybridus*; *A. caudatus* L.; *A. viridis* L.; *A. spinosus* L. and Biocoop. C2 regrouped two species, *A. cruentus* and *A. hypochondriacus*, while C3 regrouped *A. palmeri* S. Wats and *A. sp*.

4. Discussion

The *Amaranthus* genus exhibits generally a wide degree of polymorphism and diversity (Gresta et al., 2020). A high variability has been recorded across 128 accessions belonging to ten species of *Amaranthus*.

Our data revealed notable range of lipid composition (Table 1). The oil content exhibited significant variation ($P < 0.05$), ranging from 4.4 % to 9.4 %. *A. palmeri* S. Wats presented the highest oil content than the other species. This difference could be attributed to the specificity of species to accumulate oil during the plant's growth cycle. This

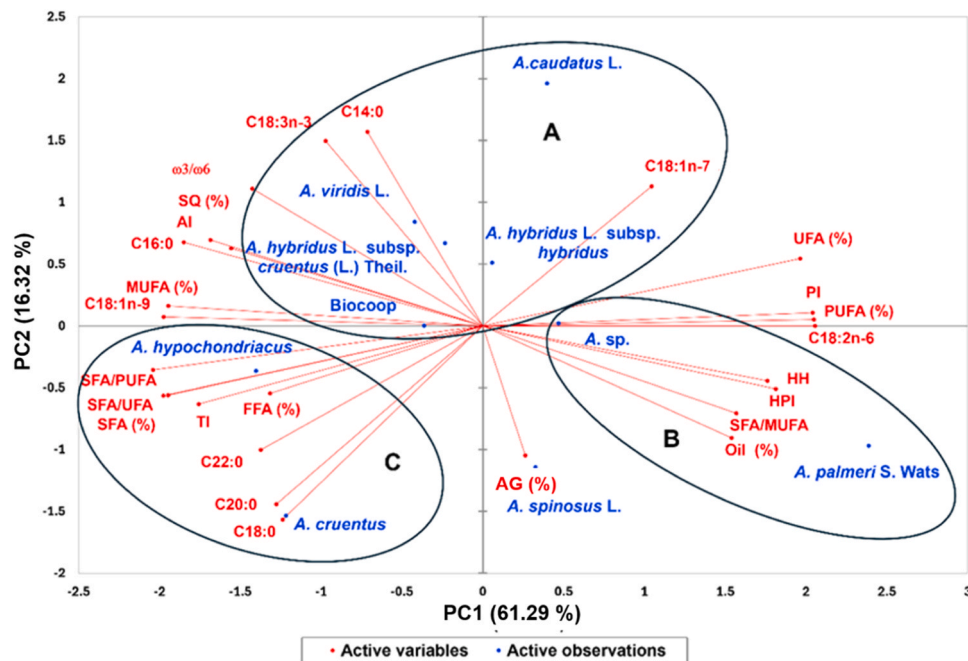


Fig. 3. PCA of the average fatty acid composition of ten *Amaranthus* species based on component correlations. First principal component: PC1, second principal component: PC2, oil content: Oil (%); squalene yield: SQ (%); free fatty acids: FFA (%); acylglycerols content: AG (%), myristic acid: C14:0; palmitic acid: C16:0; stearic acid: C18:0; oleic acid: C18:1n-9; vaccenic acid: C18:1n-7; linoleic acid: C18:2n-6; arachidic acid: C20:0; linolenic acid: C18:3n-3; behenic acid: C22:0; saturated fatty acids: SFA (%); unsaturated fatty acids: UFA (%); mono-unsaturated fatty acids: MUFA (%); poly-unsaturated fatty acids: PUFA (%); ratio saturated/unsaturated fatty acids: SFA /UFA; linolenic acid/linoleic acid ratio: $\omega 3/\omega 6$, index of atherogenicity: AI, index of thrombogenicity: TI, hypocholesterolemia/hypercholesterolemia ratio: HH, health-promoting index: HPI, peroxidation index: PI.

Table 2
Correlations between variables and the two principal components.

Traits	PC1	PC2
Oil (%)	0.733	−0.430
SQ (%)	−0.801	0.330
FFA (%)	−0.626	−0.260
AG (%)	0.125	−0.499
SFA (%)	−0.940	−0.269
MUFA (%)	−0.925	0.077
PUFA (%)	0.975	0.025
UFA (%)	0.934	0.259
C14:0	−0.340	0.747
C16:0	−0.741	0.299
C18:0	−0.589	−0.745
C18:1n-9	−0.939	0.035
C18:1n-7	0.497	0.537
C18:2n-6	0.978	0.000
C20:0	−0.607	−0.686
C18:3n-3	−0.463	0.711
C22:0	−0.653	−0.477
SFA/UFA	−0.926	−0.267
SFA/MUFA	0.746	−0.336
SFA/PUFA	−0.971	−0.169
ω3/ω6	−0.678	0.528
AI	−0.880	0.322
TI	−0.836	−0.301
HH	0.838	−0.212
HPI	0.863	−0.243
PI	0.971	0.051

First principal component (PC1), second principal component (PC2), oil content: Oil(%); squalene content SQ(%); free fatty acids/ FFA(%); acylglycerols content: AG(%), myristic acid (C14:0); palmitic acid (C16:0); stearic acid (C18:0); oleic acid (C18:1n-9); vaccenic acid (C18:1n-7); linoleic acid (C18:2n-6); arachidic acid (C20:0); linolenic acid (C18:3n-3); behenic acid (C22:0); saturated fatty acids (SFA); unsaturated fatty acids (UFAs); monounsaturated fatty acids (MUFAs); poly-unsaturated fatty acids (PUFAs); ratio saturated/unsaturated fatty acids (SFA /UFA); ratio linolenic acid/linoleic acid (ω3/ω6), index of atherogenicity (IA), index of thrombogenicity (IT), hypocholesterolemic/hypercholesterolememic ratio (HH), health-promoting index (HPI), peroxidation index (PI).

accumulation can be influenced by the expression of the genes coding the enzymes responsible for the complex set of metabolic pathways of the FA biosynthesis and their assembly into TAG, involved in the production of vegetable oils. Moreover, it has been reported that wild or spontaneous plants accumulate higher lipid content than domestic or cultivated ones. Hussain et al. (2023) have recorded from 5.2 % to 12.2 % of oil content for six wild *Amaranthus* species. It can also be affected by cultivation conditions (Tyrrus and Lykchochor, 2021), such as and/or adding fertilizer, high/less temperature, and with or without irrigation or rainfall, and soil types (Tyrrus and Lykchochor, 2021). El Gendy et al. (2018) have reported the lipid content for both *A. cruentus* and *A. hypochondriacus* under two types of soil (loamy and sandy soil) in Italy. They have reported 6.1 and 7.9 % of oil, respectively, for the two species. In the current study, we stated that the cultivation location can influence the lipid accumulation between *Amaranthus* species. Similarly to He et al. (2003) whose have investigated 104 genotypes belonging to 30 *Amaranthus* species. They have recorded an oil content ranging from 1.9 % to 8.7 %. *A. palmeri* and *A. spinosus* cultivated in China showed 4.4 and 5.7 % of oil, respectively. Likewise, *A. viridis* and *A. sp* have yielded 5.1 and 5.3 % oil (He et al., 2003). Moreover, Szabóová et al. (2020) have reported an average oil content of 5.2 % for *A. cruentus* L. cultivated in Slovakia (Nitra) and 6.5 % for *A. caudatus* cultivated in Ethiopia (Mekonnen et al. 2018). However, in the current study, *A. caudatus* L. had an average of 5.6 % (Fig. 1). Gresta et al. (2020) have investigated the lipid composition for four accessions of amaranth seeds in Calabria in southern Italy. They have found an average oil content of 6.3 % for all the collection samples. *A. cruentus* and *A. hypochondriacus* examined in our study showed an average oil content of 5.4 and 5.3 %, respectively. Our data are consistent with the previous studies, despite differences in

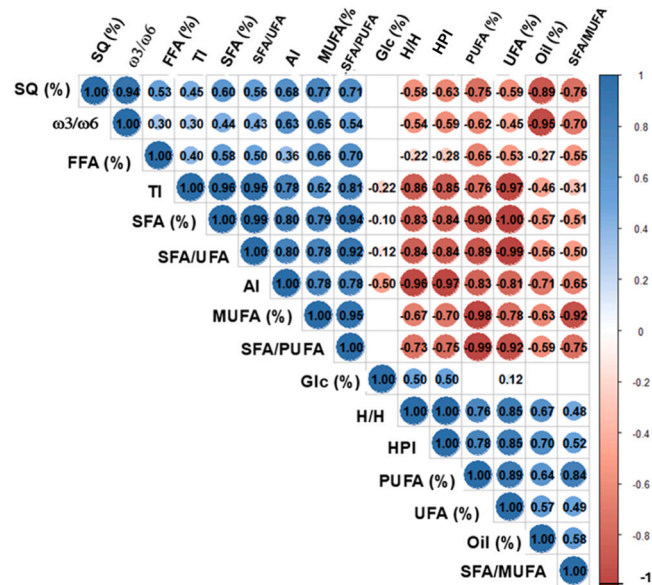


Fig. 4. Correlation coefficient between different variables. Oil content: Oil (%); squalene yield: SQ (%); free fatty acids: FFA (%); acylglycerols content: AG (%); saturated fatty acids: SFA(%); unsaturated fatty acids: UFA(%); mono-unsaturated fatty acids: MUFA(%); poly-unsaturated fatty acids: PUFA(%); ratio saturated/unsaturated fatty acids: SFA /UFA; ratio linolenic acid/linoleic acid: ω3/ω6, index of atherogenicity: AI, index of thrombogenicity: TI, hypocholesterolemic/hypercholesterolememic ratio: HH, health-promoting index: HPI, peroxidation index: PI.

the extraction parameters (process, solvent, and temperature), which can affect the oil yield. Azri et al. (2025) have applied the same extraction process. They have reported significant differences in oil content between genotypes of the same species grown at two different sites in France (Auch and Riscle). Relative to our findings, they have reported a similar oil content for *A. cruentus* (4.43–5.80), however, a higher content (5.73–6.38) for *A. hypochondriacus*. Therefore, this difference is primarily attributed to genetic and environmental factors. In addition, the amaranth oil content exceeded that of other pseudocereals such as teff (2.6 %), quinoa (6.3 %), buckwheat (2.7 %), millet (3.4–6.5 %) (Szabóová et al., 2020; Amare et al., 2021).

SQ is the precursor of all steroids (Paramasivan and Mutturi, 2022). Amaranth oil contains a much higher concentration of SQ relative to other oilseeds (Szabóová et al., 2020). In the current study, SQ yield varied from one-fold to four-fold (1.8–6.9 %) across the accessions (Table S1). The significant ($P < 0.05$) differences were mainly related to genetic factors. The obtained changes have been reported in previous studies conducted on *Amaranthus* collection (Gresta et al., 2020; He and Corke, 2003; Hussain et al., 2023; Szabóová et al., 2020). Hussein et al. (2023) have reported a range from 3.4 % to 6.1 % of SQ yield for six wild *Amaranthus* species. They have revealed that *A. cruentus* and *A. hypochondriacus* had an average SQ yield of 5.9 and 6.1 %, respectively, for both species. It should be stated that biochemical constituents, which are present in higher quantities in spontaneous plants, is frequently sacrificed in the process of optimizing biomass and yield in cultivated plants. He et al. (2003) have reported a great variability of SQ yield, ranging from trace to 7.3 % in the *Amaranthus* collection. They have reported an average SQ yield of 4.1, 5.5, 2.74, 2.70, 4.30, and 4.80 % in oil, respectively, for *A. cruentus* and *A. hypochondriacus*, *A. palmeri*, *A. spinosus*, *A. viridis*, and *A. sp* (cultivated in China). El Gendy et al. (2018) have revealed that SQ yield was 5.7 and 6.0 %, respectively, for *A. cruentus* and *A. hypochondriacus* cultivated in two soil types in Italy. Furthermore, Szabóová et al. (2020) have obtained an average SQ yield equal to 5.7 %. The variation of SQ yield between different species and genotypes may be explained by the conversion of SQ into

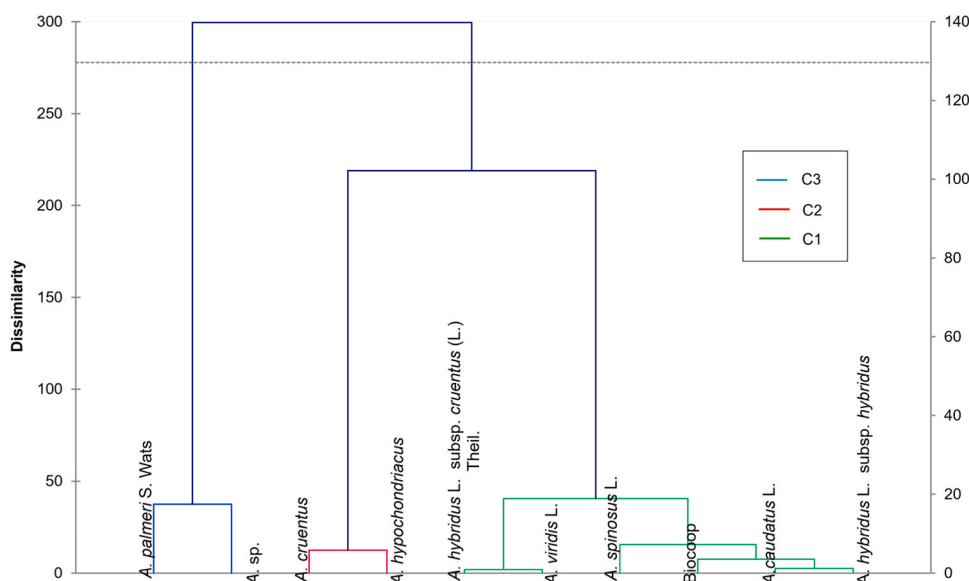


Fig. 5. Dendrogram of linkage distance of ten *Amaranthus* species in chemical composition. C1: group 1, C2: group 2 and C3: group 3.

phytosterols during the maturity period of plant seeds. Overall, the significant differences in SQ yield between the species and across genotypes were mainly related to various explanations. They could be attributed to abiotic and biotic factors (Hussain et al., 2023; Lozano-Grande et al., 2018; Szabóová et al., 2020). The studied *Amaranthus* samples collected from three different origins: France, Ethiopia, the Congo market and Biocoop, being thus from different climatic conditions, sowing times, and harvesting seasons (Tyus et al., 2023; Tyus and Lykhochvor, 2021; Yeshitila et al., 2024; Azri et al., 2025). Other experimental factors should be considered to explain the observed data, as the extraction parameters, the solvent choice polarity, the used method, and the temperature of extraction. Even when comparing our results with those obtained using the same extraction conditions (Azri et al. 2025), a notable variation remains. They have reported a SQ yield of 5.29–5.65 % in *A. cruentus*, which is similar to our data (5.1) and 6.03–7.74 % in *A. hypochondriacus*, which is higher than our results (5.5 %). This variation is mainly explained by genetic and agroclimatic factors. The significant variation could suggest the need to intercross promising accessions to introduce a wider range of genetic variation. This would enable a more efficient selection of segregated generations to improve genotypes with greater nutritional values (Sarker et al., 2016). It can be produce more SQ and other bioactive molecules, serving as renewable resources, for food, cosmetics, and pharmaceutical purposes. As account, the oil content of amaranth is higher than other pseudocereals (Amare et al., 2021). It yields notably the highest amount of SQ compared to other vegetable sources, such as maize, peanut, rapeseed, coconut, sunflower, cotton, olive oil, and rice bran (Okan et al., 2020). For knowledge, SQ, a hydrocarbon, is firstly isolated from shark liver lipids. Several studies conducted over the past few decades have shown its exceptional medicinal value (Srivastava et al., 2021). Hence, today, amaranth represents a promising alternative for producing natural plant-origin SQ, offering a renewable source of SQ and helping to avoid the slaughter of animals.

The composition of FFA (Table S1 and Fig. 2) highlighted the nutritional value and stability of lipids and oils of *Amaranthus* seeds. Our findings support the earlier studies suggesting that *Amaranthus* oil is a reliable source of FFA (Hussain et al., 2023; Srivastava et al., 2021). The FFA content widely varied between the species. This variation probably depended to the seed growth conditions and the harvesting times. The AG content are indicators of the quality, stability, and suitability of vegetable oils (Dąbrowski et al., 2019; Tymchuk et al., 2021). It ensures that the oil is suitable for nutritional, industrial, or cosmetic needs. The

AG are also a source of energy for the body and an essential component of a healthy diet (Procopet and Oroian, 2022). The current study showed that AG were the predominant constituents in amaranth seed oil. The AG ranged from 32 % to 97 % between the accessions (Table S1). The high variation in AG levels and FFA contents is probably explained by the expression of key genes involved in the Kennedy pathway to produce FA. The Kennedy pathway describes successive acylation reactions by adding a glycerol backbone for each hydroxyl group. This process may explain the reduction of FFA content to TAG stored by plants (Gill et al., 2018).

The FA profiles of 128 accessions of 10 different species analyzed to determine the relative percentage of each sample (Table 1). Our data were similar to previous published results (Amare et al., 2021; Effoe et al., 2020; Hlinková et al., 2013; Procopet and Oroian, 2022; Szabóová et al., 2020). C18:2n-6, C18:1n-9, C16:0, C18:0 and C18:1n-7 were the major amaranth oil FA, in decreasing order (Table 1). However, C14:0, C20:0, C22:0, and C18:3n-3 have been shown in much lower amounts (trace) for all samples. The therapeutic potential of amaranth seeds to alleviate atherosclerotic disorders is well known (Skwarylo-Bednarsz et al., 2020). SFA and UFA are essential in assessing the functional and nutritional qualities of fats and oils and their ratio is crucial for several healthy reasons. Some UFA, such as linoleic and linolenic acid, are exogenous acids essential for the animal body and play an important role in regulating the immune-inflammatory system, hormone synthesis, cell membrane structure, and the regulation of their permeability (Oteri et al., 2021). PUFA are well known for their capacity to protect against various metabolic diseases (Rizzo et al., 2023). PUFA play a key role in regulating cholesterol synthesis and cellular uptake by various mechanisms (Lawrence, 2021). As regards the nutritional aspects, *A. palmeri* S. Wats exhibited the highest PUFA content (77.4 %), followed by *A. caudatus* L. (75.9 %), while they also presented the lowest SFA with 20.2 and 24.1 %, respectively (Table 1). *A. hypochondriacus* and *A. cruentus* exhibited the lowest PUFA (73.2 and 73.7 %) and the highest SFA (26.8 and 26.8 %). Our findings were similar to previous studies (Bozorov et al., 2018; El Gendy et al., 2018; Gresta et al., 2020; Zhang et al., 2019). The notable difference between SFA and UFA contents can be explained by the accumulation of FA following the biosynthesis dynamics described in the Kennedy pathway, involving acyl-CoA elongase and desaturase enzymes. This process enables the reduction in SFA, which are utilized in PUFA synthesis. Relative to other oilseeds and cereals, our data revealed a high predominance of linoleic acid (ω 6), similar to sunflower (26.0–57.0 %) (Bozorov et al., 2018; El Gendy et al.,

2018; Gresta et al., 2020; Zhang et al., 2019), and a less linolenic acid ($\omega 3$) than rapeseed oil (8.7–9.6 %) (Bozorov et al., 2018; El Gendy et al., 2018; Gresta et al., 2020; Zhang et al., 2019) and chia seed (52.4–60.0 %) (Bozorov et al., 2018; El Gendy et al., 2018; Gresta et al., 2020; Zhang et al., 2019). In addition, the SFA/MUFA ratio ranged from 0.91 to 1.13. It was higher than chia oil. However, the SFA/PUFA ratio ranged from 0.40 to 0.61, which was similar to the chia oil (1.1–1.4) (Gravé et al., 2023). Moreover, amaranth oil exhibited a $\omega 3/\omega 6$ ratio similar to safflower (0.01) but lower than other oilseeds such as chia seed oil (0.3), canola oil (0.36), olive oil (0.1), atlas pistachio (1.1–3.3), and soybean oil (0.1) (Bozorov et al., 2018; El Gendy et al., 2018; Gresta et al., 2020; Maestri et al., 1998; Roche et al., 2016, 2019; Zhang et al., 2019). Although there is no specific value recommended for $\omega 3/\omega 6$ ratio, according to the European Food Safety Authority (Beyzi et al., 2019; Gravé et al., 2019; Nakonechna et al., 2024).

There are only two references described the AI, TI, and H/H indices in amaranth oils (Gresta et al., 2020; Oteri et al., 2021). The AI characterized the atherogenic potential of FA and indicated the relationship between the sum of SFA, without C18:0, which is considered pro-atherogenic because it promotes lipid head adhesion in cells of the circulatory and immunological systems (González-Félix et al., 2016; Monteiro et al., 2018; Omri et al., 2019), and the sum of UFA (Chen and Liu, 2020). The UFA are considered an anti-atherogenic because they inhibit the accumulation of plaque and reduce the phospholipids, cholesterol, and esterified FA levels (Monteiro et al., 2018; Omri et al., 2019). Therefore, the consumption of nutritional products with a lower AI can reduce the levels of total cholesterol and LDL-C (Low-Density Lipoprotein) in human blood plasma (Yurchenko et al., 2018). For the knowledge, the AI value for crops ranged between 0.084 and 0.55 (Chen and Liu, 2020). Our data revealed that amaranth oil contains a normal AI index (0.24–0.28) relative to AI crops. Previous studies recorded an AI 0.46–0.53 for Cumin (*Cuminum cyminum*), 0.22 for Guar seed (*Cyamopsis tetragonoloba*), 0.55 for Scabiosa stellata, 0.084–0.107 for White lupine (*Lupinus albus*), 0.05–0.07 for Camelina oil (*Camelina sativa*), and 0.09–0.11 for sunflower oil (Chen & Liu, 2020). Additionally, Kabiri et al. (2011) have reported a significant reduction in the AI in atherosclerotic rabbits supplemented with amaranth extracts. The TI characterized the thromogenic potential of FA. This parameter indicates the tendency to form clots in blood vessels and indicates the relationship between pro-thrombogenic and anti-thrombogenic FA. Hence, the consumption of nutritional products with a lower TI is beneficial for cardiovascular health (Chen and Liu, 2020; Ulbricht and Southgate, 1991). Amaranth oil revealed a range from 0.54 to 0.64 of the TI indices. These results conform to standards and are consistent with those reported for other crops such as Cumin (*Cuminum cyminum*) (0.46–0.56) and Guar seed (*Cyamopsis tetragonoloba*) (0.53); however, it's higher than Camelina oil (*Camelina sativa*) (0.1) (Chen and Liu, 2020). The H/H ratio assessed the nutritional value of the oil. It calculated based on the functional effects of the individual FA on cholesterol metabolism. A H/H ratio ranged from 11.7 to 14.7, with a low AI and TI contributing to a decrease in the incidence of coronary heart disease (CHD). Our results showed that amaranth oil presented a higher H/H ratio than Camelina oil (*Camelina sativa*), which ranged from 11.2 to 15.0 (Chen and Liu, 2020). The HPI assesses the nutritional value of dietary lipids, for example, dairy products with high HPI values are assumed to be more beneficial to human health (Chen and Liu, 2020). Our data exhibited some differences between AI, TI, and H/H ratio, HPI, and PI indices values conducted in this study (0.29, 0.64, 4.20, 4.16, and 57.72, respectively). The PI was highly varied between the *Amaranthus* species. It observed that PI index increases with an increase in the PUFA. The PI value reflected the different PUFA contents, being higher in our samples (ranging between 44.93 and 57.72) than that calculated by Oteri et al. (2021) in four accessions of *A. hypochondriacus* (34.4, on average) and by Gresta et al. (2020) in *A. cruentus* seeds (27.6, on average).

Current biochemical evidence indicates a relationship between different components in *Amaranthus* seed genotypes. Fig. 4 presented the

correlation matrix (Pearson (n)). The analysis was carried out based on the coefficient correlation to assess the strength and direction of the relationship between the variables. The blue color indicated a positive correlation, and the red indicated a negative correlation; however, no color indicated any correlation between the variables (Fig. 4). The SQ yield and the MUFA (%) were positively correlated at around 0.8. It correlated also with FFA content (0.2), SFA (0.5), $\omega 3/\omega 6$ (0.09), AI (0.6), and TI (0.4) (Fig. 4). This relationship could indicate the global regulation mechanisms by a common precursor (acetyl-CoA). However, no relationship observed between oil content and SQ yield (Fig. 4). This divergence can be explained by several biochemical and physiological properties in plant systems. Notably, SQ and oil do not share the same biosynthetic pathway. Oil is predominantly composed of essential FA and TAG, and its accumulation is largely influenced by genetic and environmental factors (temperature, rainfall) (Azri et al., 2025). In contrast, SQ serves as a precursor for hopanoids and is extensively converted into phytosterols during grain maturation. Fig. 4 indicated the positive correlation between oil and PUFA (%), UFA (%), SFA/MUFA (%), HH ratio, HPI, and PI with R-value from 0.5 to 0.7. This correlation may be explained by the dominant FA revealed in amaranth oils, such as SFA, UFA, and PUFA. The SFA strongly correlated with AI (0.8), TI (0.95), SFA/PUFA (0.9), and MUFA (%) (0.7). However, the MUFA positively correlated with $\omega 3/\omega 6$ (0.6), AI (0.7), and TI (0.6). As regards nutritional indices, the AI positively correlated with TI (0.78), however, HPI correlated strongly with the H/H ratio (0.96), while PI was highly correlated with HPI (0.77).

The dendrogram (Fig. 5) clearly showed three main classes. These groups indicated significant differences in the lipid composition of the samples, revealing distinct biochemical profiles. This dissimilarity is probably related to genetic diversity. The different accumulation levels of lipid compounds are regulated by biosynthesis pathways, which involve different enzymatic activities between species. For instance, the similarity of species in group C2 was due to the high accumulation of FFA and saturated FA. C1 selected species with high levels of AG, linoleic acid, and low levels of FFA (Fig. 5). C3 group was selected based on their SQ, FFA, oil, and AG contents. The analyzed relationships between the ten *Amaranthus* species (Fig. 5) were similar to those observed by He et al. (2003) and Wolosik and Markowska (2019). The close relationships between *A. hybridus* and *A. spinosus*, *A. viridis*, reported by He et al. (2003), have been observed in this scatter plot (Fig. 5). Additionally, the separation of *A. palmeri* from the other species could be due to its low SQ yield (Fig. 5). The genotype profiles of several species, *A. hypochondriacus*, *A. hybridus*, and *A. sp.*, were widely dispersed in the scatter plot, similar to that published by He et al. (2003). The possible reason could be their high genetic variation for these traits.

Multivariate analysis of collection species showing similar lipid composition suggested a common adaptation to similar genetic traits and/or environmental biotopes. These analyses help to discriminate between species and highlight those rich in bioactive molecules for future research.

5. Conclusions

Amaranth is among the major sources of SQ and UFA; the present study investigated the lipid composition of 128 genotypes belonging to ten species of *Amaranthus* seed. This research aimed to refine and select genotypes according to their importance and stability.

Our data clearly showed a wide variability of lipid compositions in our collection. The oil content varied twice between 4.4 % and 9.4 %, and the squalene yield varied from 1.8 % to 6.9 %. *Amaranthus* presented a high level of essential FA, particularly linoleic and oleic acids. Indeed, AG presented the major constituent of oil composition in the studied collection (reached 97 % on *A. hybridus* L. subsp. *hybridus*). Multivariate analysis enhances the selection of species with their biochemical traits.

Moreover, *Amaranthus* seeds are a greater source of SQ compared to

other cereal and pseudocereal sources. On account that clinical and nutraceutical benefits of squalene gain greater recognition, the exploitation of this molecule is expected to grow steadily. This increasing demand will promote the large-scale production of *Amaranthus* seed, both as a sustainable source of SQ and for other value-added applications. The residues of amaranth seed could be used in different bakery industries or construction sectors.

The current collection is interesting and should be studied under various conditions to evaluate the bioaccumulation of its different components. This paper advances the knowledge of the nutritional value of this crop, aiming to foster new market opportunities, share comprehensive data on nutritious food availability, and identify target ingredients for the formulation of novel functional foods.

CRedit authorship contribution statement

Romain Valentin: Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Ahlem Azri:** Writing – original draft, Investigation, Formal analysis, Data curation. **Othmane Merah:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Mohamed Debouba:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Conceptualization. **Jalloul Bouajila:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **Mekonnen Yeshitila:** Writing – original draft, Visualization, Resources, Methodology, Formal analysis. **Muriel Cerny:** Writing – original draft, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Eric Lacroux:** Writing – original draft, Resources, Methodology, Investigation, Formal analysis. **Sameh Sassi Aydi:** Writing – original draft, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Samir Aydi:** Writing – original draft, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Hewan Demissie Degu:** Writing – review & editing, Validation, Resources, Conceptualization. **Lucas Tricoulet:** Writing – original draft, Software, Resources, Investigation, Formal analysis, Conceptualization. **Patrice Galaup:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization.

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.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.jfca.2025.108305](https://doi.org/10.1016/j.jfca.2025.108305).

Data availability

Data will be made available on request.

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