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Plant oils as a source of vitamin E in the human diet

Bachelor's Thesis

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Food Quality and Processing of Agricultural Products

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Declaration

I hereby declare that I have authored this bachelor's thesis carrying the name „Plant oils as a source of vitamin E in the human diet “independently under the guidance of my supervisor. Furthermore, I confirm that I have used only professional literature and other information sources that have been indicated in the thesis and listed in the bibliography at the end of the thesis. As the author of the bachelor's thesis, I further state that I have not infringed the copyrights of third parties in connection with its creation.

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Plant oils as a source of vitamin E in the human diet

Summary:

According to the classical concept, vitamin E includes four tocopherols (α -, β -, γ -, and δ -tocopherol) and four tocotrienols (α -, β -, γ -, and δ -tocotrienol), collectively referred to as tocochromanols or tocols. This group of amphipathic lipid-soluble molecules generally consists of a polar part derived from tyrosine and a hydrophobic polyprenyl side chain derived from the isoprenoid structure. Tocochochromanols are synthesized by photosynthetic organisms, therefore plant products provide the only natural dietary sources of these substances. The primary site of accumulation of tocochochromanols is plastids, where their biosynthesis takes place. The formation of the polar chromanol ring from homogentisate is mediated via shikimate pathway, whereas the methylerythritol phosphate pathway provides the lipophilic prenyl tail from geranylgeranyl diphosphate and phytyl diphosphate for the synthesis of tocotrienols and tocopherols, respectively.

The key role of tocochochromanols in plants is their complex system of protective mechanisms that together protect light-harvesting tissues from photooxidative damage. They are particularly important during intense light stress or in the absence or failure of other protective mechanisms. Tocochochromanols, especially α -tocopherol, effectively neutralize singlet oxygen molecules. In the human body vitamin E plays a significant role as an antioxidant. The main principle of the antioxidant action of tocopherols and tocotrienols is to break the radical chain reaction by quenching peroxy radicals. Vitamin E may also be involved in the regulation of gene expression and the maintenance of physiological functions of the immune system, such as the stimulation of phagocytic function, which is important in defending the body against infectious diseases.

Since all the natural forms of vitamin E are of plant origin, vegetable oils are the most important and concentrated dietary source of vitamin E for humans. Many oilseeds are currently being used as functional foods, primarily because oils derived from the seeds of field crops are often high in unsaturated fatty acids. Coconut, cottonseed, olive, palm, peanut, rapeseed/canola, soybean, and sunflower oils are the most common plant oils. Usually, α -tocopherol (102-575 mg/kg) and γ -tocopherol (15-592 mg/kg) are the most occurring tocopherols among these oils from their total tocopherol content. However, non-traditional oils that could diversify our diet are poppy seed oil and soybean oil, due to their content of β - and δ -tocopherol, which are not commonly abundant. Poppy seed oil contains β -tocopherol roughly in scale from 261 to 268 mg/kg and δ -tocopherol in soybean oil is from 182 to 185 mg/kg of its total tocopherol content. Furthermore, palm fruit is the richest source of tocotrienols among all plant oils. Tocotrienols make up almost 70% of vitamin E in palm oil, with the remaining 30% being tocopherols.

However, in order to reasonably determine the suitability of including different plant oils in the human diet, it will be necessary to conduct scientific research to evaluate the influence of genetic as well as environmental factors on the tocol content and profile of different oil crops.

Keywords: vitamin E, tocopherols, tocotrienols, lipophilic antioxidants, rapeseed oil, poppy seed oil, sunflower seed oil

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1 Introduction

Vegetable oils are an integral part of the human diet and based on the historical records, first references to the consumption of olive oil go back to around 6000 BC in Israel. Furthermore, palm and coconut oils were detected in artifacts in Egyptian pyramids, approx. 4000 BC. Much later, at about 1000 AD, in the east, soybean oil was discovered. The consumption and trade of plant oils continued to grow over time, especially around late 1800s, when knowledge of the chemistry of fats and oils in Europe led to the application of new technologies in the industrial production of fats and oils.

Today, the most widely consumed plant oils include palm, soybean, rapeseed, and sunflower oil, which are used mainly for their sensory and technological properties. However, plant oils can also provide health benefits to the consumer as they can be a significant source of vitamin E, as well as other biologically active substances. Nowadays, as people are increasingly focusing on a healthy lifestyle, there is a growing awareness of the importance of vitamins and biologically active substances for human health and an interest in finding natural sources of these substances that could be easily incorporated in the diet.

Vitamin E is well known for its strong antioxidant properties, which are important for the plants that produce these substances as part of their secondary metabolism, as well as for humans who consume these substances in their diet. In the human body, vitamin E is particularly important in terms of protecting cellular macromolecules from oxidative damage, which is an important factor in the pathogenesis of many human diseases, such as coronary heart disease, atherosclerosis, cancer, the aging process, and many disease states *in vivo*.

In the context of growing interest in healthy and possibly plant-based diets, it is essential to be aware of the nutritional value of commonly used and less traditional vegetable oils that can be used effectively to meet vitamin E needs and support the overall health of consumers.

2 Aims of the thesis

The objective of the Bachelor Thesis is to present the current knowledge on the forms of tocochromanols occurring in selected plant oils. To describe their chemical structure, biosynthetic pathway and to evaluate their importance in the human diet.

3 Literature review

3.1 Tocochromanols

Tocochromanols, abbreviated as tocots, include eight different, structurally similar substances that are divided into two basic groups, tocopherols and tocotrienols. The term vitamin E, which is often used in connection with tocots, indicates all entities exhibiting the biological activity of natural α -tocopherol, the main function of which is to protect cellular structures from oxidative damage. In plant tissues, all forms of vitamin E actually show the activity, but in the context of the human organism only α -tocopherol can be called a vitamin, since it is the only one of all tocots that has been shown to protect the organism against diseases caused by its deficiency (Azzi 2018).

The discovery of vitamin E is related to the research of Evans and Bishop (1922), who identified a component in the lipid fraction of plant material essential for the normal function of the reproductive system of rats. It was called "factor X" also referred to as "anti-sterile factor" and it was classified as vitamin E fourteen years later. In the following years, vitamin E was isolated from wheat germ oil and named α -tocopherol derived from the Greek words *tocos* (childbirth) and *feroin* (bringing), with the suffix -ol indicating the compound is an alcohol. Subsequently, the chemical structure, method of synthesis, and the relevance of preventing deficiency of this substance were recognized. Over the last 30 years or so, it has become clear that adequate intake of vitamin E (along with other antioxidants) may play an essential role in preventing the onset and development of cardiovascular and some other diseases (Eitenmiller & Lee 2004; Preedy & Watson 2007). This finding prompted further research on tocopherols, which has, in particular, led to the discovery of several other compounds with vitamin E activity, as well as some previously undescribed mechanisms of action of this vitamin *in vivo*. According to the classical concept, vitamin E comprises four tocopherols (α -, β -, γ -, and δ -tocopherol), and four tocotrienols (α -, β -, γ -, and δ -tocotrienol), collectively referred to as tocochromanols (Fišnar & Réblová 2022). All these naturally occurring forms of tocochromanols were recognized to exhibit the biological activity of vitamin E (Eitenmiller & Lee 2004).

3.1.1 Chemical structure

All eight identified forms of tocochromanols are amphipathic, lipid-soluble organic molecules with a common basic structure, which consists of a polar moiety of a chromanol ring (they are bicyclic phenols) and a hydrophobic side chain originating from the isoprenoid structure (Mène-Saffrané & DellaPenna 2009). The individual forms of tocots differ in the number and location of methyl groups substituted on the aromatic ring and in the side chain saturation (Preedy & Watson 2007). Saturated side chain (an aliphatic phytyl side chain) is characteristic for tocopherols, the basic structure of which is formed by 2-methyl-2-(4,8,12-trimethyltridecyl) chroman-6-ol. On the other hand, tocotrienols are characterized by the presence of three double bonds in the side chain (an unsaturated farnesyl side chain) at positions 3', 7', and 11', thus the basis of their structure is 2-methyl-2-(4,8,12-trimethyltrideca-3,7,11-trienyl) chroman-6-ol (Tiwari & Cummins 2009). The four different homologues of tocopherols

or tocotrienols, namely α -, β -, γ -, δ -, differ in the number and location of the methyl substituent in the hydrophilic head of 6-chromanol (Figure 1) affecting the possibility of formation of various isomeric forms (Szewczyk et al. 2021).

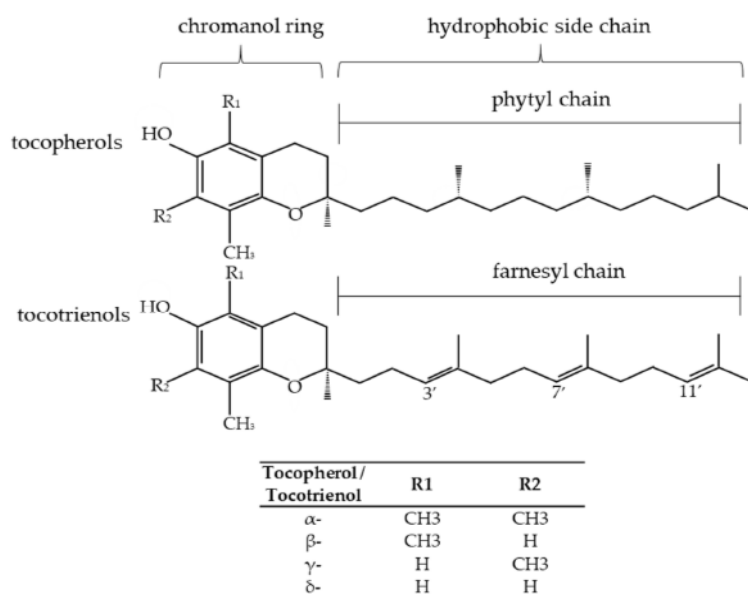


Figure 1. The basic structure of tocopherols and tocotrienols and their individual forms (Szewczyk et al. 2021).

α -tocopherol (α -T) and α -tocotrienol (α -T3) are trimethylated, whereas β -tocopherol (β -T), β -tocotrienol (β -T3), γ -tocopherol (γ -T), and γ -tocotrienol (γ -T3) are dimethylated, and δ -tocopherol (δ -T) as well as δ -tocotrienol (δ -T3) are monomethylated. The term tocol is used as the generic trivial title for 2-methyl-2-(4',8',12'-trimethyltridecyl) chroman-6-ol. The tocopherol(s) should be applied as a general name for all mono, di, and trimethyl tocols. All of these forms can generally be referred to as tocols, however, this designation should not be confused with the term vitamin E (Eitenmiller & Lee 2004).

According to the IUPAC-IUB Joint Commission on Nomenclature the term vitamin E represents the universal designation for all tocol and tocotrienol derivatives exhibiting qualitatively the same biological activity as α -T and it should be used in derived terms like vitamin E deficiency, vitamin E activity, and vitamin E antagonist (Eitenmiller & Lee 2004).

Due to the presence of three chiral centers at positions 2, 4', and 8' of the phytyl tail, tocopherols may exist in eight (2^3) different stereoisomeric forms (Figure 2). The natural forms of tocopherols have an "R" configuration at all of these chiral centers, therefore there is a 2-R, 4'-R, 8'-R- or shortly RRR- prefix in their name (Preedy & Watson 2007). These natural forms have stronger biological effects than their synthetic equivalents, which are a racemic mixture of all eight possible stereoisomers (Azzi 2018; Szewczyk et al. 2021). Tocotrienols have only one chiral center at C-2, but unlike tocopherols they have two more sites of geometric isomerism at C-3' and C-7' due to the presence of the double bonds. Natural tocotrienols occur in the 2-R, 3'-*trans*, 7'-*trans* configuration (Bramley et al. 2000).

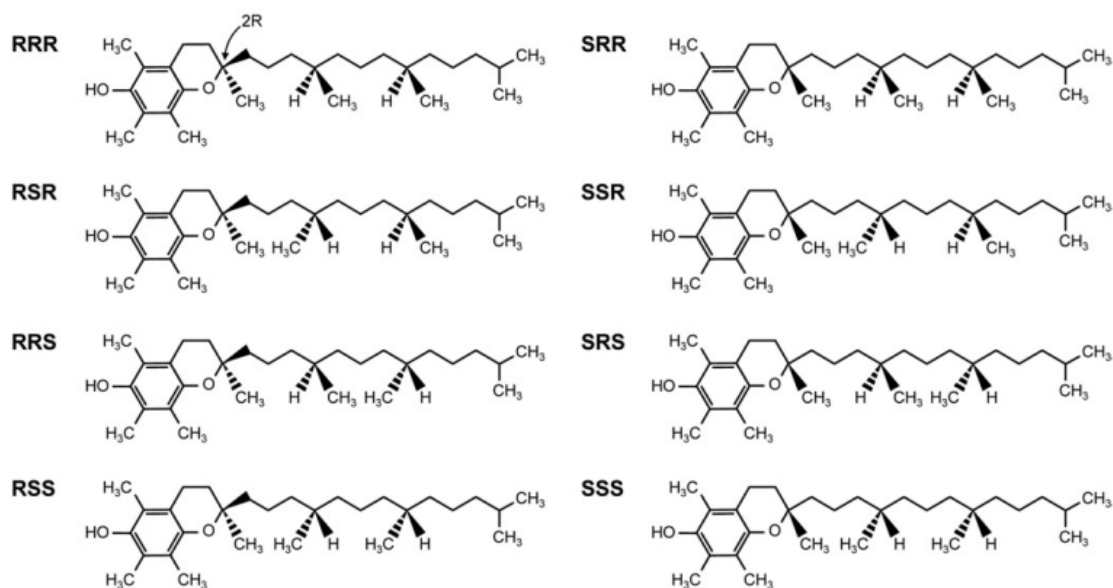


Figure 2. Structures of RRR- α -T and the seven stereoisomers (Biesalski 2009)..

Of all the forms, the greatest biological activity is exhibited by natural RRR- α -T. The activity of the other tocol forms, expressed as the α -tocopherol equivalent (%), is as follows: β -T 50%, γ -T 10%, 3% for δ -T, 30% for α -T3, 8% for γ -T3, and 5% for β -T3. The equivalent has not been established for δ -T3 (Szewczyk et al. 2021).

At the end of the 20th century, other substances structurally similar to tocols were discovered, some of which have already experimentally shown to have the biological activity of vitamin E. These compounds include, for example, tocomonoenols (Figure 3), desmethyl- and didesmethyl tocotrienols and tocodienols (Fišnar & Réblová 2022). The vitamin E activity is also exhibited by other derivatives such as tocopheryl and tocotrienyl esters (e.g. α -tocopheryl acetate, α -tocotrienyl acetate) (Eitenmiller & Lee 2004).

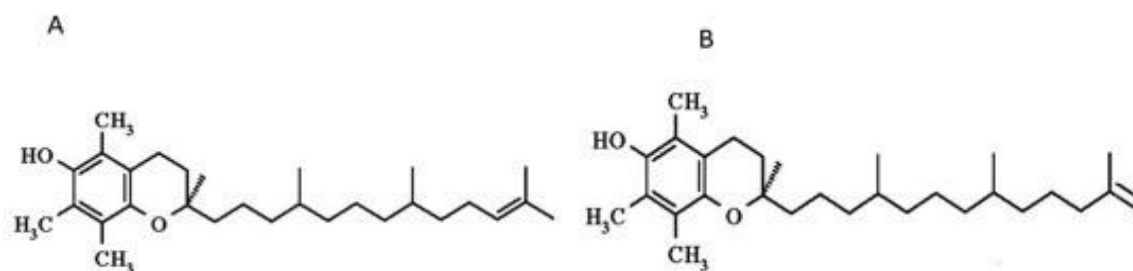


Figure 3. Chemical structure of (A) α -tocomonoenol of palm oil and (B) an isomeric α -tocomonoenol from the lipophilic fraction of salmon eggs having an unusual methylene unsaturation at the end of isoprenoid chain (Azzi 2019).

3.1.2 Biosynthesis

Tocopherol biosynthesis takes place at the inner envelope of plastids through a combination of two main pathways. The shikimate pathway gives rise to the polar chromanol ring from homogentisate (HGA), whereas the methylerythritol phosphate (MEP) pathway provides the lipophilic prenyl tail from geranylgeranyl diphosphate (GGDP) and phytyl

diphosphate (PDP) for the synthesis of tocotrienol and tocopherol, respectively (Figure 4). An additional pathway for PDP production from chlorophyll degradation is a phytol recycling pathway (Muñoz & Munné-Bosch 2019).

3.1.2.1 Biosynthesis of chromanol moiety

The first step in the biosynthesis of the chromanol moiety is the synthesis of *p*-hydroxyphenylpyruvate (HPP), which can be synthesized in the shikimate pathway via a prephenate intermediate or by tyrosine transamination (Figure 5). The resulting HPP is converted to HGA by the activity of the enzyme *p*-hydroxyphenylpyruvate dioxygenase. It is a complex, irreversible enzymatic reaction involving oxidative decarboxylation of the side chain, its migration to position 2 of the aromatic ring and hydroxylation at position 1 (Fritsche et al. 2017).

The condensation of precursor molecules of the lipophilic hydrocarbon chain and the polar chromanol moiety is essential for the tocol biosynthetic pathway. Therefore, in the next step, HGA and PDP or GGDP are condensed to form 2-methyl-6-phytylplastoquinol (MPBQ) or 2-methyl-6-geranylgeranylplastoquinol (MGGBQ). These reactions are catalyzed by the activity of the enzyme homogentisate prenyltransferase (HPT) or homogentisate geranylgeranyltransferase (HGGT), respectively. This step is the main site of regulation of the biosynthetic pathway and the activity of HPT and HGGT is crucial in the process of tocopherol and tocotrienol formation (Muñoz & Munné-Bosch 2019). MPBQ and MGGBQ are the first common intermediates for the synthesis of all tocopherols and tocotrienols (Bramley et al. 2000; DellaPenna & Pogson 2006; Fritsche et al. 2017).

Methylation of the benzene ring of MPBQ or MGGBQ at position 3 results in the formation of 2,3-dimethyl-6-phenyl-1,4-benzoquinone (DMPBQ) or 2,3-dimethyl-6-geranylgeranyl-1,4-benzoquinone (DMGGBQ). MPBQ and DMPBQ (or MGGBQ and DMGGBQ) are substrates for the enzyme tocopherol cyclase, which produces δ -tocopherol from MPBQ (δ -T3 from MGGBQ), which can be further converted via the enzyme γ -T methyltransferase to β -T (or β -T3). The same enzymes act in a section of the biosynthetic pathway derived from DMPBQ (or DMGGBQ). In this case the first product is γ -T (or γ -T3), from which α -T (or α -T3) is subsequently formed (Figure 4) (DellaPenna & Pogson 2006; Fritsche et al. 2017).

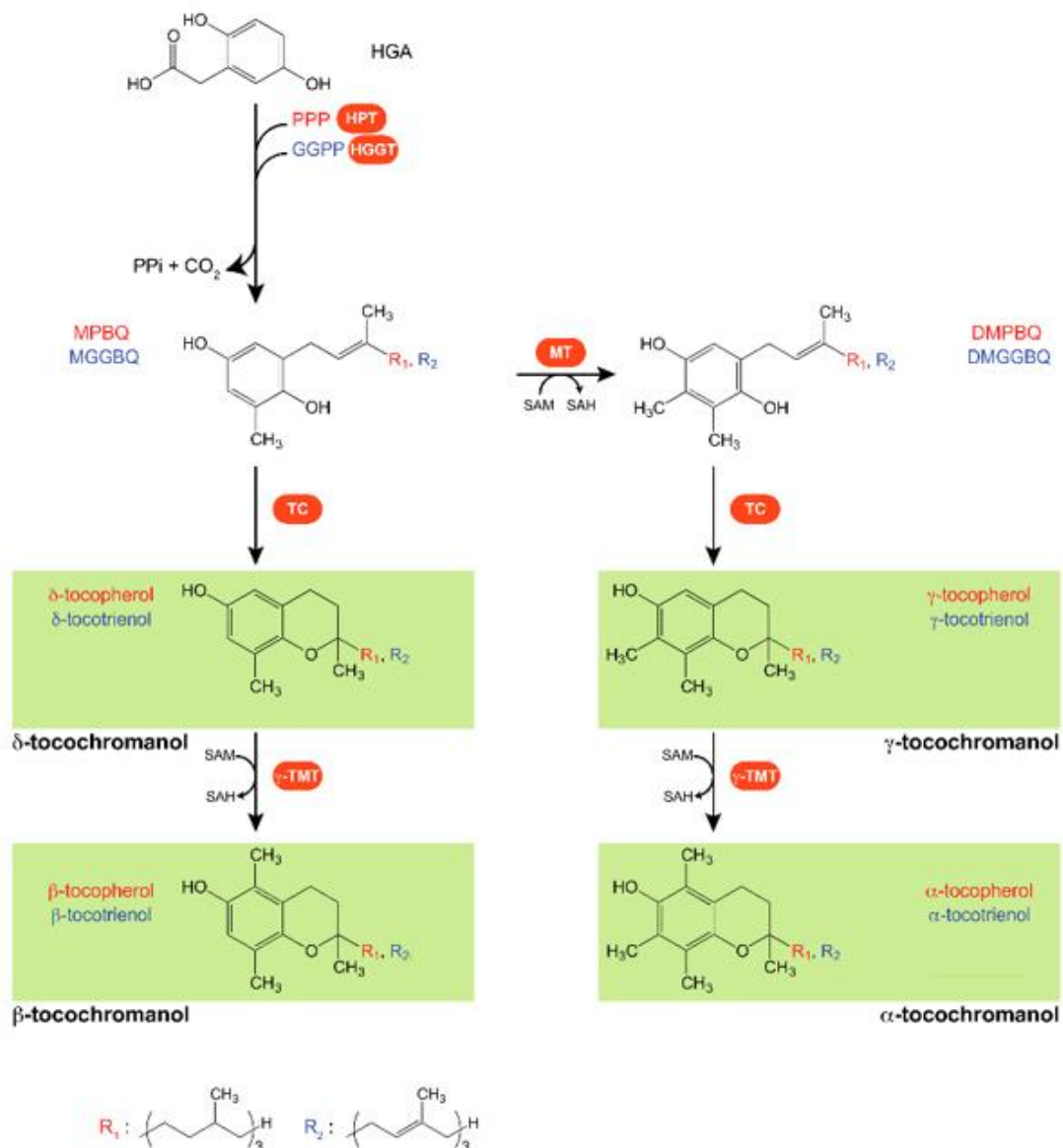


Figure 4. Tocochromanol biosynthetic pathways in plants. Tocochromanol and prenyl benzoquinol chemical structures and biosynthetic enzymes (highlighted in orange). Tocochromanol and prenyl benzoquinol names are color-coded to distinguish each tocochromanol pathway: red for the tocopherol pathway and blue for the tocotrienol pathway (edited by Mène-Saffrané 2018). HGA homogentisate, HGGT homogentisate geranylgeranyltransferase (EC 2.5.1.116), HPT homogentisate phytyltransferase (EC 2.5.1.115), GGPP geranylgeranyl pyrophosphate, γ -TMT γ -tocopherol methyltransferase (EC 2.1.1.95), MT methyltransferase (EC 2.1.1.295), PPI pyrophosphate, SAM S-adenosyl-l-methionine; SAH S-adenosyl-l-homocysteine, TC tocopherol cyclase (EC 5.5.1.24), THGGPP tetrahydrogeranylgeranyl pyrophosphate.

3.1.2.2 MEP pathway

The essential pathway for the synthesis of plastidic terpenoids (including plant tocochromanols) is the MEP route (also referred to as non-mevalonate pathway), which probably developed in cyanobacteria. The genes encoding the enzymes necessary for the course of this pathway were integrated into the nuclei of plant organisms by endosymbiosis of

a precursor of monoterpenes, FDP of sesquiterpenes and triterpenes, and GGDP is used for the synthesis of 20- to 40-carbon structures, including the isoprenoid chain of tocochromanols (Styrczewska et al. 2013; Chang et al. 2021). GGDP is the precursor for the synthesis of tocotrienols. To form tocopherols, GGDP must be first converted to PDP by the enzyme GGDP reductase, which reduces three of the four double bonds in the GGDP molecule to form PDP (DellaPenna & Pogson 2006).

3.1.2.3 *Phytol recycling pathway*

This pathway was discovered almost 15 years ago due to the identification and characterization of the gene (*vte5-1*) that determines vitamin E synthesis in *Arabidopsis thaliana*. Although the tocochromanol biosynthetic pathway in photosynthetic organisms had been proposed from radio traces studies for over 30 years, it is only during the past decade that the enzymes and genes of the pathway were isolated. During the past decade, several groups around the globe focused on the molecular, biochemical, and genetic dissection of tocochromanol synthesis in two complementary model systems, *Synechocystis* sp. PCC6803 and *Arabidopsis*, with the result that all core tocochromanol pathway enzymes have now been cloned and studied in detail (DellaPenna 2005; Muñoz & Munné-Bosch 2019).

The alternative metabolic route, allowing phytol recycling, was recently completely described in *Arabidopsis* with the characterization of the phytyl-phosphate kinase *vte6*, which catalyzes the second step of this pathway, the phytol phosphorylation (Figure 6). Chlorophyll degradation occurs not only in plant responses to environmental stresses but also during a few developmental processes, such as leaf senescence or seed maturation, as well as during the ripening of several fruits and the senescence of some flowers. Many studies (Muzzalupo 2011; Obranovic et al. 2015; Muñoz et al. 2018; Gramegna et al. 2019) have shown a strong correlation between chlorophyll loss and tocopherol production through these physiological processes (Muñoz & Munné-Bosch 2019).

3.1.2.4 *Accumulation in plant tissues*

Tocochromanols are synthesized only by photosynthetic organisms such as plants, algae and some cyanobacteria (Mène-Saffrané & DellaPenna 2009). Synthesis has not been documented in any other organisms, and therefore plant products provide the only natural dietary sources. The conclusions of the early studies, by Visser et al. 1991 and by Gibson et al. 1993, on α -T showed it is formed in both photosynthetic and nonphotosynthetic tissues of higher plants and is concentrated in the chloroplasts. Other tocopherols and tocotrienols are in higher concentrations in nonphotosynthetic tissues. Leaves of *Calendula officinalis* contain α -T only in chloroplasts, whereas γ -T and δ -T were found in chloroplasts, mitochondria, and microsomes. No tocopherols were present in Golgi apparatus membranes and cytosol (Eitenmiller & Lee 2004). The primary site of accumulation of tocochromanols is plastids, where their biosynthesis takes place, but their occurrence has also been reported in vacuoles and cell nuclei of barley leaves or in mitochondria of green algae. In cereals, they may also be present in the lipid bodies of the cell cytosol, where large amounts of storage lipids are

accumulated and tocopherols are involved in their protection against oxidative damage (Falk & Munné-Bosch 2010; Mène-Saffrané & DellaPenna 2010).

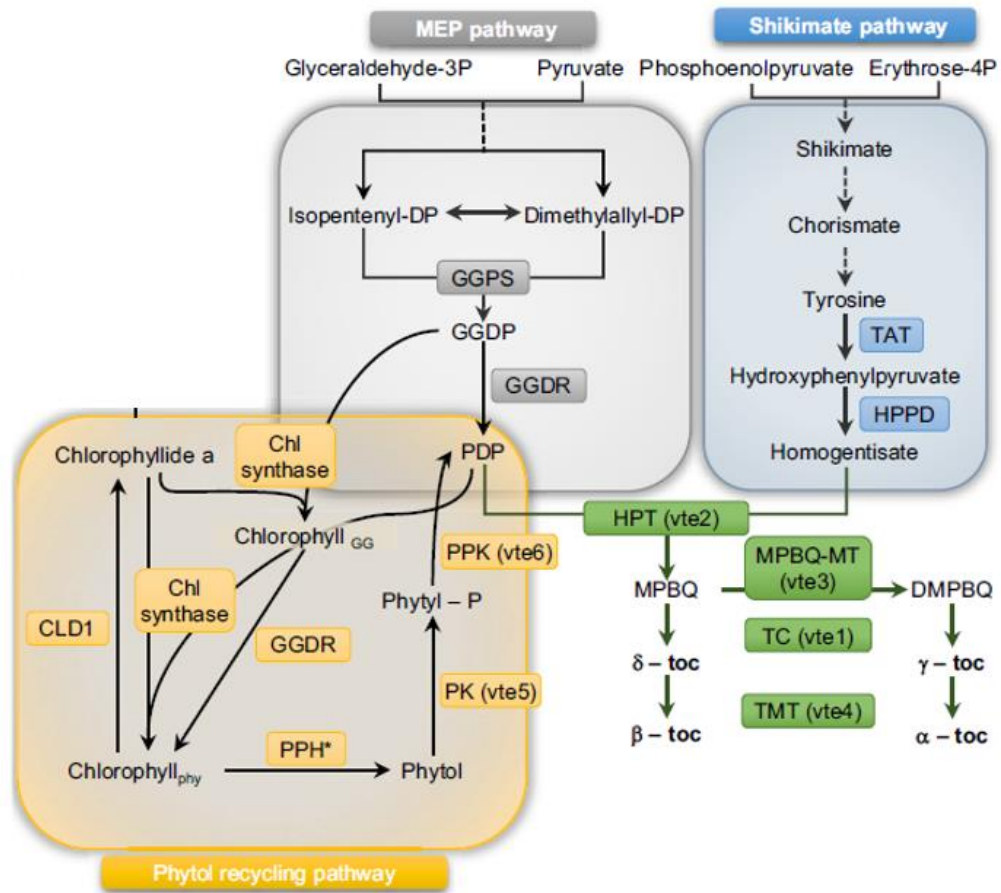


Figure 6. Linking tocopherol biosynthesis with chlorophyll degradation in plants

(edited by Muñoz & Munné-Bosch 2019). PPH pheophytin pheophorbide hydrolase (EC 3.1.1.14), PK phytyl kinase (EC 2.7.1.182), PPK phytyl phosphate kinase (EC 2.7.4.-), CLD1 chlorophyll dephytylase (EC 3.1.3.26), DMPBQ dimethylphytylbenzoquinol, GGDR geranylgeranyl diphosphate reductase (EC 1.3.1.83), GGPS geranylgeranyl diphosphate synthase (EC 2.5.1.29), HPPD hydroxyphenylpyruvate dioxygenase (EC 1.13.11.27), HPT homogentisate phytyltransferase (EC 2.5.1.115), MEP methylerythritol phosphate, MPBQ methylphytylbenzoquinol, MPBQ-MT MPBQ methyltransferase (EC 2.1.1.295), PDP phytyl diphosphate, TAT tyrosine aminotransferase, TC tocopherol cyclase (EC 5.5.1.24), TMT tocopherol methyltransferase (EC 2.1.1.95).

Tocopherols were detected in different plant tissues including leaves, seeds, roots, tubers, fruits, stems, hypocotyls, and cotyledons of higher plants but tocopherol content and composition is very heterogeneous. The tocol contents reported range from 150 ng/g fresh weight (FW) in potato tubers up to several mg/g FW in oil palm leaflets. Leaves generally accumulate ten to twenty times less tocopherols than seeds. The tocol content of leaves has been measured in many plant species and ranges from 10 to 50 µg/g FW with the prevailing form being α-T, whereas seeds contain 300 to 2000 mg/kg, with α-T often representing only a minor component. Accumulation of α-T has also been observed in nonphotosynthetic cell culture systems such as safflower, indicating that the capacity for tocopherol biosynthesis is not dependent on photosynthesis (DellaPenna 2005; Preedy & Watson 2007). In the model plant *Arabidopsis*, the

spectrum in leaf tissue is composed of 90% α -T and 10% γ -T, whereas in seeds, γ -T is the major form (95%), with minor amounts of δ -T (4%) and α -T (1%). Tocotrienols appear to be less widespread in the plant kingdom, because of their rare presence in photosynthetic tissues. They are often present in plants as esters and tocopherols exist only in their free forms (Preedy & Watson 2007; Mène-Saffrané & DellaPenna 2010; Combs & McClung 2016).

In summary, the content and abundance of each form varies widely, but in photosynthetic tissues α -T is the predominant form, whereas tocotrienols are often more abundant in the seeds of monocotyledonous plants. In cereal grains, tocopherols are mainly found in the germ and pericarp, while tocotrienols are primarily located in the aleurone layer and endosperm (Falk & Munné-Bosch 2010; Mène-Saffrané & DellaPenna 2010).

3.1.3 Significance for plants

Tocochromanols are part of a complex system of protective mechanisms that together protect light-harvesting tissues from photooxidative damage. They are particularly important during intense light stress or in the absence or failure of other protective mechanisms (Falk & Munné-Bosch 2010). Tocochromanols, especially α -T, effectively neutralize singlet oxygen ($^1\text{O}_2$) molecules through two different mechanisms. The first method (physical) involves resonance transfer and subsequent thermal dissipation of excess energy, whereby a single molecule of α -T can deactivate up to 120 $^1\text{O}_2$ molecules before it is completely degraded. The second method (chemical) is based on a direct reaction leading to the breaking/opening of the chromanol cycle to form tocopheryl quinones, in which one molecule of tocopherol is consumed to neutralize one molecule of $^1\text{O}_2$. However, quinones can be regenerated to the starting tocochromanol molecules through NADPH-dependent quinone oxidoreductase, under the simultaneous action of ascorbate, glutathione, and tocopherol cyclase (Muñoz & Munné-Bosch 2019).

By participating in the stabilization of thylakoid membrane structures and in the regulation of the redox state in chloroplasts, tocochromanols make a major contribution to the protection of photosystems from the harmful effects of $^1\text{O}_2$. Some forms of tocochromanols may also be involved in plant physiological processes such as seed germination, flowering, leaf senescence, or responses to various abiotic stress factors. Tocopherols play a key role in the regulation of lipid peroxidation during germination and early plant growth. Tocopherol deficiency can also cause a reduction in the transport and distribution of carbohydrates in plants, the excessive accumulation of which can lead to growth defects and premature senescence, but also promote the formation of anthocyanins, which can partially compensate for the lack of tocopherols and protect plant tissues from photooxidation (Falk & Munné-Bosch 2010).

3.1.4 Significance in human diet

Bioavailability, which is determined by the efficiency of an absorption from the digestive tract into the bloodstream, is a prerequisite for the manifestation of the physiological action of tocols in the body (Bohn et al. 2015; Umbreen et al. 2021). Due to similar physicochemical properties, the metabolism of tocochromanols in the gastrointestinal tract is analogous to the process undergone by other lipophilic substances (Combs & McClung 2016).

The presence of lipids in the intestinal lumen and secretion of bile acids ensuring micelle formation is essential for the absorption of tocopherols into intestinal cells, which is facilitated by various transport molecules. From enterocytes, tocopherols in the form of chylomicrons are transported to the liver, where they are hydrolytically released into the cytosol of liver cells. The free tocopherols may be subsequently degraded in the liver and incorporated into very low-density lipoprotein particles. Secretion of tocopherols from the liver and their incorporation into plasma lipoproteins occurs via the α -T transfer protein (α -TTP), which has different affinities for different forms depending on their structure. The binding affinity of α -TTP is determined by the arrangement of the phytyl side chain, the presence of a hydroxyl group, and the degree of methylation of the chromanol ring, with the methyl group at the C5 position being the principal one. The tocopherols have similar lipid-soluble antioxidant activities *in vitro* but the *in vivo* vitamin E activity of individual tocopherols differ by orders of magnitude, with α -T having the highest vitamin E activity. α -T best matches these characteristics, which is the reason for its preferential distribution over other forms that have relatively lower affinity for α -TTP (α -T, 100%; β -T, 38%; γ -T, 9%; δ -T, 2%; α -T3, 12%). Due to the binding to α -TTP, the molecules are protected from hydroxylation (DellaPenna 2005; Combs & McClung 2016; Schmölz et al. 2016; Arai & Kino 2021). In the blood plasma, α -T and other tocopherols are also found as part of other lipoprotein particles, between which they are easily transferred by the phospholipid transport protein (PLTP). Through PLTP α -T is also transferred to red blood cells, which contain up to 25% of its total amount in blood plasma, and also to the cells of the central nervous system and adipose tissue, which is the main site of vitamin E deposition in the human body (Combs & McClung 2016; Schmölz et al. 2016).

The function of vitamin E was attributed solely to its antioxidant activity until 1988, when an alternative molecular mechanism was proposed to regulate the activity of protein kinase C (Mahoney & Azzi 1988). The ability to inhibit this enzyme is the basic principle of vitamin E's protective action against the development of inflammation, various cardiovascular complications or platelet aggregation. Vitamin E may also be involved in the regulation of gene expression and the maintenance of physiological functions of the immune system, such as the stimulation of phagocytic function, which is important in defending the body against infectious diseases. The originally recognized effect of vitamin E on fertility in rats has not been confirmed in humans, instead extremely low levels of this substance in humans have been linked to a disease called ataxia with isolated vitamin E deficiency (AVED), a rare disorder caused by mutations in the gene encoding α -TTP, which is required for vitamin E distribution to peripheral tissues and its retention. Typical symptoms of this disease are mainly disturbances of the body's immune response and peripheral nerves manifested by numbness, tingling or pain in parts of the limbs, impaired coordination of movement and degenerative changes in the spine. AVED is the only known vitamin E deficiency disease that can be prevented by α -T supplementation. The ability to prevent and treat AVED has not yet been demonstrated in other forms of tocopherols, which is why these forms cannot be called vitamers or forms of vitamin E (Khadangi & Azzi 2019; Szewczyk et al. 2021).

3.1.4.1 Antioxidant activity of tocochromanols

Antioxidants are substances that can prevent or slow down oxidative damage to cells caused by physiological oxidants with significant positive reducing potential, such as reactive oxygen species (ROS) and free radicals (Apak et al. 2016; Pérez-Gálvez et al. 2020). ROS are part of the primary immune defense of phagocytic cells against foreign substances or microorganisms and are also involved in cell signaling (Gulcin 2020). Free radicals are generally highly reactive, unstable molecules that have at least one unpaired electron in their electron shell and are capable of independent existence, at least for a short time (Pláteník 2009). In an attempt to achieve stability, they may transfer or withdraw an electron to another molecule, from which a new free radical is formed. In biological systems, free radicals can exist in various forms, the most important of which are ROS, which can also cause the most serious tissue damage, so-called oxidative damage. The level of free radicals in the body is regulated by the activity of antioxidant enzymes, but also by non-enzymatic substrates with antioxidant properties. However, if the balance of oxidative and antioxidant factors in the body is disturbed, the antioxidant defenses may be overwhelmed, promoting a condition known as oxidative stress. One of the most studied consequences of ROS exposure is the chain oxidation of unsaturated fatty acids, which leads to the formation of highly reactive peroxy radicals that alter the structure and biological functions of the affected molecules, such as cell membrane lipids (Murray et al. 2012).

The antioxidant properties of tocochromanols are mainly due to the ability of their heterocyclic system to donate phenolic hydrogen to free radicals. The most efficient hydrogen donors are the α -, then β -, γ - and finally δ -forms of tocochromanols (Falk & Munné-Bosch 2010). The main principle of the antioxidant action of tocopherols and tocotrienols is to break the radical chain reaction by quenching peroxy radicals, whose reaction rate with tocopherols is many times higher than that with unsaturated fatty acids. The transfer of a hydrogen proton from the phenol group of tocochromanols to the peroxy radical results in the formation of a hydroperoxide and a chromanoxyl radical, which is more stable than the original peroxy due to the delocalization of the unpaired electron in the benzene ring. Chromanoxyl radicals, which are referred to as α -tocopheroxyl radicals in the case of the antioxidant action of α -T, can be regenerated via the ascorbate-glutathione cycle, whose activity is stimulated by low levels of α -T. Chromanoxyl radicals can also react with another peroxy radical molecule to form non-radical oxidation products of tocochromanols, most commonly quinones or epoxides, thereby terminating (Falk & Munné-Bosch 2010; Muñoz & Munné-Bosch 2019).

Thanks to their amphipathic molecular structure, tocochromanols play an important role in stabilizing biological membranes, where they protect lipid components from peroxidation. Tocochromanols are anchored in cell membranes by a polyprenyl chain, with the chromanol moiety located at the interface between the membrane and the surrounding polar environment. Due to the presence of an unsaturated side chain, tocotrienol molecules are more efficiently distributed in cell membranes, which is probably the reason for their proven better stabilizing effects compared to tocopherols (Atkinson et al. 2008). The antioxidant action is supported by the ability of movement of tocochromanol molecules in membrane structures (flip-flop movement), which makes the hydroxyl groups providing the hydrogen proton more accessible

and represents an effective means of scavenging peroxy radicals (Muñoz & Munné-Bosch 2019).

3.1.5 Tocochromanols in the human diet

Vitamin E and other antioxidant components (e.g. vitamin C, carotenoids, selenium or flavonoids) have been put to the front of the medical and nutritional sciences thanks to significant advances in the understanding of the relationship of oxidative stress to the onset and/or control of many chronic diseases. Of many such dietary components, vitamin E has received the most of interest because of its availability, strong marketing potential, overall health impact, and central role in preventing oxidation at the cellular level (Eitenmiller & Lee 2004). Moreover, when used as a food additive, it inhibits the oxidation of foods to extend their shelf life and overall quality (Shahidi et al. 2021).

Since all natural forms of vitamin E are of plant origin, vegetable oils are the most important and concentrated dietary source of vitamin E for humans. The second most concentrated source of vitamin E next to the plant oils are nuts and seeds. Additionally, some, such as pistachios, macadamia, and cashews, contain tocotrienols, adding diversity to the profile of tocopherols and tocotrienols in the diet. Almonds, compared to other nuts, show the highest α -T level with small quantities of β -, γ -, and δ -T. Interestingly, even though the tocochromanol content of peanuts rates below some other nuts and seeds, peanut butter alone accounts for 2.3% of total vitamin E available in the U.S. diet. Another relevant source of vitamin E in the human diet is cereals, which are distinguished by the presence of tocotrienols (Eitenmiller & Lee 2004). Consumption of cereal-based products can meet the intake recommendations for vitamin E without increasing the amount of oils and fats in the diet (Tiwari & Cummins 2009). The vitamin E content of baked grain products originates not only from the grain fraction (flour, bran) but also from the fat ingredients, such as shortening, margarine, or butter. Variability of the vitamin E content in baked cereal products is due to the processing technology and storage, but also to the formulation, with, for example the vitamin E content of margarines varies greatly, depending upon types of oils used in their preparation (Eitenmiller & Lee 2004).

Vitamin E is also important in terms of oxidative stability of foods, as particularly for edible oils, the addition of vitamin E was found to enhance their oxidative stability when submitted to heating, a common processing step upon cooking (Shahidi et al. 2021). Alizadeh et al. (2019) observed that the addition of tocopherol to mayonnaise slowed the primary oxidation stage more efficiently than tertiary-butylhydroquinone (TBHQ), a common synthetic antioxidant.

The demand for vitamin E products has rapidly increased over the past two decades and therefore, in addition to natural sources, synthetically produced tocochromanols are also widely used (Shahidi et al. 2021). The methods of synthesis currently used for the commercial production of vitamin E are based on successful synthesis reactions. Synthesis follows formation of the chromanol ring by a Friedl-Crafts alkylation reaction that attaches the alkyl side chain of phytol, isophytol, or phytyl halides onto the benzene ring of trimethylhydroquinone (TMHQ) resulting in a ring closure. Subsequent condensation of TMHQ with isophytol results in the formation of all-rac- α -T. Approximately 80% of the world production (> 25,000 tonnes) of vitamin E is produced by this synthesis route. Synthesis of β -,

γ -, and δ -T can be accomplished by using the same reaction scheme by altering the placement and number of methyl groups on the hydroquinone ring. A large percentage of synthetic all-rac- α -T is esterified into all-rac- α -tocopheryl acetate with conversion of smaller quantities into succinate and nicotine esters. It was reported that 71% of the world's production of all-rac- α -T is utilized by the feed industry, 24% by the pharmaceutical industry, 3% in cosmetics manufacture, and only 2% in human food production (Eitenmiller & Lee 2004). The use of vitamin E as a dietary supplement and the health claims associated with it are restricted. European and Canadian agencies prohibit any claims that vitamin E intake cures diseases. The maximum daily intake of vitamin E for adults varies from 500 mg (Chile) to 1 000 mg (Argentina, Brazil, and Canada). In commercial supplements, vitamin E is used in its esterified form (α -tocopheryl acetate). Although this form is less susceptible to oxidative degradation, the real concentration of vitamin E in supplements decreases with time and its stability is influenced by packaging and matrix (tablet, suspension, gel, etc.) characteristics (Shahidi et al. 2021).

Food, feed, pharmaceutical, and cosmetic industries along with market demand has increased in the number of available product types, however, the oxidative stability of vitamin E products is required for all applications. Commercial forms include the following categories: pure standards, oils and concentrates, dry granula powders, water-dispersible free-flowing powders, and gelatin microcapsules. Technology to manufacture products for specific applications is sophisticated, including microencapsulation and enrobing technologies. The use of microencapsulation or coatings to protect tocopherols and tocotrienols by forming oxygen barriers allows wider use of non-esterified forms (Eitenmiller & Lee 2004).

The European Food Safety Authority Panel on Food Additives (EFSA) concluded that the use of tocopherols as food additives does not represent any safety concern (EFSA ANS Panel 2015). Similarly, the U.S. Food and Drug Administration (FDA 2023) classified the use of tocopherols as food additives as "Generally Recognized as Safe" (GRAS). Updated in 2019, the Codex Alimentarius provides a maximum level of tocopherols that can be added to food to act as additive. These levels vary greatly depending on the food type; from 5 mg/kg for alcoholic beverages (like beer and wine), 200 mg/kg for breakfast cereals, cakes, cookies, cream analogues, dried fruit and much more, up to even 5000 mg/kg for edible casings and flours (GSFA 2023). Widely regarded as safe, tocopherols represent a natural alternative to lipid-soluble synthetic antioxidants in the food industry (Shahidi et al. 2021).

3.2 Plant oils

Oilseeds are an important group of crops whose oil can be used for human consumption. They are grown all over the world in a variety of agroclimatic conditions and are a vital commodity in the trade and business of many economies. Their increasing production is mainly due to the growing demand for oilseed products and is made possible mainly by increasing the area under cultivation and also by breeding high-yielding varieties (Sharma et al. 2012). Oilseeds are particularly important in the food industry, where they are used to produce vegetable oils or for direct consumption. They are also used in livestock nutrition, mainly in the form of cake, or for the production of biofuels and (Hrtúsová 2021). Of the total production of oils and fats, about 80% is used for food purposes, 6% is used in animal feed, and the remaining 14% provides the basis of the oleochemical industry (Gunstone 2002).

Vegetable oils are a group of fats that are derived from some seeds, nuts, cereal grains, and fruits. Not all of vegetable oils are produced in commercial quantities, and of those that are, not all are considered edible as in the sense of being a typical dietary component (Hammond 2003). The most widely used oilseeds in Europe are rapeseed, mustard, poppy, and sunflower, and in the other parts of the world, sunflower, soybeans, peanuts, and palm trees (Hrtúsová 2021). Among these, coconut, cottonseed, olive, palm, peanut, rapeseed/canola, soybean, and sunflower oils are the most common vegetable oils. In 2019/2020, palm oil was the most produced vegetable oil (73 million metric tonnes) worldwide, followed by soybean (58 million metric tonnes) and rapeseed/canola (28 million metric tonnes) oils (Shahidi et al. 2021). Most edible plant oils are obtained from beans or seeds, which generally provide two valuable commodities – an oil and a protein-rich meal (Gunstone 2002).

Oilseeds play an important role in the human diet mainly because of their fat content, but also for their protein, and saccharide content. Many oilseeds are currently being used as functional foods, primarily because oils derived from the seeds of field crops are often high in unsaturated fatty acids (Lampi et al. 2002; Bozan & Temelli 2008). Furthermore, edible oils are the major source of dietary tocopherols (Shahidi et al. 2021).

Tocopherols are present in various plant tissues in many species, while the distribution of tocotrienols seems to be less widespread in the plant kingdom. The presence of tocotrienols in nature is often associated with monocotyledonous species, such as oil palm (*Elaeis guineensis*, Aracaceae family) and cereal grasses (*Avena sativa*, *Triticum spp.*, *Secale cereale*, *Hordeum vulgare*, *Oryza sativa*, *Zea mays*, Poaceae family). In the case of dicotyledonous species in which tocotrienols are present, no taxonomic relation has been found (Siger & Górnaś 2023). Tocotrienols are natural compounds found in a number of vegetable oils, wheat germ, barley, and certain types of nuts and grains. Particularly palm oil and rice bran oil contain higher amounts of tocotrienols (Table 3). Palm fruit is the richest source of tocotrienols among all vegetable oils. Tocotrienols make up almost 70% of vitamin E in palm oil, with the remaining 30% being tocopherols. Other sources of tocotrienols include grape seed oil, oats, hazelnuts, maize, olive oil, buckthorn berry, rye, flax seed oil, poppy seed oil, and sunflower oil (Ahsan et al. 2015).

3.2.1 Seed extraction

Oilseeds have been cultivated since ancient times. Rapeseed and sesame are described in Indian Sanskrit writings dating back to 2000 BC. Historically, extraction of oil seems to have been a batch process. Seeds were stored in bags or boxes were pressed to extract the oil. The separated oil, after purification, was used for both food and non-food purposes. The resulting cakes were used as animal feed or thrown away in the fields to help improve soil fertility. Through the time, humans discovered the uses of oil and other oilseed products for various other food and non-food purposes (Nagaraj 2009).

Vegetable oils can be extracted from oilseeds by various pressing systems, solvent extraction or a combination of both methods. Seeds with high oil content are pre-pressed and then solvent extracted, or direct solvent extraction can be carried out for seeds with lower oil content. The extraction technology can be chosen depending on production costs, material properties, availability, usage goal of the cake, and environmental factors. Depending on the

structure and composition of the oilseeds, some fractions of the oil may remain in the meal or cake. This should be taken into account when comparing the oil yield and composition of the meal in press and cold press. To increase the oil yield from cold pressing, some pretreatments such as enzyme application, microwave treatment, steaming and roasting could be applied to the seeds before pressing (Ramadan 2020).

Extraction is usually followed by the refining process that is applied to remove undesirable compounds (phospholipids, monoacylglycerols, diacylglycerols, free acids, pigments, oxidized materials, flavour components, trace metals, and sulfur compounds) but may also remove valuable minor components which are antioxidants and vitamins such as tocopherols. These processes must therefore be designed to maximize the first and to minimize the second. Some of the useful minor components can be recovered from side streams to give valuable products such as phospholipids, tocopherols, carotenes, and sterols. Some oils, such as virgin olive oil, are used without further treatment but most are refined in some measure before use (Gunstone 2002). It has been noted in the literature (Koski et al. 2002; Azadmard-Damirchi et al. 2010; Kreivaitis et al. 2013) that solvents help to leach the tocopherols from the seeds into the oil, and therefore cold pressed oils exhibit lower tocopherol concentrations and typically lower oxidative stability than solvent extracted oils (Flakelar et al. 2015).

Vegetable oils are usually classified into different grades according to their values of quality and sanitation indexes (e.g. acid values, peroxide value, iodine value, etc.). The grade of oil is closely related to the degree of oil refinement. The refining degree of first-grade oil is higher than that of fourth-grade oil, which may imply that the tocopherols loss of the first-grade oil is higher than that of the fourth-grade oil. However, the specific correspondence between the oil grade and tocopherols content is rarely reported (Wen et al. 2020)

The pressing process of cold pressed oil (CPO) does not require the use of chemical solvents or high energy expenditure. Only centrifugation or filtration is necessary to obtain high-quality CPO. These oils are not refined, thus they contain many substances accompanying lipids. A producer could select the production type based upon the aim of production, uses of oil and cake, and the amount of processed seeds. CPO usually contain unique phytochemicals with health-promoting traits (Siger et al. 2015; Ramadan 2020).

3.2.1.1 Oilseed press cake

Oilseed press cake and meal are main co-products of the extraction of oil from oilseeds. The term “cake” refers to the co-product coming directly from the expeller, whereas the term “meal” is used when it has undergone an additional, usually organic solvent-based de-oiling process. Nevertheless, there is certain ambiguity in the use of both terms (Arrutia et al. 2020). Both the oilseed press cake and the meal are composed mainly of protein, fibre (lignocellulosic materials) and minerals (Lomascolo et al. 2012). Depending on the type of meal, it contains up to 50% of proteins on a dry basis and about 20% of carbohydrates including soluble sugars (Gerzhova et al. 2016). Oilseed press cakes collected after cold pressing are usually used for animal feeding. However, they might also be a potential source of biologically active substances beneficial to human health. After oil extraction, more polar antioxidants remain in the oilseed press cake and are not significantly destructed during the oilseed processing. Content of antioxidant compounds in the form of simple phenols or flavonoids in oilseed press cakes

depends on the type of seeds, location of cultivation, climate, harvest time, as well as solvents and conditions used in an extraction procedure. Antioxidant compounds (e.g. polyphenols) are also present in defatted oilseeds in free and/or bound forms. A minor part of the oilseed press cake contains lignans and their degradation products (Chmelová et al. 2018).

Oilseed press cake and meal could represent a suitable alternative protein source to cover the increasing world demand for protein foods, which is expected to double by 2050. Since 2010 there has been a swift growth in the use of plant-based protein sources as the need for renewable and sustainable sources of proteins is growing. Diets containing more plant protein are increasing due to several reasons, such as the negative environmental impacts of animal protein production, the increasing vegetarianism and veganism trends, and inadequate consumer acceptance of food grade insects (Pojić et al. 2018).

3.2.2 Chemical composition

Edible oils are mainly composed of fatty acids (FAs) in the form of triacylglycerols (TAGs), which represent the source of energy for the human body. Additionally, edible oils are sources of minor compounds such as tocopherols, tocotrienols, carotenoids, and phytosterols (Shahidi & Costa de Camargo 2016).

Plant-based oils as used in foods, are comprised of a complex mixture of TAGs (usually > 95%) with some minor amounts of diacylglycerols (usually < 5%). Other minor components are tocopherols/tocotrienols (up to 900 mg/kg) and phytosterol and their esters (up to 1%). The vegetable oils might be characterized using chromatographic analysis by determining its TAG composition, together with the composition of FAs and the minor components (Table 1) (Hammond 2003).

3.2.2.1 Fatty acids

Lipids are composed of FAs classified mostly according to the presence or absence of double bonds as saturated (SFAs – without double bonds), monounsaturated (MUFAs – with one double bond) and polyunsaturated fatty acids (PUFAs – with more than two double bonds). Furthermore, *cis* and *trans* isomers are distinguished based on the configuration of the double bonds, and PUFAs are classified as n-3 or n-6 depending on the position of the first double bond from the FA methyl-end. The *cis*- configuration is found in most naturally occurring unsaturated FAs, whereas the *trans*- configuration is the result of technology processing, such as hydrogenation. The most important PUFAs are α -linolenic (ALA, 18:3, n-3) and linoleic acid (LA, 18:2, n-6) from which other important PUFAs are derived (Orsavova et al. 2015). The human body cannot synthesize n-3 and n-6 PUFAs because of the absence of appropriate enzymes. These acids are therefore referred to as essential fatty acids (EFAs) and must be obtained from the diet, particularly by the consumption of fish and fish oils. PUFAs are considered to be necessary components of cell membranes, they play a key role in many cell processes and have an anti-inflammatory effect because of decreasing the production of cytokines and adhesion molecules (Hlinková et al. 2019). Furthermore there is the potential of reducing the risk of serious diseases, especially cardiovascular diseases, cancer osteoporosis, diabetes and other health promotion activities. Following from their complex influence on concentrations of lipoproteins, fluidity of biological membranes, function of membraned

enzymes and receptors, modulation of eicosanoids production, blood pressure regulation, and finally, on the metabolism of minerals (Orsavova et al. 2015).

LA is generally the most abundant PUFA in the human diet. In addition to being a source of energy for the human body, like all other FAs, it is also a precursor of arachidonic acid (20:4, n-6), which can subsequently be converted into eicosanoids. A certain level of these compounds in the body is necessary for normal metabolic function of cells and tissues. However, if eicosanoids are produced in excessive amounts over a long period of time, they can contribute to the development of certain chronic diseases (inflammation, cancer) (Whelan & Fritsche 2013). ALA is important in the human diet mainly because it is a precursor of eicosapentaenoic acid (EPA, 20:5, n-3) and docosahexaenoic acid (DHA, 22:6, n-3) that are essential for proper tissue function in the human body (Burdge & Calder 2006). Most oils are characteristic of having a wide spectrum of FAs depending on the variety, growing conditions, and maturity of the seed (Table 1) (McCance & Widdowson 2002).

However, the intake of medium-chain FAs, which are present in palm kernel and coconut oil, increases the level of total cholesterol leading, to atherosclerosis, and increases the risk of cardiovascular disease. A similar effect is caused by the intake of palmitic acid-rich fats such as palm oil/fat. Therefore, the intake of these FAs should be reduced in the diet. Stearic acid is the only SFA that does not affect the level of cholesterol in the blood and, therefore, does not affect the onset cardiovascular disease. There are not many stearic acid-rich fats, and they are often very expensive, such as cocoa butter or the stearin fraction of shea butter (Romanić 2020).

Table 1. Values of fatty acids and of vitamin E in selected plant oils per 100 g edible portion (edited by McCance & Widdowson 2002; edited by Özcan & Atalay 2006).

Oils	Fatty acids [g/100g]		
	Saturated	Monounsaturated	Polyunsaturated
Coconut	86.5	6.0	1.5
Corn	14.4	29.9	51.3
Olive	14.3	73.0	8.2
Palm	47.8	37.1	10.4
Peanut	20.0	44.4	31.0
Poppy	17,9	19,61	60,5
Rapeseed	6.6	59.3	29.3
Safflower	9.7	12.0	74.0
Sesame	14.6	37.5	43.4
Soya	15.6	21.3	58.8
Sunflower	12.0	20.5	63.3
Walnut	9.1	16.5	69.9
Wheatgerm	18.6	16.6	60.4

Vegetable oils are typically liquid at room temperature. However, oils rich in SFAs, including coconut, cottonseed, and palm oil, are often more viscous or semi-solid at room temperature (Colón 2023). Oils generally act as medium of heat transmission in frying, serve as a lubricant in various formulations, but also affect the stability of food emulsion products

and gives characteristic flavours to food and a feeling of satiety. They can carry fat-soluble vitamins and supply FAs including EFAs that poses health-benefiting roles (Figure 7) (Bhattacharya 2023). Tocotrienols might improve the oxidative stability of edible oils. For example, the good oxidative stability of palm oil during frying processes to its high tocotrienol and low LA contents (Shahidi et al. 2021).

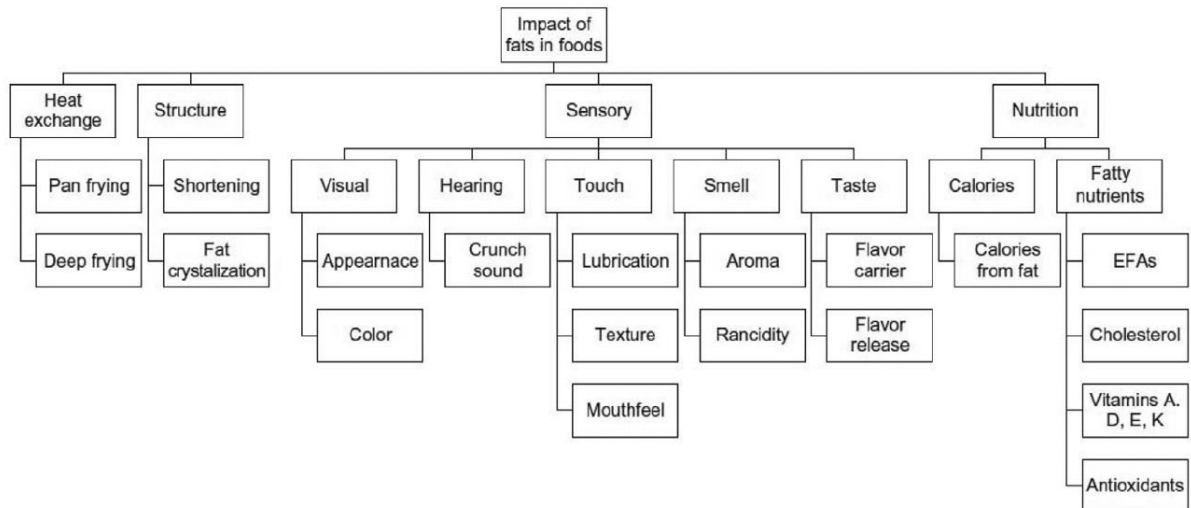


Figure 7. Key functions of fats in food systems and attributes impacted by fats (Bhattacharya 2023).

FA composition and tocopherols in seed determine the quality of vegetable oil and their content changes depending on genotypes and some other factors such as environmental conditions, planting and harvesting time etc. (Sharma & Goyal 2015).

3.2.2.2 Tocols

Oil tocopherol concentration presents inter- and intra- species variability. Gunstone et al. (1994) stated the tocopherol content of the different oilseed species varies considerably, ranging from 271 to 2,188 mg/kg of oil, with significant variations occurring also between genotypes of the same crop. Nolasco et al. (2006) reported variation in tocopherol content from 708 to 936 mg/kg of oil for sunflower genotypes grown in a trial including 7 locations. Izquierdo et al. (2011) observed variability in tocopherol concentration in soybean, corn and rapeseed (e.g. from 1,304 to 2,732, from 1,304 to 2,732 and from 520 to 940 mg/kg of oil, respectively) depending on the environmental conditions. The reasons, that cause such variation in antioxidant oil concentration, even within genotype, are not known (Belo et al. 2017).

Figure 8 shows seed oils of crops show considerable variation in the profile of tocopherols contained, with 96% of α -T in sunflower seed oil but only 7% in soybean oil, which in contrast contains high levels of γ -T (70%) and δ -T (22%). In palm seed oil, α -T (30%) and γ -T (40%) are the main tocopherol representatives (Preedy & Watson 2007). Shadidi & De Camargo (2016) says that α -T is the major tocopherol in many edible oils as exemplified by almond, peanut, olive, and sunflower oils. The content of γ -T in some edible oils such as canola, corn, linseed, soybean, and walnut oils are similar or higher than that of α -T. Furthermore, the study of Gliszczynska-Świągło et al. 2007 shows the total tocopherol content

in plant oils ranges from 121 mg/kg in grapeseed oil to 829 mg/kg in corn and soybean oil (Table 2). Besides tocopherols, some common edible oils also contain high levels of tocotrienols. Pokkanta et al. 2019 reported 139 mg/100 g of tocotrienols in rice bran oil, accounting for almost 90% of total tocols, with γ -T3 representing 59% of this total. Palm oil is recognized as a rich source of tocotrienols as well, they make up almost 70% of vitamin E in palm oil, with the remaining 30% being tocopherols (Ahsan et al. 2015; Shahidi et al. 2021).

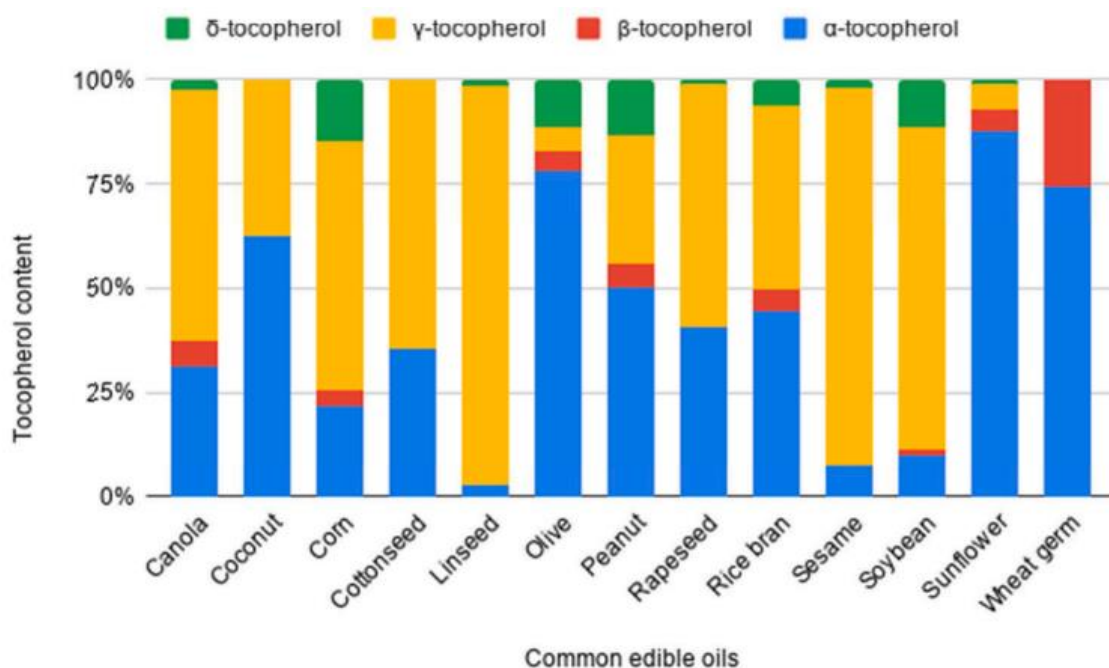


Figure 8. Relative tocopherol composition in selected common edible oils (Shahidi et al. 2021).

Table 2. Tocopherol content of selected plant oils (mg/kg) (edited by Gliszczynska-Świgło et al. 2007).

Oil	Characteristic	α	(β+γ)	δ	Total tocopherol
Corn	Refined	207±11	592±20	30,0±1,0	829±23
Grapeseed	Refined	103±5	15,0±4,0	3,4±1,6	121±6
Linseed	Cold-pressed	-	363±7	5,2±0,8	367±8
Olive	Extra virgin	163±3	12,3±0,4	1,6±0,3	177±3
Peanut	Refined	102±3	112±2	12,0±0,1	226±4
Rapeseed	Refined	178±25	281±13	12,0±2,0	468±28
Rapeseed	Cold-pressed	181±5	244±7	9,3±0,1	434±9
Soybean	Refined	152±1	494±12	182±3	829±12
Sunflower	Refined	575±11	25,2±0,4	8,8±0,4	609±11
Sunflower	Cold-pressed	490±8	30,8±0,5	10,1±0,1	535±8

Table 3. Presence of different tocotrienols in various vegetable oils (Ahsan et al. 2015).

	α -T3 [mg/l]	γ -T3 [mg/l]	δ -T3 [mg/l]	Total tocotrienols [mg/l]
Palm	205	439	94	738
Rice bran	236	349	-	585
Wheat germ	26	-	-	26
Coconut	5	1	19	25
Cocoa	2	0	0	2

3.2.3 Rapeseed oil

Oilseed rape (*Brassica napus*) is a member of the Brassicaceae family, grown as a cold-season annual crop predominantly for the extraction of its oil (Woodfield & Harwood 2017). It has been grown since the 16th century in Europe, but it is only since the 1960s that it has become a major world crop (Robson et al. 2002).

It is the third largest source of plant-derived oil in the world after palm oil and soybean, with approximately 24 million tonnes being produced per year. Production has been steadily rising since the crop entered the food market in the 1970s and is predicted to continue in this upward trend as global oil consumption increases. Oilseed rape is grown predominantly in Western Europe, Canada, China, and India (Woodfield & Harwood 2017).

Oilseed rape is very beneficial in crop rotation that generally represents a key component of successful organic arable systems, as it helps maintain optimal soil parameters (fertility, organic matter, nitrogen levels, and structure). Rotations can be optimized to conserve and recycle nutrients and minimize the use of pesticides, disease, and weed problems. The main benefit which oilseed rape brings to a rotation is its effect on soil structure. Actively growing root systems have the potential to ameliorate subsoil under poor physical conditions by “biological drilling” and tap-rooted species such as oilseed rape are generally considered superior to grasses in their ability to ameliorate poorly structured soils (Robson et al. 2002). In practice, it is used as a cereal sequence breaker. It is a very high quality pre-crop because it leaves a large amount of post-harvest residue. It should be spaced at least 4 years apart in the rotation. The most suitable production area for this crop is the potato-growing area, where average annual temperatures are around 6.5-8.5°C. It needs sufficient moisture especially before sowing and during the period of 4 true leaves, when the generative organs are developing. Soils are ideally loamy, deep, with sufficient nutrients and a pH of 6-6.5 (Hrtúsová 2021).

Brassica napus is a hybrid species resulting from interspecific breeding between *Brassica rapa* and *Brassica oleracea*. Thanks to this hybridization event, oilseed rape is allotetraploid (containing four genomes from two different species). Historically, oilseed rape was high in erucic acid (22:1) (which had poor nutritional properties) and glucosinolates which gave the oil an unpleasant bitter taste, consequently the oil was mainly for industrial usage rather than for human or animal consumption. Therefore, cultivars with low glucosinolates and low erucic acid, with a more palatable taste, were developed through conventional breeding. These varieties were initially produced in Canada with the trade name Canola, which has since

become the common term for these “double-low” cultivars in many English-speaking countries, especially in North America and Australia. In Europe it is still called ‘rapeseed’, and the terms HEAR and LEAR are used for high- and low-erucic acid varieties, respectively. Other cultivars have since been bred with various oil compositions including low-linolenic and high-oleic varieties. Oilseed rape is a highly productive plant with a diverse range of applications in both industrial and consumer markets. There are many breeding programs underway to improve on the quality and quantity of oil produced by oilseed rape (Woodfield & Harwood 2007).

Typically, canola varieties of oilseed rape contain palmitic (4%), stearic (2%), oleic (62%), LA (22%), and ALA (10%) acids. The rapeseed oil comparison of the FA composition of LEAR and HEAR is shown in Table 4 (Woodfield & Harwood 2017).

Table 4. Fatty acid composition of rapeseed oils expressed as percentages (Woodfield & Harwood 2007).

	LEAR	HEAR
Total saturated acids	5.1	5.0
16:0	3.6	4.0
18:0	1.5	1.0
Total monounsaturated acids	63.2	69.9
18:1	61.6	14.8
20:1	1.4	10.0
22:1	0.2	45.1
Total polyunsaturated acids	31.3	23.2
18:2	21.7	14.1
18:3	9.6	9.1

LEAR cultivars (canola) have much lower levels of SFAs than any other commodity oil and have a favourable n-6/n-3 ratio, both of which are considered to be healthy qualities, making oilseed rape popular in the food industry. Rapeseed is put to various culinary uses, for instance in salad oils, frying and cooking oils, spreads, and shortenings. Rapeseed oil has also become more prevalent in the biofuel industry, in heated fuel systems, or the methyl esters are mixed with mineral oil to produce a more sustainable biodiesel. Across the world approximately 60% of rapeseed oil is used for food, 38% for industrial uses, and 3% for feed, however, these proportions vary significantly by region. Although grown predominantly for its oil, the processing of rapeseed produces a high protein content meal as a by-product which is used for animal feed. This rapeseed meal, or oil cake, is also used in certain parts of the world as a fertilizer (Woodfield & Harwood 2007).

Crude rapeseed oil contains high concentrations of α -T and γ -T approximately 270 and 420 mg/kg, respectively, which is comparable to those found in palm and sunflower oils, but considerably higher than olive oils. In rapeseed oil, γ -T is consistently present at higher concentrations than α -T, and also than δ -T, which is usually lowest of all tocopherols. Codex standards (Codex committee on Fats and Oils 2011) define the content of α -T, γ -T, δ -T, and total tocopherols for crude rapeseed oil as 100-386, 189-753, 0-22 and 430-2,630 mg/kg, respectively (Flakelar et al. 2015).

3.2.4 Sunflower oil

Sunflower (*Helianthus annuus*) is a relatively new crop among the world's field crops and is unique in several aspects, including the fact that it has been bred for distinctly different purposes. Among the uses of sunflower are oil production, birdseed uses, and it is used as an ornamental plant for home gardens and a colourful array of sunflowers for the cut-flower industry (Seiler & Gulya 2016). Sunflower was domesticated as a food crop in North America, perhaps as early as 3000 BC. The crop was introduced to Europe in the 1600s and was successfully developed as an oil crop in Russia in the early 1800s. Russian plant breeders were able to increase the oil content in sunflower seed from less than 30% to over 50%, which was the major factor enabling the development of sunflower as an oil crop for the temperate areas of the world (McVetty et al. 2016). Among oilseeds, sunflower generally ranks fifth behind soybeans, rapeseed, cottonseed, and peanuts, with an average annual world production of 21-27 million metric tonnes (Bhattacharya 2023).

Sunflower is drought-resistant crop that is grown worldwide in temperate and subtropical climates. Cereals are suitable pre-crops for sunflower, while root crops are considered unsuitable. Sunflower should be spaced at least 8 years apart in the crop rotation. It can germinate at 4°C, but temperature around 10-12°C is optimal. Sunflowers are a crop of warm temperate regions and are therefore best suited to the maize production area. Manure fertilization is appropriate for this crop as it requires a soil well supplied with nutrients. For a high yield, sulphur and boron should be applied, as well as phosphorus and potassium preferably at autumn preparation, and nitrogen at a rate of 80 kg/ha (Hrtúsová 2021).

Unlike soybean, sunflower is primarily an oil crop, with high protein meal being a by-product. Sunflower oil is retrieved by the mechanical pressing of sunflower seeds. The oil is mainly used for cooking, shortening, and for preparing salad dressings and margarines. Sunflower oil is a health-benefitting oil due to its low content of SFAs, high levels of PUFAs, MUFAs, as well as vitamin E. It has good oxidative stability, and the high-oleic sunflower oil is suitable for industrial frying. Lecithin, wax, and tocopherol are also obtained from sunflower oil (Bhattacharya 2023). Nutritionally, sunflower oil has a greater proportion of unsaturated FAs (oleic, LA, ALA), than many other vegetable oils, which is particularly pronounced in the high oleic content and NuSun varieties (Table 5) (Gulya 2004). Although sunflower oil is considered premium oil, with a correct equilibrium between LA and tocopherols, the benefits of MUFAs to health have encouraged the production of new sunflower oils. Thus, several new variants of sunflower oils have appeared with the aim of catering to the demand for oils richer in oleic acid, such as the high-oleic-acid sunflower oil (HOSO), and with much lower price than olive oils. Moreover, due to both the 'neutrality' under lipoprotein metabolism point of view and the stability at high temperature of stearic acid, new sunflower oils have appeared in the market, such as high-stearic-acid sunflower oil (HSSO) and high-oleic-acid-high-stearic-acid sunflower oil (HOHSSO), with very promising properties (Sánchez-Muniz et al. 2016). Plant breeding methods have been applied to obtain the desirable varieties of sunflower with a focus on the content of oleic and LA (Bhattacharya 2023). Belo et al. (2017) reported LA concentration ranging from 32.5 to 71.9% among traditional and 0.8 to 20.4% among high oleic genotypes. In addition, high stearic sunflower oil can be a healthier alternative to other fats rich in SFAs. The advantage of this oil is the richness of tocopherols (Romanić 2020).

Table 5. Fatty acid composition of traditional, high oleic, and NuSun sunflower oil in comparison with other plant oils (Gulya 2004).

Crop	Saturated FA [%]	Unsaturated FA [%]		
	Palmitic and Stearic	Oleic	Linoleic	Linolenic
Sunflower, traditional	12.5	20	66	0.1
Sunflower, high oleic	6.7	80	12	0.1
Sunflower, NuSun	9.5	60	30	0.1
Olive	15	75	9	1
Rapeseed	6	63	20	8.6
Soybean	14	28	50	7
Corn	13	29	57	1

The study of Belo et al. 2017 shows the variation of tocopherols content per grain between 9.4-22.1; 16.4-25.6; and 22.4-30.2 μg . The main tocopherol was α -T followed by β -T, which represented, in average, 97% and 2% of total tocopherols, respectively. Numerous authors stated associations between tocopherols and FA composition in vegetable oils. For example, Gotor et al. (2015) reported correlations of -0.70, -0.21, and 0.40, between tocopherol concentration in sunflower oil and the percentage of palmitic, stearic, and oleic acid, respectively. Similarly, in soybean oil with low ALA content, Whent et al. (2009) discovered correlations of -0,38 and 0,49 between oil tocopherol concentration and the percentage of palmitic and oleic acid, respectively. Dolde et al. (1999) as well as Kamal-Eldin & Andersson (1997) also reported the relation between tocopherols and FA compositions in sunflower, soybean, rapeseed, and wheat oil.

3.2.5 Poppy seed oil

Poppy (*Papaver somniferum*) is a plant cultivated worldwide for medicinal, food or ornamental purposes. Turkey is the country with the largest harvest poppy area, which in 2018 was 45,123 ha producing 26,991 tonnes of poppy seeds. The world's second largest producer of poppy seeds is the Czech Republic (26,608 ha, 13,666 tonnes) and the third in this ranking is Spain, with a cultivation area of 11,452 ha and seed production quantity of 12,360 tonnes (Dabrowski et al. 2020). Poppy is mainly grown in the temperate zone of the northern hemisphere and is absent in the tropical zone. About 12 species of poppy grow wild or are cultivated in the Czech Republic, of which 6 are considered native taxa (Vašák et al. 2010). Genotypes of technical poppy with a high content of opium alkaloids are the basic raw material for pharmaceutical purposes (as a source of opium and morphine), while low morphine genotypes of food poppy serve as an edible seed source for the bakery and confectionery industries and the production of edible oil (Dabrowski et al. 2020).

Due to more than 100 described species of poppy (*Papaver* sp.), this genus has been gradually subdivided into lower categories – sections, which have been continuously refined since the first half of the 19th century. In this classification, the morphological diacritical characters of the species, their distribution ranges and, since the end of 20th century, also the composition of their alkaloid spectra are mainly used. Poppies contain about 14 types of alkaloids, e.g. rhoeadin, aporphine, protopine, promorphinan, morphinan, etc., the production of which is a constant, genetically fixed trait. Poppy alkaloids are nitrogenous secondary metabolites which, like other secondary metabolites, are thought to originate from complex plant defence mechanism (Vašák et al. 2010). The pharmaceutical industry demands poppy cultivars exhibiting high amounts of the pharmacological active substances, which are standardized with regard to their individual concentration in the plant (Schulz et al. 2004). Poppy latex – opium (juice from immature poppies) can contain up to around 80 different alkaloids, the most abundant of which is morphine (Casado-Hidalgo et al. 2021). Despite continuous advances in the knowledge of synthetic chemistry, to this point the extraction of alkaloids (typically morphine) from poppy plants is still much more economically viable compared to the use of synthetic alkaloids (Brook et al. 2017). Total alkaloid content in poppy latex ranges between 5-10% (Pushpangadan et al. 2012). Morphine accounts for about 10-15% of the total alkaloids in opium (Schulz et al. 2004). The Czech Regulation number 399/2013 determines, with effect from 1 January 2014, that only poppies containing up to 25 mg of morphine alkaloids on the seed surface in 1 kg of poppy seeds may be used for food purposes (Vyhláška č. 399/2013 Sb.).

The poppy seeds themselves do not contain alkaloids, but they may be contaminated to some extent during harvesting (Knutzen et al. 2018; Casado-Hidalgo et al. 2021) when poppy straw dust, which may contain alkaloids, adheres to the seeds (Lachenmeier et al. 2010). Contamination of the final product with opium alkaloids may occur due to the use of poppy seeds, which are a by-product of the cultivation of technical poppy varieties (López et al. 2018). However, when food-grade varieties are used, the risk is negligible and poppy seeds can be considered a very healthy food (Hlinková et al. 2019).

Seeds of poppy as part of a rational diet are typical of Central and Eastern Europe, but some poppy seed desserts are also commonly served in Turkey and India. The most common uses of poppy seeds as food are as fillings for buns and cakes, or as a sprinkling on pastries or as a pressed oil for direct consumption. The oil is obtained by solvent or mechanical extraction and the remaining poppy seed cake is crushed and used for cattle feed (Fist 2001; Musa Özcan & Atalay 2006; Chmelová et al. 2018). Poppy seed oil is used as a food stabilizer which, thanks to the antioxidant potential of several substances contained in poppy seed oil, serves as a preservative to prevent spoilage (Bozan & Temelli 2008).

Quality and nutritive value of poppy seeds is based on lipid content and mainly PUFAs. Generally, poppy seeds contain 28-53% of edible oil, depending on the cultivar, cultivation location and other environmental conditions (Hlinková et al. 2019; Dabrowski et al. 2020). The protein content of poppy seeds ranges between 18-22% (Azcan et al. 2004; Gök 2015), the content of saccharides is about 23%, and there is approximately 6% of ash (Nergiz & Ötles 1994). Of the minerals, poppy is particularly rich in calcium, which reaches a level of approximately 12.9 g/kg (Saini & Davar 2012). Other elements present are sodium, potassium, and magnesium (Senila et al. 2020; Levent et al. 2020). PUFAs are the most dominant group

of FAs in poppy seed oil and occupy approximately 56.4-74.8% (Bozan & Temelli 2008; Rahimi et al. 2011; Lančaričová et al. 2016). The dominant FA in the profile of poppy fat is LA, whose share varies from 53% to 74% (Dabrowski et al. 2020). The second PUFA present in poppy seed oil is ALA, the proportion of which is significantly lower and occupies about 0.4-1.2% (Azcan et al. 2004; Hlinková et al. 2019; Satranský et al. 2021). Less abundant are oleic acid (13-24%) and palmitic acid (8-19%), accompanied by 1-2% of stearic acid and ALA. In the majority of poppy oils, the share of PUFAs ranges from about 61% to 76%, and therefore poppy seeds and their products are susceptible to auto-oxidation – rancidity (Lančaričová et al. 2016). The composition of FAs of poppy oil is not ideal from a nutritional point of view due to the predominance of LA. However, poppy oil contains other healthy compounds such as tocopherols, phytosterols, and phenolics. High variation in the content and composition of these compounds in the same seed material can be primarily affected by the method of oil production (Dabrowski et al. 2020).

The study of Ghafoor et al. 2019 researched poppy seed oil. The most abundant tocopherol in poppy seed oil samples was γ -T, followed by β -, α -, and δ -T. The γ -T contents were in ranges from 251.94 to 281.5 mg/kg. The second major tocopherol was β -T which was observed in scale from 261.3 to 268.1 mg/kg. Erinc et al. 2009 reported that PSO contained 195.37-280.85 mg/kg γ -T and 21.99-45.83 mg/kg α -T. According to Özcan & Atalay 2006, poppy seed oil contains 26.8-37.2 mg/kg α -T, 309.5-567.3 mg/kg β -T, and 6.1-18.6 mg/kg δ -T (Ghafoor et al. 2019). In contrast to Özcan & Atalay 2006, the research by Özbek & Ergönül 2020 did not detect δ -T in any poppy seed oil in their study and only two of their samples contained traces of β -T. The dominant tocopherols in their study were α - and γ -T isomers with contents of 8.48 to 88.8 mg/100g and 29.72 to 40.33 mg/100g, respectively.

3.2.6 Soybean oil

Soybean (*Glycine max*) is botanically classified as a member of the legume family (*Fabaceae*), but due to its high oil content is also considered as an important oil crop in food and feed industry. Geographical and historical evidence suggests that soybean first emerged as a domesticate in the eastern part of northern China (around 1500-100 BC) and was introduced from there into other regions of Asia. In the early 1900s, interest in this crop grew in Europe and the USA. In the USA, soybean was grown predominantly as a forage crop for many years before it was grown for grain (Kumudini 2010). In the first half of the 20th century, China was the world's largest soybean producer and exporter. In the 1950s, soybean production expanded rapidly in the USA, which is now the largest soybean producer in the world (Qiu & Chang 2010).

Soybeans are a subtropical crop, but the breeding of varieties tolerant of conditions in northern latitudes now allows their cultivation as far north as Canada and Sweden. When effectively modified, soybeans can derive up to 40% of their N from fixation. Soybeans are sensitive to soil N status and on heavily fertilized soil may derive only up to 25% of their N through fixation. Soybeans can be sown with a bean, beet, or grain drill, as long as it provides good depth control to within 1 cm. The crop is combinable and therefore is mechanically compatible with cereals. However, the capacity of the soybean crop depresses the yields of subsequent crops of wheat is a major disincentive to place the in a wheat rotation as a break

crop (Robson et al. 2002). Mature soybeans are oval shaped, and their sizes are variety-dependent. The seed consists of three major parts: seed coat or hull, cotyledon, and germ or hypocotyls (Table 6) (Gunstone 2002).

The two main products of the soybean are seed oil and the protein-containing meal. Soybean contains 18-23% of oil which is an important source of tocopherols and 38-44% protein on a moisture-free basis (Hymowitz 2008; Sharma & Goyal 2015). Soybean oil is used for cooking, to make margarines, and for a range of industrial products including paints, linoleum, inks, and soap. Soybean protein consists of a balanced proportion of all nine essential amino acids required by the human body, thus, it is considered as a healthy source of complete protein. The soybean meal is used primarily as a source of high-protein feeds for the production of pork, poultry, eggs, fish, beef, and milk, but can be also processed into protein isolates and meals for human consumptions (Robson et al. 2002; Hymowitz 2008).

Table 6. Chemical composition (wt%) of soybean and its components (dry weight basis) (Gunstone 2002).

Components	Yield	Protein	Oil	Ash	Carbohydrate
Whole seed	100.0	40.3	21.0	4.9	33.9
Cotyledon	90.3	42.3	22.8	5.0	29.4
Hull	7.3	8.8	1.0	4.3	85.9
Hypocotyl	2.4	40.8	11.4	4.4	43.4

Soybean seed oil contains three major unsaturated FAs; oleic acid (25%), LA (55%), and ALA (8%). Furthermore, the study of Sharma & Goyal 2015 says that soybean oil contains three major tocopherol isomers (α -, γ -, and δ -T), which accounts for 4-10, 60-70, and 20-25% respectively. In comparison, Wang 2008 determined all tocopherol isomers in soybean oil (Table 7).

Table 7. Tocopherol content and composition of mechanically pressed and solvent-extracted soybean oil (Wang 2008).

Tocopherol	Mechanically Pressed Soybean Oil	Solvent-extracted Soybean Oil
Total tocopherol [ppm]	1257	1370
α -T [%]	9.3	10.5
β -T [%]	1.2	1.2
γ -T [%]	62.8	63.5
δ -T [%]	26.7	25.0

As for other crops, the tocopherol content of soybean is affected by environmental conditions, with high temperature and high precipitation sites producing seeds with high α -T and total tocopherol content, whereas low temperature decreases total tocopherol content, which has been attributed to the loss of γ -T. Free α -T content increased in soybean seeds under warmer growing conditions during seed maturation (Sharma & Goyal 2015). Although there

are some controversial topics regarding soybean toward human health, it is considered as one of the most economical and valuable agricultural commodities (Naresh et al. 2019).

4 Conclusion

Plant oils, derived from various parts of plants, play a crucial role in the human diet. In the form of oilseed press cake or meal, oil crops are also important part of feed for the livestock, as they represent a valuable source of proteins and minerals. Moreover, the use of oilseed crops as biofuels takes its importance to contribute to renewable energy sources. Among the most cultivated oil crops in Europe are oilseed rape, sunflower, soybean, and poppy, the oil of which is characterized by its content of polyunsaturated fatty acids and vitamin E. Due to these nutritional components, plant oils represent a valuable commodity with potential health benefits.

Plant oils usually contain the essential polyunsaturated fatty acids, α -linolenic (n-3) and linoleic acid (n-6), which must be obtained from the diet because they cannot be synthesized in the human body. These compounds are considered to be necessary components of cell membranes, they play a key role in many cell processes and have an anti-inflammatory effects because of decreasing the production of cytokines and adhesion molecules. Furthermore, their consumption can help reduce the risk of serious diseases, especially cardiovascular diseases, cancer osteoporosis, diabetes and other health promotion activities. Sunflower oil has the highest content of oleic, linoleic, and α -linolenic acid among other plant oils, thanks to the breeding of cultivars with high content of these fatty acids.

Vitamin E (referred to as tocopherols) contribute to overall health by acting as strong antioxidant, supporting the immune system, and potentially preventing cardiovascular diseases, cancer osteoporosis, and diabetes. Vitamin E is also important in terms of oxidative stability of foods, as particularly for edible oils, the addition of vitamin E was found to enhance their oxidative stability when submitted to heating, a common processing step upon cooking. Although the vitamin E content of plant oils is generally high, the composition of different forms of tocopherols varies. In the commonly used oils (rapeseed, sunflower), α - and γ -tocopherol predominate, while the less conventional poppy seed oil is characterized by a high content of β -tocopherol. From a nutritional point of view, it may be worth including in the diet some of the less traditionally used oils, which may represent a valuable source of these health promoting substances.

However, in order to provide a reasonable assessment of the advisability of including various plant oils in the daily diet, it will be necessary to carry out scientific research to evaluate the effect of genetic but also environmental factors on the tocopherol content and profile of different oil crops.

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6 List of abbreviations and symbols

ALA	α -linolenic acid
AVED	ataxia with isolated vitamin E deficiency
CLD1	chlorophyll dephytylase
CO ₂	carbon dioxide
CPO	cold pressed oil
DHA	docosahexaenoic acid
DMAPP	dimethallyl diphosphate
DMGGBQ	2,3-dimethyl-6-geranylgeranyl-1,4-benzoquinone
DMPBQ	2,3-dimethyl-6-phenyl-1,4-benzoquinone
DXP	1-deoxy-D-xylulose-5-phosphate
EFA	essential fatty acid
EFSA	European Food Safety Authority
EPA	eicosapentaenoic acid
FA	fatty acid
FDA	Food and Drug Administration
FDP	farnesyl diphosphate
FW	fresh weight
GGDP	geranylgeranyl diphosphate
GGDR	geranylgeranyl diphosphate reductase
GDP	geranyl diphosphate
GGPP	geranylgeranyl pyrophosphate
GGPS	geranylgeranyl diphosphate synthase
GRAS	Generally Recognized as Safe
HEAR	high-erucic acid variety
HGA	homogentisate acid
HGGT	homogentisate geranylgeranyltransferase
HOHSSO	high-oleic-acid-high-stearic-acid sunflower oil
HOSO	high-oleic-acid sunflower oil
HPP	<i>p</i> -hydroxyphenylpyruvate
HPPD	hydroxyphenylpyruvate dioxygenase
HPT	homogentisate prenyltransferase
HSSO	high-stearic-acid sunflower oil
IPP	isopentenyl diphosphate
LA	linoleic acid
LEAR	low-erucic acid variety
MEP	methylerythritol phosphate
MGGBQ	2-methyl-6-geranylgeranylplastoquinol
MPBQ	2-methyl-6-phytylplastoquinol
MPBQ-MT	2-methyl-6-phytylplastoquinol methyltransferase
MT	methyltransferase

MUFA	monounsaturated fatty acid
PDP	phytyl diphosphate
PK	phytyl kinase
PLTP	phospholipid transport protein
PPH	pheophytin pheophorbide hydrolase
PPi	pyrophosphate
PPK	phytyl phosphate kinase
PUFA	polyunsaturated fatty acid
ROS	reactive oxygen species
SAH	S-adenosyl-l-homocysteine
SAM	S-adenosyl-l-methionine
SFA	saturated fatty acid
α -T	α -tocopherol
β -T	β -tocopherol
γ -T	γ -tocopherol
δ -T	δ -tocopherol
α -T3	α -tocotrienol
β -T3	β -tocotrienol
γ -T3	γ -tocotrienol
δ -T3	δ -tocotrienol TAG triacylglycerol
TAT	tyrosine aminotransferase
TBHQ	tertiary-butylhydroquinone
TC	tocopherol cyclase
THGGPP	tetrahydrogeranylgeranyl pyrophosphate
TMHQ	trimethylhydroquinone
TMT	tocopherol methyltransferase
γ -TMT	γ -tocopherol methyltransferase
α -TTP	α -tocopherol transfer protein

