GABA, a non-protein amino acid ubiquitous in food matrices

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Abstract: GABA has attracted great attention over the last several decades due to its ubiquity in life. It is an important molecule naturally present in considerable amounts in many feed and food matrices of vegetable and animal origin. GABA occurs naturally in plants, animals and microorganisms, having diverse physiological functions and great potential health benefits. Extensive data demonstrates that GABA content is usually higher in plants than in animals and its concentration is in the range of mg g\(^{-1}\) depending on plant matrix, development stage and postharvest processing conditions. In animals, GABA was found at significantly high levels in the brain and central nervous system and some specific peripheral tissues like livestock muscles in the range of \(\mu g\) g\(^{-1}\). Food items produced by different types of animals, such as eggs, milk or honey, also show remarkable GABA content without any processing steps. A healthy diet following the set of recommendations of WHO national food-based dietary guidelines (FBDG) or/and the Healthy Eating Plate (Harvard) will provide a considerable amount of GABA as a natural nutrient. Additionally, considering its potential health benefits, many efforts are being allocated to developing new technological processes for GABA enhancement in traditional foodstuffs or avoiding losses after processing treatments.

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Dr. Roberto Ramos Ruiz is technical director at Servalesa, a company aiming to offer products for farming which provide a differential value through their innovation and contribution to ensure healthier crops for healthier consumers. Amongst other responsibilities, Roberto is in charge of research and development. Servalesa has developed for the past decade several research projects in collaboration with different universities and research organizations. The fundamental objective of these projects is to offer farmers technologies able to mitigate the effects caused by different kind of plant stress with impact on crops, either biotic or abiotic, with an acceptable efficacy, no residues, a minimal impact on the environment and a toxicological profile with no effect on users and consumers through food treated with these products. Within this research activity, Servalesa has a particular interest in studying the effects on crops and impacts on human health and the environment of naturally occurring substances.

PUBLIC INTEREST STATEMENT

Tendency of experts and consumers towards a healthy diet includes an increasing interest on details about the nutrients (e.g. carbohydrates, fat, protein, vitamins and minerals) needed to achieved a healthy balance diet. GABA is a non-protein amino-acid that occurs naturally in plants, animals, and microorganisms, having diverse physiological functions and great potential health benefits. Over the last several decades GABA has attracted great attention due to its different positive effects on mammalian physiology. The aim of this review is to compile the levels of GABA measured in nature, specifically in plant and animal products for the food industry.
1. Introduction

Gamma-amino-butyric acid (γ-amino-butyric acid, GABA, CAS [56–12-2]) is a well-known, non-protein amino acid that was first identified in potato tubers (Steward, Thompson, & Dent, 1949) and found one year later in mammalian brains (Awapara, Landua, Fuerst, & Seale, 1950; Roberts & Frankel, 1950; Udenfriend, 1950). Since then, GABA has been investigated in many organisms including bacteria, fungi, plants and animals (Dhakal, Bajpai, & Baek, 2012; Erdö, 1992; Lin et al., 2013; Minuk, 1992; Seher, Filiz, & Melike, 2013; Tanaka, 1985). This small molecule has been found in almost every living organism and many essential roles and functions have been described.

It has been reported that GABA induces different positive effects on mammalian physiology. Some examples of GABA activity include hypotensive effects and relaxation (Mody, De Koninck, Otis, & Soltesz, 1994; Yang, Jhou, & Tseng, 2012; Yoshimura et al., 2010), enhancement of immunity under stress conditions (Abdou Adham, Higashiguchi, Horie, Mujo Kim, & Yokogoshi, 2008), prevention of cancer cell proliferation (Oh & Oh, 2004), prevention of diabetic conditions (Hagiwara, Seki, & Ariga, 2004) or modulation of blood cholesterol levels (Roohinejad et al., 2009). Due to all of these biological functions, GABA is a potentially bioactive component of foods and pharmaceuticals (Boonstra et al., 2015; Diana, Quílez, & Rafecas, 2014). Due to its relevance, GABA is also becoming recognized as an essential nutrient for a healthy balanced diet.

GABA is metabolized via a three-enzyme pathway known as the GABA shunt, which bypasses two steps of the tricarboxylic acid (TCA) cycle (Michaeli & Fromm, 2015; Watanabe, Maemura, Kanbara, Tamayama, & Hayasaki, 2002).

GABA is mainly produced from glutamate by the irreversible reaction of the cytosolic enzyme glutamate decarboxylase (GAD; EC 4.1.1.15) which involves cytosolic acidification and/or Ca+2/calmodulin activation (Roberts & Kuriyama, 1968; Shelp, Bozzo, Trobacher, Chiu, & Bajwa, 2012). However, GABA synthesis may also occur via polyamine (putrescine and spermidine) degradation (Fait, Fromm, Walter, Galli, & Fernie, 2008) and possibly by a non-enzymatic reaction from proline under oxidative stress (Signorelli, Dans, Coitino, Borsani, & Monza, 2015).

GABA catabolism occurs by the action of GABA transaminase (GABA-T; EC 2.6.1.19) to produce succinic semi-aldehyde (SSA). SSA in turn, is oxidized to succinate by SSA dehydrogenase (SSADH) (Bouché, Fait, Bouchez, Moller, & Fromm, 2003; Roberts & Hammerschlag, 1972, Tunnicliff, 1986), or alternatively, reduced to γ-hydroxybutyrate via SSA reductase (SSAR) activity (Hildebrandt, Nunes, Araujo, & Braun, 2015).

This review aims to give an overview of the natural occurrence of GABA, not only in plants, animals and environment, but also focused on GABA concentrations in food and feed. GABA concentrations in these matrices are reported to reach considerable levels. Data coming from original references have been maintained and, if required, values with harmonized units are incorporated in square brackets in the text or in a separate column within tables.

2. GABA in plants

GABA is a ubiquitous non-protein amino acid that is present in almost every plant. During the last few decades, research related to GABA in plants was focused on understanding GABA metabolism and its role in plant growth and response to stress (Bouché, Lacombe, & Fromm, 2003; Bown & Shelp, 1997; Ham, Chu, Han, & Ryu, 2012; Kinnersley & Turano, 2000; Satya & Nair, 1990; Shelp, Bown, & McLean, 1999).
More recent studies show that GABA is also involved in various physiological processes and could have a potential role as a signalling molecule (Bouché, Fait, Zik, & Fromm, 2004; Bown, MacGregor, & Shelp, 2006; Bown & Shelp, 2016; Fait, Yellin, & Fromm, 2006; Gillham & Tyerman, 2015; Häusler, Ludewig, & Krueger, 2014; Michaeli & Fromm, 2015; Shelp, Bown, & Zarei, 2017; Shelp, Van Cauwenberghe, & Bown, 2003).

GABA levels are influenced by many factors, including species and variety, environmental conditions, stress during cultivation and even post-harvest treatments. It is well known that GABA accumulation occurs in response to biotic and/or abiotic stresses such as hypoxia, cytosolic acidification, cold shock, mechanical stimulation, water stress and light (Ham et al., 2012; Kinnersley & Turano, 2000). GABA content also changes depending on the plant growth and development stage and its level increases during germination of food grains (Chalorcharoenying, Lomthaisong, Suriharn, & Lertrat, 2017; Karladee & Suriyong, 2012; Kim et al., 2013; Li, Bai, Jin, Wen, & Zhenxin, 2010).

The aim of this review is to compile the levels of GABA measured in plants in nature, also reporting the evolution of GABA content during product life. Plants have been considered as food and feed products mainly coming from agriculture. Taking into account regulations on health issues related to production and consumption of plants, plant classification within the review is aligned with the classification described in Commission Regulation (EU) 2018/62 of 17 January 2018.²

2.1. GABA in fruits and treetnus

2.1.1. Citrus fruits

Citrus is one of the most widely produced and popular types of fruits, with a related industry constantly developing processing technologies to produce juices and high value derivatives coming from its wastes and by-products. Citrus are rich in phenolic compounds as well as vitamins, minerals, dietary fibre, essential oils and carotenoids. The first quantitative data reported by (Clements & Leland, 1962), showed that GABA content in lemon juices (Eureka and Lisbon lemon, 7 mg 100 mL⁻¹ [0.07 mg mL⁻¹] of juice) was lower than in orange juices of different varieties (mature Valencia, Washington navel oranges and Dancy tangerines, with 32, 24 and 18 mg of GABA 100 mL⁻¹ of juice respectively [0.32, 0.24 and 0.18 mg mL⁻¹]). Bergamot juice was reported to have 25.7 μgm L⁻¹ [0.026 mg mL⁻¹] GABA (Mazzotti et al., 2012).

A complex analytical method was developed using positive electrospray ionization and a triple quadrupole mass spectrometer (MS) operating in multiple reaction monitoring (MRM) mode. This method allows low level detection of GABA in its native form from freshly squeezed orange juice (Zazzeroni, Homan, & Thain, 2009). The concentration of GABA measured in orange juice, using this new method, increased slightly to 344 μg mL⁻¹ [0.344 mg mL⁻¹]. It is relevant to note that different methods of measuring GABA concentration, along with L-Arginine and L-Aspartic acid, have been used to differentiate the quality of commercial orange juices (Simó, Martin-Alvarez, Barbas, & Cifuentes, 2004).

The fermentation of fruit produces significant changes in their nutritional composition. Determination of the influence of controlled alcoholic fermentation and thermal pasteurization on the amino acid profile of orange juice has been studied (Cerrillo et al., 2015). An UHPLC (Ultra High Performance Liquid Chromatography) system coupled with a 6460 tandem triple quadrupole mass spectrometer was used for the analysis of orange juice samples. GABA was the ninth most abundant amino acid in orange juice (187 mg L⁻¹ [0.187 mg mL⁻¹]), but this amount decreased in fermented orange juice after 15 days (167 mg L⁻¹ [0.167 mg mL⁻¹]) and appears to be lower in fermented-pasteurized (85°C for 30 s) orange juice (126 mg L⁻¹ [0.126 mg mL⁻¹]).

A different technique, High-Resolution Magic Angle Spinning (HR-MAS) NMR spectroscopy (Mucci, Parenti, Righi, & Schenetti, 2013), was used to identify several metabolites of intact specimens
from flavedo, albedo, pulp, seeds and the content of oil glands obtained from shelf samples of lemon (Citrus limon) and citron (Citrus medica). Only in albedo and pulp was it possible to detect GABA, with a relative average molar content of 0.26 and 0.28 in pulp of lemon and citron respectively. Using the same technique, (Corsaro et al., 2015), studied the cultivar “Interdonato” lemon, which is a hybrid between a cedar and a lemon. They evaluated the lemon juice for different samples of both Protected Geographical Indication (PGI) Interdonato lemon of Messina and Interdonato lemon from Turkey. In the Turkish lemon there was a higher amount of GABA (2.40 mM [0.247 mg mL⁻¹]) than in the Italian lemon (1.05 mM [0.108 mg mL⁻¹]).

(Sun et al., 2013) measured variations of GABA content in Hirado Buntan Pomelo (HBP; Citrus grandis). The harvested HBP fruits were stored at ambient temperature (16–20°C) and 85–90% relative humidity for 132 days. The average content of GABA in the pulp fruit was more than 140 μg g⁻¹ [0.140 mg g⁻¹] Fresh Weight (FW). This content slightly increased in the fruit over time from 145 μg g⁻¹ FW [0.145 mg g⁻¹] at day 12–190 μg g⁻¹ FW [0.190 mg g⁻¹] at day 78.

2.1.2. Tree nuts
This group comprises fruits that are composed of an inedible hard shell and a seed which is generally edible. It includes a wide variety of dried seeds, the most common being almonds, brazil nuts, cashew nuts, chestnuts, coconuts, hazelnuts/cobnuts, macadamias, pecans, pine nut kernels, pistachios and walnuts. Even though the concentration of GABA in chestnuts is significant (188 nmol g⁻¹ Dry Weight (DW), [0.019 mg g⁻¹] (Oh, Moon, & Oh, 2003)) not much information related to GABA content has been reported.

The cola nut is a caffeine-containing nut from evergreen trees of the genus Cola. These are consumed, fresh or fermented, for their excitant properties. These properties could be attributed to the richness of the seeds in purine alkaloids, polyphenols and sugars. (Onomo, Niemenak, Ndoumou, & Lieberei, 2010) studied the GABA contents of accessions of Cola acuminata and Cola anomala, harvested randomly from trees from different sites in Cameroon. GABA content was measured in mature seeds, germinated seeds and seedlings and the amounts of GABA always increased in that order. Only the sample from Zoatele of the six accessions of C. acuminata had a lower amount of GABA in seedlings (1,241.3 μg g⁻¹ DW [1.241 mg g⁻¹]) than in mature germinated seeds (3,128.8 μg g⁻¹ DW [3.129 mg g⁻¹]). Except for mature seeds (1,054.3–1,452.6 μg g⁻¹ DW [1.054–1.453 mg g⁻¹]), GABA content of both, germinated seeds (2,788.0–3,102.4 μg g⁻¹ DW [2.788–3.102 mg g⁻¹]) and seedlings (3,546.8–4,004.3 μg g⁻¹ DW [3.547–4.004 mg g⁻¹]) of C. acuminata was higher than the quantities detected in C. anomala (1,650.6–1,663.2; 2,300.0–2,309.6; 2,475.9–2,502.7 μg g⁻¹ DW [1.651–1.663, 2.300–2.310, 2.476–2.503 mg g⁻¹] respectively).

GABA is found in coconut (Cocos nucifera L.) water, the aqueous part of the coconut endosperm (Yong, Ge, Ng, & Tan, 2009). The chemical composition of this edible part varies with the age and type of coconuts. (Arndtii, 2009) reports 820 μg mL⁻¹ [0.820 mg mL⁻¹] of GABA in coconut water. (Tulecke, Weinstein, Rutner, & Laurencot, 1961) determined GABA content in coconut water at different fruit ages: young green (1.90 μg mL⁻¹ [0.002 mg mL⁻¹]), mature green (34.60 μg mL⁻¹ [0.035 mg mL⁻¹]), mature (168.80 μg mL⁻¹ [0.169 mg mL⁻¹]) and mature (autoclaved) (173.20 μg mL⁻¹ [0.173 mg mL⁻¹]).

2.1.3. Pome fruits
Apple was one of the first fruits to be studied for its amino acid content, including GABA (Hulme & Arthington, 1950). Since then, many studies have shown that apple contains low amounts of this non-protein amino acid; that is (Oh et al., 2003) reported 2 nmol of GABA g⁻¹ [0.00021 mg g⁻¹] DW, (Zazzeroni et al., 2009) detected 7.11 μg g⁻¹ [0.007 mg g⁻¹] in the epicarp/mesocarp mixture. Although GABA contents vary among varieties of apples, it is always present within a similar range of concentrations (Deewatthanawong & Watkins, 2010; Deyman, Brikis, Bozzo, & Shelp, 2014; Vasanits, Kutlan, Sass, & Molnar-Perl, 2000): Jonagored 2.55 μg g⁻¹ Wet Pulp (WP) [0.003 mg g⁻¹], Idared 4.38 μg g⁻¹ WP [0.004 mg g⁻¹], Jonica 3.66 μg g⁻¹ WP [0.004 mg g⁻¹], Florina 4.45 μg
g\(^{-1}\) WP [0.004 mg g\(^{-1}\)], Freedom 3.93 μg g\(^{-1}\) WP [0.004 mg g\(^{-1}\)], Empire, 25–40 nmol g\(^{-1}\) FW [0.003–0.004 mg g\(^{-1}\)].

(Zhang, Pengmin, & Cheng, 2010) investigated the developmental changes of several compounds in “Honeycrisp” apple flesh. Fruits were sampled at 2-week intervals from 2 weeks after full bloom. Initial GABA content was around 100 μg g\(^{-1}\) FW [0.1 mg g\(^{-1}\)]. The concentration increased from 2 to 4 weeks after bloom to more than 140 μg g\(^{-1}\) FW [0.14 mg g\(^{-1}\)], and then decreased exponentially to harvested fruits to approximately 10 μg g\(^{-1}\) FW [0.01 mg g\(^{-1}\)]. On a whole fruit basis, GABA content increased rapidly in the first 6 weeks reaching 2.3 mg fruit\(^{-1}\), decreased slightly in the next 4 weeks, and then increased gradually to fruit harvest (up to 2.6 mg fruit\(^{-1}\)).

During storage under Controlled Atmosphere (CA) conditions, GABA accumulated in apple fruit (Malus × domestica Borkh. cv. Empire), probably as a stress response. GABA only accumulated slowly in fruit stored in 1% CO\(_2\) over an 8-week storage period (from 33 to 60 nmol g\(^{-1}\) FW [0.003–0.006 mg g\(^{-1}\)]), while GABA accumulated to reach maximum concentrations by week 4 in fruit stored in 2.5 and 5% CO\(_2\) (135 nmol g\(^{-1}\) FW [0.014 mg g\(^{-1}\)]). GABA concentrations in the elevated CO\(_2\) treated fruit subsequently declined to levels similar to those in fruit stored at 1% CO\(_2\) (Deewatthanawong & Watkins, 2010). (Deyman et al., 2014) presented results of longer lasting experiments in the same fruit variety. During their CO\(_2\) treatments GABA accumulated in a linear fashion over the storage period (50 weeks). Notably, fruit receiving 2.5 kPa CO\(_2\) accumulated almost twice as much GABA (∼2 nmol g\(^{-1}\) Fresh Matter week\(^{-1}\) [0.0002 mg g\(^{-1}\) week\(^{-1}\)]) as fruit receiving 0.03 kPa CO\(_2\).

(Troebacher et al., 2013) maintained “Empire” apples for 10 months under controlled atmospheric conditions (2.0 kPa CO\(_2\), 2.5 kPa O\(_2\), 3°C; GABA level entire fruit: 942 ± 217 nmol g\(^{-1}\) FW [0.097 ± 0.022 mg g\(^{-1}\)]). After 10 months, the apples were transferred from storage to ambient conditions (0.038 kPa CO\(_2\), 21 kPa O\(_2\), 25°C; GABA level whole apple: 370 ± 48 nmol g\(^{-1}\) FW [0.038 ± 0.005 mg g\(^{-1}\)]) for 3 h and the fruits dissected into peel (GABA, 172 ± 28 nmol g\(^{-1}\) FW [0.044 ± 0.008 mg g\(^{-1}\)]) and flesh (GABA, 428 ± 73 nmol g\(^{-1}\) FW [0.044 ± 0.008 mg g\(^{-1}\)]) and core (GABA, 905 ± 179 nmol g\(^{-1}\) FW [0.093 ± 0.018 mg g\(^{-1}\)]), a process that took approximately 2 min. GABA contents decreased in intact fruit by approximately 60% after the transition between storage conditions. Removal of the stress conditions rapidly resulted in a net decline in GABA level, indicating that the GABA was being catabolized.

Accumulation of GABA was also observed in loquat fruit under cold conditions (Cao, Cai, Yang, & Zheng, 2012). The content of GABA increased steadily during storage time. After 35 days at 1°C the amount of GABA in loquat pulp was 49 μg g\(^{-1}\) FW [0.049 mg g\(^{-1}\)], almost three times more than at harvest (18 μg g\(^{-1}\) FW [0.018 mg g\(^{-1}\)]).

2.1.4. Stone fruits
GABA is present in very low concentrations in peach fruits (Prunus persica L. Batsch). GABA content is independent of fruit acidity, as demonstrated in “Jalousia” low acid fruit or “Fantasia” normal acid fruit (Moing et al., 1998). (Jia, Okamoto, & Hirano, 2000) evaluated the influence of fertilizer levels on GABA concentration in Hakuho peach fruit at harvest. Liquid fertilizer (Ohtsuka House) was used at three different nitrogen application rates; L-40 ppm, M-80 ppm and H-160 ppm. GABA content increased with increased fertilizer concentration, from 0.08 μmol mL\(^{-1}\) [0.008 mg mL\(^{-1}\)] (L) to 0.15 μmol mL\(^{-1}\) [0.015 mg mL\(^{-1}\)] (H).

2.1.5. Berries, grapes and small fruits
2.1.5.1. Berries. One of the first studies related to GABA content on berry fruits appeared in 1965 for blueberry (Strech & Copellini, 1965). Since then, different studies reported that blueberry is one of the fruits of this group with less GABA content, that is 89.27 g\(^{-1}\) [0.089 mg g\(^{-1}\)] (Zhang et al., 2014) and 7.9 mg 100 g\(^{-1}\) FW [0.079 mg g\(^{-1}\)] (Lee et al., 2015). Mulberry seems to be the berry with
highest content of GABA. (Choi et al., 2010) analyzed the GABA content in mulberry fruits from 7 Morus alba L. cultivars, including Daejappong, Iksuppong, Daesungppong, Yongppong, Cheongilppong, Gwasang 1 and Gwasang 2 with results in the range of 86.08–185.63 mg 100 g−1 DW [0.86–1.86 mg g−1]. Black raspberry and raspberry contained intermediate GABA levels; 19.4 mg 100 g−1 FW [0.194 mg g−1] and 10.1 mg 100 g−1 FW [0.101 mg g−1] respectively (Lee et al., 2015).

More recently, (Lee & Hwang, 2017) investigated changes in the physicochemical properties of mulberry fruits at seven maturity stages during ripening. Content of GABA decreased during ripening. GABA contents of the immature mulberry fruits were 113.2 and 59.6 mg 100 g−1 [1.132 and 0.596 mg g−1] respectively. These concentrations were significantly higher than those of the mature fruits (MS-3–6, 17.1–33.6 mg 100 g−1 DW [0.171–0.336 mg g−1]). Final GABA content in the fully mature phase increased slightly to 42.1 mg 100 g−1 DW [0.421 mg g−1]. The concentrations of GABA in the leaf, stem, and root bark of mulberry have also been reported. (Kwon, Kim, Hwang, & Park, 2013), using a simple high-performance anion-exchange chromatography-integrated pulsed amperometric detection method, determined that GABA content was 2.22 ± 0.20 mg g−1 in leaf, 2.84 ± 0.20 mg g−1 in stem, and 1.87 ± 0.14 mg g−1 in root bark. These results are in line with those previously reported, showing that GABA content of mulberry root bark ranged from 1.70 to 2.62 mg g−1 (Bang, Lee, Choi, & Kim, 1998) and of mulberry leaf were 2.36 mg g−1 (Yoo, Kim, Kim, & Rhee, 2002).

GABA concentrations in four strawberry (Fragaria ananassa Duch) cultivars, “Allstar”, “Earliglow”, “Jewel” and “Northeast” were studied (Deewatthanawong, Nock, & Watkins, 2010). “Allstar” and “Earliglow” had the lowest GABA concentrations of 0.15 mmol kg−1 [0.0155 mg g−1] at harvest. The highest GABA levels were detected in “Jewel” with an average of 0.35 mmol kg−1 [0.036 mg g−1], while in “Northeast” the GABA concentration was 0.24 mmol kg−1 [0.025 mg g−1]. GABA behaviour in strawberries during storage was also studied. When berries were stored in air, GABA concentrations showed different behaviour; in “Allstar” and “Earliglow” the concentration of GABA decreased, in “Jewel” the GABA concentration remained unchanged and in “Northeast” the GABA concentration increased. For CO2 treated fruit, the amounts of GABA were always higher than fruit stored in air, increasing by 2.2-fold in “Allstar” to 7.1-fold in “Northeast”. (Zhang et al., 2014) reported a GABA content in freeze-dried samples of strawberry (Fragaria × Ananassa) of 548.17 μg g−1 [0.548 mg g−1], slightly higher than GABA concentrations in stored strawberries. (Ordóñez et al., 2015) analyzed samples of strawberry purée. The concentration of GABA was 1.89 ± 0.89 mg L−1 [0.002 ± 0.0009 mg mL−1]. GABA content increased during fermentation of strawberry purée, using a surface culture of three strains of different acetic acid bacteria species.

Omija fruit is another example of a berry which contains GABA (Kim et al., 2008) at a substantial amount of 10 mg 100 g−1 [0.1 mg g−1] of fruits. It has also been reported (Kim, Lim, & Yang, 2016) that in the ethanolic extract of the stems of Elaeagnus umbellata Thunb., GABA was the major free amino acid (300.17 mg 100 g−1 [3.002 mg g−1]).

2.1.5.2. Grapes. The amino acid profiles of grape berries harvested at a similar maturity from six different cultivars of Vitis vinifera L. were investigated (Stines et al., 2000). GABA content for Sangiovese, Riesling, Pinot Noir, Cabernet Sauvignon, Muscat Gordo and Grenache were 82.51, 152.70, 174.30, 146.60, 79.56 and 90.53 mg g−1 FW respectively. The GABA distribution in seeds, skin and pulp was determined for berries of Riesling (RI) and Cabernet Sauvignon (CS). In both varieties, more than 65% of GABA was found in the pulp (RI, 85.36 mg g−1 FW, CS, 107.72 mg g−1 FW). Riesling berries had a higher GABA content in the seed than in the skin (30.88 and 14.03 mg g−1 FW respectively) and the contrary was observed for Cabernet Sauvignon berries (9.30 and 20.04 mg g−1 FW respectively). Data of GABA content in leaves of grapevines of Chardonnay (0.257 μmol g−1 DW [0.027 mg g−1]) and Meski (0.200 μmol g−1 DW [0.021 mg g−1]) have also
been reported (Hatmi et al., 2015). Under drought stress GABA content increased significantly to more than 3,400 μmol g⁻¹ DW [350.6 mg g⁻¹].

A chemical study was carried out on de-seeded berries of Carlos and Noble muscadine grapes (V. rotundifolia) during berry maturation (Marcy, Carroll, & Young, 1981). HIS plus GABA (also with Thr) were the predominant free amino acids in both cultivars at an immature berry stage (229.9 nm g⁻¹ [0.024 mg g⁻¹] fresh de-seeded weight). At full berry maturity, HIS plus GABA content increased (397.0 nm g⁻¹ [0.041 mg g⁻¹]) and was only surpassed by Arg content. The mean concentration (nm g⁻¹ fresh de-seeded weight) of HIS plus GABA for three V. rotundifolia cultivars determined at normal harvest were very similar (Regale, 688.7 [0.071 mg g⁻¹], Pride, 699.8 [0.072 mg g⁻¹] and Magnolia, 714.3 [0.074 mg g⁻¹]). The amount of HIS plus GABA for the Dixie cultivar was lower (444.0 nm g⁻¹ [0.046 mg g⁻¹]).

Data on GABA behaviour during maturation was reported by (Murch, Hall, Le, & Saxena, 2010) for wine grapes of Merlot varieties. GABA was found at approximately 115 μg g⁻¹ [0.115 mg g⁻¹] in 77% of early stage green grapes (pre-lag) and there was a significant linear decrease in both prevalence and concentration as the grapes matured through the process of véraison (green: 80 μg g⁻¹ [0.080 mg g⁻¹], transition, 70 μg g⁻¹ [0.070 mg g⁻¹] and purple 40 μg g⁻¹ [0.040 mg g⁻¹]).

The analysis of metabolite variation throughout the physiological development was also analyzed for the Sardinian Vermentino grape berry (Mulas et al., 2011). The variability in metabolite concentration was investigated as a function of the clone, the position of berries in the bunch or growing area within the vineyard, environmental factors and grape maturity. GABA contents varied between 6 and 67 mg kg⁻¹ [0.006–0.067 mg g⁻¹] depending on these factors.

2.1.5.3. Musts, wines and vinegars. Free amino acid contents are of great physiological significance for the final taste and quality of wines and vinegars. They are considered as barcodes to wine authenticity. Many studies have been reported showing the detailed chemical composition and, more specifically, the GABA content of these products (see Table 1).

Reported data are generally comparable within the different grape varieties (Bouloumpasi, Soufferos, Tsarchopoulos, & Biliaderis, 2002; Carlavilla, Moreno-Arribas, Fanali, & Cifuentes, 2006; Erbe & Brückner, 1998; Herbert, Cabrita, Ratola, Laureano, & Alves, 2006; Kliewer, 1970), with consideration of geography (Table 1), raw material (Kliewer, 1970), processing (Callejón et al., 2008; Guitart, Hernandez-Orte, & Cacho, 1997; Martínez-Pinilla, Guadalupe, Hernández, & Ayestarán, 2013) and vintage (Martínez-Pinilla et al., 2013). GABA content seems to be higher in white wines than red wines. The amount of GABA is also higher in varieties of grapes harvested at a later stage of fruit maturity.

Considering vinegars, acetatos balsámico di Modena are the ones with the higher GABA content. Sherry vinegars (Spain) show much lower content. Red wine vinegars contain more GABA than vinegars from white wine.

2.1.6. Miscellaneous fruits
The amounts of GABA of different parts of jujube fruits were analyzed (Collado et al., 2014). Data indicated that edible parts (peel and flesh) with 1.4 g kg⁻¹ (DW) [1.4 mg g⁻¹] contain more GABA than the pits (shell plus seed), which contain 0.3 g kg⁻¹ (DW) [0.3 mg g⁻¹]. Contents decreased with low irrigation and limited soil water conditions.

Among small fruits with inedible peel, kiwi has been well studied. (Macrae & Redgwell, 1992) investigated the distribution of GABA in different tissues of kiwi fruit (Actinidia delicosa) and changes in GABA concentration during maturation. Although amino acid concentrations in the fruit decreased during maturation, GABA, along with Arg, increased to become the predominant amino acids in fruit harvested at the end of May (GABA + Arg: 76.9 μg g⁻¹ FW [0.077 mg g⁻¹]) compared to 140.7 μg g⁻¹ FW [0.141 mg g⁻¹] in fruits harvested in February. Considering the outer
| Variety          | Origin       | Beverage       | GABA content       | GABA content (harmonized units) | Reference                                      |
|------------------|--------------|----------------|--------------------|----------------------------------|------------------------------------------------|
| Syrah            | France       | Grapejuice     | 25-60 mg L\(^{-1}\) | 0.025-0.060 mg mL\(^{-1}\) | (Kelly, Blaise, & Larroque, 2010)             |
| Marsh            | US           | Grapejuice     | 190 mg L\(^{-1}\)  | 0.19 mg mL\(^{-1}\)            | (Clements & Leland, 1962)                     |
| Several          | –            | Musts          | 2-580 mg L\(^{-1}\) | 0.002-0.580 mg mL\(^{-1}\)     | (Boch, Sauvage, Dequin, & Camarasa, 2009)     |
| Tempranillo      | La Rioja, Spain | Red Must      | 89.43 mg L\(^{-1}\) | 0.089 mg mL\(^{-1}\)           | (Garde-Cerdán, Portu, López, & Santamarina, 2016) |
| Several          | Alentejo region, Portugal | Red Must      | 20.2-110.3 mg L\(^{-1}\) | 0.020-0.110 mg mL\(^{-1}\)     | (Herbert et al., 2006)                        |
| Several          | Alentejo region, Portugal | White Must   | 29.9-118.1 mg L\(^{-1}\) | 0.030-0.118 mg mL\(^{-1}\)     | (Herbert et al., 2006)                        |
| Airen variety    | La Mancha    | White Must     | 109.2 mg L\(^{-1}\) | 0.109 mg mL\(^{-1}\)           | (Hernández-Orte, Ibarz, Cacho, & Ferreira, 2003) |
| Chardonnay       | Spain        | White Must     | 57.4 mg L\(^{-1}\)  | 0.057 mg mL\(^{-1}\)           | (Guitart et al., 1997)                        |
| Grenache (late stage fruit maturity) | – | Red Wine       | 125 µmol 100 mL\(^{-1}\) | 0.129 mg mL\(^{-1}\)           | (Kliewer, 1970)                                |
| Corinongne (late stage fruit maturity) | – | Red Wine       | 410 µmol 100 mL\(^{-1}\) | 0.423 mg mL\(^{-1}\)           |                                                |
| Gamay (early stage fruit maturity) | – | Red Wine       | 61 µmol 100 mL\(^{-1}\) | 0.063 mg mL\(^{-1}\)           |                                                |
| Alicante Bouschet (early stage fruit maturity) | – | Red Wine       | 294 µmol 100 mL\(^{-1}\) | 0.303 mg mL\(^{-1}\)           |                                                |
| Xinomavro, Agiorgitiko, Mandilara, Katsifali | Greek | Red Wine       | 15.3-30.8 mg L\(^{-1}\) | 0.015-0.031 mg mL\(^{-1}\)     | (Bouloumpasi et al., 2002)                     |
| Cabernet Sauvignon, Merlot, Syrah, Grenache rouge | Greek | Red Wine       | 9.5-17.5 mg L\(^{-1}\) | 0.009-0.017 mg mL\(^{-1}\)     |                                                |
| Cannonau         | Italy        | Red Wine       | 43.1 mg L\(^{-1}\)  | 0.043 mg mL\(^{-1}\)           | (Tuberoso, Giovanni, Congiu, Serrelli, & Mameli, 2015) |
| Hungarian red wine | Hungary      | Red Wine       | 6.9 mg L\(^{-1}\)   | 0.007 mg mL\(^{-1}\)           | (Kutlán & Molnár-Perl, 2003)                   |
| Several          | Alentejo region, Portugal | Red Wine   | 2.5-85.4 mg L\(^{-1}\) | 0.002-0.085 mg mL\(^{-1}\)     | (Herbert et al., 2006)                        |

(Continued)
| Variety                        | Origin            | Beverage  | GABA content | GABA content (harmonized units) | Reference                          |
|-------------------------------|-------------------|-----------|--------------|-------------------------------|-----------------------------------|
| Tempranillo (after alcohol. ferment.) | La Rioja, Spain   | Red Wine  | 48.2–14.8 mg L<sup>-1</sup> | 0.048–0.015 mg mL<sup>-1</sup> | (Martínez-Pinilla et al., 2013)  |
| Tempranillo (after malolact. ferment.) | La Rioja, Spain   | Red Wine  | 44.9–16.1 mg L<sup>-1</sup> | 0.045–0.016 mg mL<sup>-1</sup> |                                    |
| Monastel (after alcohol. ferment.) | La Rioja, Spain   | Red Wine  | 25.9–14.7 mg L<sup>-1</sup> | 0.026–0.015 mg mL<sup>-1</sup> |                                    |
| Monastel (after malolact. ferment.) | La Rioja, Spain   | Red Wine  | 11.1–15.1 mg L<sup>-1</sup> | 0.011–0.015 mg mL<sup>-1</sup> |                                    |
| Maturana (after alcohol. ferment.) | La Rioja, Spain   | Red Wine  | 10.7–5.2 mg L<sup>-1</sup>  | 0.011–0.005 mg mL<sup>-1</sup> |                                    |
| Maturana (after malolact. ferment.) | La Rioja, Spain   | Red Wine  | 15.1–5.8 mg L<sup>-1</sup>  | 0.015–0.006 mg mL<sup>-1</sup> |                                    |
| Grey Riesling (early stage fruit maturity) | –                  | White Wine | 53 μmol 100 mL<sup>-1</sup> | 0.055 mg mL<sup>-1</sup>     | (Kliewer, 1970)                   |
| Orange Musca (early stage fruit maturity) | –                  | White Wine | 208 μmol 100 mL<sup>-1</sup> | 0.214 mg mL<sup>-1</sup>     |                                    |
| Grey riesling (late stage fruit maturity) | –                  | White Wine | 140 μmol 100 mL<sup>-1</sup> | 0.144 mg mL<sup>-1</sup>     |                                    |
| Flora (late stage fruit maturity) | –                  | White Wine | 420 μmol 100 mL<sup>-1</sup> | 0.433 mg mL<sup>-1</sup>     |                                    |
| Vermentino                     | Italy              | White Wine | 130 mg L<sup>-1</sup>      | 0.13 mg mL<sup>-1</sup>      | (Tuberoso et al., 2015)           |
| Badacsonyi Szurkebarát         | Hungary            | White Wine | 16.6 mg L<sup>-1</sup>     | 0.017 mg mL<sup>-1</sup>     | (Kutlán & Molnár-Perl, 2003)     |
| Several                       | Alentejo region, Portugal | White Wine | 2.1–183.5 mg L<sup>-1</sup> | 0.002–0.183 mg mL<sup>-1</sup> | (Herbert et al., 2006)            |
| Airen variety                  | La Mancha          | White Wine | 36 mg L<sup>-1</sup>       | 0.036 mg mL<sup>-1</sup>     | (Hernández-Orte et al., 2003)    |
| Chardonnay                    | Spain              | White Wine | 114.8° mg L<sup>-1</sup>   | 0.115 mg mL<sup>-1</sup>     | (Guitart et al., 1997)           |
Table 1. (Continued)

| Variety                                      | Origin | Beverage | GABA content (harmonized units) | Reference                                  |
|----------------------------------------------|--------|----------|---------------------------------|--------------------------------------------|
| Wine vinegar with extracts of herbs          | Italy  | Vinegar  | 0.8 μg mL⁻¹                     | 0.0008 mg mL⁻¹ (Carlavilla et al., 2006)   |
| Acetatos balsámico di Modena                 | Italy  | Vinegar  | 62.9–159.4 μg mL⁻¹              | 0.063–0.159 mg mL⁻¹                        |
| Balsamic vinegar                             | Italy  | Vinegar  | 64.8–151.9 mg L⁻¹               | 0.065–0.152 mg mL⁻¹ (Erbe & Brückner, 1998) |
| Balsamic vinegar                             | Italy  | Vinegar  | 6.09–164.47 mg kg⁻¹             | 0.006–0.164 mg g⁻¹ (Chinnici, Duran-Guerrero, & Riponi, 2016) |
| Sherry vinegars                              | Spain  | Vinegar  | 9.9–21.0 μg mL⁻¹                | 0.010–0.021 mg mL⁻¹ (Carlavilla et al., 2006) |
| Sherry vinegars                              | Spain  | Vinegar  | 15.6–23.1 mg L⁻¹                | 0.016–0.023 mg mL⁻¹ (Erbe & Brückner, 1998) |
| Sherry vinegars                              | Spain  | Vinegar  | 44.61–96.69 mg kg⁻¹             | 0.045–0.097 mg g⁻¹ (Chinnici et al., 2016) |
| Sweet Sherry vinegars                        | Spain  | Vinegar  | 57.15–106.17 mg kg⁻¹            | 0.057–0.106 mg g⁻¹                        |
| White wine vinegar                           | Spain  | Vinegar  | 7.9 μg mL⁻¹                     | 0.008 mg mL⁻¹ (Carlavilla et al., 2006)    |
| White wine vinegar                           | Germany| Vinegar  | 2.6–7.9 mg L⁻¹                  | 0.003–0.008 mg mL⁻¹ (Erbe & Brückner, 1998) |
| Hungarian wine-vinegar                       | Hungary| Vinegar  | 21.5 mg L⁻¹                     | 0.021 mg mL⁻¹ (Kutlán & Molnár-Perl, 2003) |
| 3 different red wines                        | Spain  | Vinegar  | 4.60–31.80 mg L⁻¹               | 0.005–0.032 mg mL⁻¹ (Collejón et al., 2008) |
| Red wine vinegar                             | France, Germany | Vinegar | 9.3–34.5 mg L⁻¹                | 0.009–0.034 mg mL⁻¹ (Erbe & Brückner, 1998) |
| Cava vinegar                                 | Spain  | Vinegar  | 1.6 μg mL⁻¹                     | 0.0016 mg mL⁻¹ (Erbe & Brückner, 1998)     |
| Spirit vinegar                               | Germany| Vinegar  | 0.0–0.2 mg L⁻¹                  | 0.0–0.0002 mg mL⁻¹ (Erbe & Brückner, 1998) |

* Data for Vintage 2009–Vintage 2010
§ Data after 18 h fermentation and 6 months of bottle ageing, other examples reported
cortex, Arg/GABA content increased significantly during development in the stem ends (from 26 to 44 μg g⁻¹ FW [0.026 to 0.044 mg g⁻¹]) and decreased in middle of the fruit and blossom (17 to less than 5 μg g⁻¹ FW [0.017 to 0.005 mg g⁻¹]). The same tendency was observed in the inner cortex, demonstrating increasing Arg/GABA concentrations in stem ends (from 120 to 195 μg g⁻¹ FW [0.120–0.195 mg g⁻¹]) and decreasing in middle of the outer cortex and blossom (from around 100 to less than 25 μg g⁻¹ FW [0.100–0.025 mg g⁻¹]). In the core, the Arg/GABA content showed the same pattern in all the parts of the fruit, being lower in May than in February (blossom: from 1750 to 1300 μg g⁻¹ FW [1.75 to 1.3 mg g⁻¹]; middle of the fruit: from 1200 to 200 μg g⁻¹ FW [1.2–0.2 mg g⁻¹]; stem: from 600 to 75 μg g⁻¹ FW [0.6–0.075 mg g⁻¹]). It could be theorized that as the fruit ripens GABA is transported from the leaf to the fruit (Redgwell & Macrae, 1992).

GABA is the most abundant amino acid in lychee flesh (1.7–3.5 mg g⁻¹ FW), with a concentration approximately 100 times higher than in other fruits (Wu et al., 2016). The concentration varies among cultivars but remains relatively constant during development and maturation. When the amino acid composition of five kinds of lychee juices from cultivars of five regions in China were analyzed, GABA was found to be one of the major amino acids, with an average content of 104.69 mg 100 mL⁻¹ [1.05 mg mL⁻¹] (Cui et al., 2011). GABA was also found in other small fruits of inedible peel, such as in the flesh of rambutan, with a low concentration of 0.71 ± 0.23 mg g⁻¹ (Meeploy & Deewatthanawong, 2016); or in “Chuliang” and “Shixia” cultivars of Longan fruit (Dimocarpus longan Lour.) with a GABA content of 13–14 mmol kg⁻¹ FW [1.341–1.444 mg g⁻¹] (Zhou, Ndeurumio, Zhao, & Zhuoyan, 2016).

The presence of GABA in large fruit with inedible peel has also been reported. GABA content in banana fruit just after harvest was 23 μg g⁻¹ FW [0.023 mg g⁻¹]. The GABA concentration increased after 20 days of storage to 40.5 μg g⁻¹ [0.040 mg g⁻¹] (Wang, Luo, Mao, & Ying, 2016). The GABA content increased 41.1% during storage with nitrogen oxide treatment. In freshly harvested cherimoya fruit, GABA concentration was determined to be 0.045 μmol g⁻¹ FW [0.005 mg g⁻¹] increasing to 0.1 μmol g⁻¹ FW [0.010 mg g⁻¹] during storage. In treatments with CO₂, GABA content increased to 0.45 μmol g⁻¹ FW [0.047 mg g⁻¹] (Merodio, Muñoz, Del Cura, Buitrago, & Escribano, 1998). GABA concentrations in cherimoya varied between 2 and 6% of the total free amino acids content (Torres, Lazaro, Periago, Gil, & Faus, 1995). Pineapple juice was reported to have 40.1 μg mL⁻¹ [0.040 mg mL⁻¹] of GABA content (Mazzotti et al., 2012). Pepino (Solanum muricatum) extract was reported to have a very similar GABA concentration of 62.7 ± 0.9 μg mL⁻¹ [0.063 ± 0.0009 mg mL⁻¹] (Chang, Chiu, & Fu, 2015).

(Booz, Kerbasy, Guerra, & Pescador, 2009) reported the levels of endogenous GABA and investigated its role in different stages of somatic embryogenesis in guava (Acca sellowiana Berg. (Myrtaceae)). The highest level of GABA was detected from the third to the ninth day of culture (12.77 μmol g⁻¹ FW [1.317 mg g⁻¹]), during the period of intense cell proliferation in the explants. A decrease of GABA and other amino acids occurred during the different developmental stages of somatic embryos, being the lowest in cotyledonary-staged somatic embryos (0.08 μmol g⁻¹ FW [0.008 mg g⁻¹]).

### 2.2. GABA in vegetables

#### 2.2.1. Root and tuber vegetables

Potato tuber was the vegetable in which GABA was detected for the first time (Steward et al., 1949). Many further studies have been undertaken since this first analysis. (Table 2). GABA is usually found in higher concentrations than other plant metabolites (Choi, Kozukue, Kim, & Friedman, 2016; Golan-Goldhirsh, Hogg, & Wolfe, 1982) and the content varies depending on the potato tissue (Choi et al., 2016; Talley, Toma, & Orr, 1983), type of cultivar (Choi et al., 2016; Nakamura, Nara, Noguchi, Ohshiro, & Koga, 2006; Talley et al., 1983), environmental conditions and postharvest processing (Kim & Yoon, 2013; Sullivan, Kozempel, Egoville, & Talley, 1985; Talley...
| Potato tissue                      | Potato variety       | GABA content (μmol g⁻¹ FW) | GABA content (harmonized units) | Reference                          |
|-----------------------------------|----------------------|-----------------------------|---------------------------------|------------------------------------|
| Potato tuber                      |                      | 5.66                      | 0.54 mg g⁻¹                    | (Jaarma, 1969)                     |
| Raw whole potato                  | Katahdin//Pontiac    | 18.4                       | 0.017 mg g⁻¹                   | (Oh et al., 2003)                  |
| Potato                            | 22 varieties         | 16–61                      | 0.16–0.61 mg g⁻¹                | (Nakamura et al., 2006)           |
| Whole potato                      | Atlantic//Goun//K1//K20|| 783//1.41//2.51//1.05//1.64 mg g⁻¹ | (Choi et al., 2016)             |
| Peeled potato                     | –                    | 27% of total free aa       |                                 | (Galan-Goldhirsh et al., 1982)    |
| Raw flesh                         | Katahdin//Pontiac    | 22.1                       | 2.279 mg g⁻¹                   | (Talley et al., 1983)             |
| Pulp                              | Atlantic//Goun//K1//K20| 154//1.99//3.57//1.282 mg 100 g⁻¹ DW | 1.54//1.99//3.57//1.65//2.82 mg g⁻¹ | (Choi et al., 2016)             |
| Peel                              | Superior             | 108–143                    | 1.08–1.43 mg g⁻¹                | (Choi et al., 2016)               |
| Potato juice                      | –                    | 110–240                    | 1.10–2.40 mg mL⁻¹               | (Kim & Yoon, 2013)                |
| Sweet potato                      | –                    | 137 nmol g⁻¹ DW            | 0.014 mg g⁻¹                    | (Oh et al., 2003)                  |
| Peeled Bo flesh                   | Katahdin//Pontiac    | 25.4                       | 2.619 mg g⁻¹                   | (Talley et al., 1983)             |
| Flesh from BoU whole potato       | –                    | 21.3//26.8                  | 2.196//2.764 mg g⁻¹              | (Talley et al., 1983)             |
| Flesh from MC whole potato        | –                    | 25.9//20.3                  | 2.671//2.093 mg g⁻¹              | (Talley et al., 1983)             |
| Flesh from OB whole potato        | –                    | 25.8//27.3                  | 2.660//2.815 mg g⁻¹              | (Talley et al., 1983)             |
| Peel from Bo whole potato         | –                    | 14.4//19.9                  | 1.485//2.052 mg g⁻¹              | (Talley et al., 1983)             |
| Peel from MC whole potato         | –                    | 14.0//15.5                  | 1.444//1.598 mg g⁻¹              | (Talley et al., 1983)             |
| Peel from OB whole potato         | –                    | 14.1//21.7                  | 1.454//2.238 mg g⁻¹              | (Talley et al., 1983)             |
et al., 1983). Sweet potato has similar amounts of GABA (137 nmol g$^{-1}$ DW [0.014 mg g$^{-1}$]) to potato (Oh et al., 2003).

Radish (Raphanus sativus L.) has been reported to contain 0.28 ± 0.01 mg of GABA per g of dry weight (DW) of root radish at harvest (Kato et al., 2015) and 1 µmol g$^{-1}$ FW [0.103 mg g$^{-1}$] in mature leaves (Streeter & Thompson, 1972). Powdered sprouts of radish had a GABA concentration of 18.7 mg 100 g$^{-1}$ DW [0.187 mg g$^{-1}$] (Nakamura et al., 2016). Post-harvest processing, such as dehydration by sun-drying or salt-pressing process, caused an increased of GABA content in roots to 7.30 ± 1.57 and 4.98 ± 0.06 mg g$^{-1}$ DW, respectively. Leaves also showed an increase of GABA content when submitted to anaerobic stress.

Carrot is another example of root vegetables with low GABA contents, <0.14 µg g$^{-1}$ FW [0.00014 mg g$^{-1}$] (Fan, Higashi, Lane, & Jardetzky, 1986) and 28 nmol g$^{-1}$ DW [0.003 mg g$^{-1}$] (Oh et al., 2003). GABA concentration was reported to be higher in dehydrated carrots, 2.3–2.8 g kg$^{-1}$ DW [2.3–2.8 mg g$^{-1}$] (Gamboa-Santos, Soria, Corzo-Martinez, Villamiel, & Montilla, 2012). In beet roots, GABA content was quantified in the range of 0–16 mg g$^{-1}$ (Westall, 1950). Jerusalem artichoke (Helianthus tuberosus L.) tubers contain GABA, as demonstrated using 1H-NMR (Claussen, Bach, Edelenbos, & Bertram, 2012). Flour from six varieties of taro roots, grown in Cameroon and Chad, were reported to contain 1.61 and 2.40 g GABA 100 g$^{-1}$ respectively (Lim, 2015).

### 2.2.2. Bulb vegetables

There have been few studies to determine GABA content of bulb vegetables, such as onions, garlics and shallots, among others. (Oh et al., 2003) showed that onions contain a low amount of GABA, 12 nmol g$^{-1}$ DW [0.001 mg g$^{-1}$]. However, (Moreno, Marta Corzo-Martinez, Del Castillo, & Villamiel, 2006) were not able to find GABA, measured as 2-furoylmethyl derivative (2-FM-GABA), neither in dehydrated onion nor in garlic. FM-GABA was only detected at low levels in stored onion. Thus, 2-FM-GABA showed a maximum concentration of 247 mg 100 g$^{-1}$ [2.47 mg g$^{-1}$] protein and remained constant from the fourth to the tenth day of storage.

### 2.2.3. Fruiting vegetables

Tomato (Solanum lycopersicum L.; Solanaceae) is a major crop worldwide. It has become an excellent model for the analysis of fruit development, ripening, metabolism and genomic research of solanaceous plants ((Rastogi & Davies, 1990; Takayama & Ezura, 2008; Yin et al., 2010) and references therein). In comparison with other plants, this vegetable accumulates a large amount of GABA in the fruits (Choi et al., 2014; Morini, Stingone, Cornali, & Sondei, 2015), although the content differs greatly among the varieties (Table 3). GABA content in other parts of the plant has also been reported but is usually found in lower quantities.

Drastic changes in GABA levels have been observed during fruit development, increasing during the mature green stage and rapidly decreasing during the ripening stage (Kader, Stevens, Albright, & Morris, 1978; Inaba, Yamamoto, Ito, & Nakamura, 1980; Akihiro et al., 2008; Perez et al., 2011). In order to improve tomato fruit quality, several analyzes have been reported to evaluate the influence of GABA content during plant development or postharvest storage under conditions of stress. It is generally reported that amounts of GABA increased compared to control samples (Bolarín, Santa-Cruz, Cayuela, & Pérez-Alfocena, 1995; Deewatthanawong & Watkins, 2010; Mae et al., 2010; Saito et al., 2008; Selman & Cooper, 1978; Zushi & Matsuzoe, 2007; Zushi, Matsuzoe, Yoshida, & Chikushi, 2005).

Data on GABA content of tomato-processed products has also been reported (Morini et al., 2015). A recent example is the quantification of GABA for each step of the production of tomato vinegar (Koyama et al., 2015): raw tomato juice (422 mg 100 mL$^{-1}$) [4.22 mg mL$^{-1}$], tomato wine after alcohol fermentation (348 mg 100 mL$^{-1}$) [3.48 mg mL$^{-1}$] and tomato vinegar after acetic acid fermentation (398 mg 100 mL$^{-1}$) [3.98 mg mL$^{-1}$].
| Tomato variety * | Tissue* | Stage * | GABA content | GABA content (harmonized units) | Data comments | Reference |
|------------------|---------|---------|--------------|----------------------------------|---------------|-----------|
| Solanum lycopersicum | Fruits | Days after flowering (DAF) | 1250–140 mg 100 g⁻¹ FW | 12.50–1.40 mg g⁻¹ | 27 DAF—45 DAF | (Akihiro et al., 2008) |
| L. esculentum Mill. | Leaves | Development | 1–2.1 μmol mL⁻¹ | 0.103–0.217 mg mL⁻¹ | day 0–day 8 | (Balarin et al., 1995) |
| L. esculentum Mill. | Root | | ≤0.2–0.6 μmol mL⁻¹ | ≤0.021–0.062 mg mL⁻¹ | day 0–day 8 | |
| L. pennelli (Correll) D'Arcy (wild salt tolerant) | Leaves | | 0.6–0.8 μmol mL⁻¹ | 0.062–0.082 mg mL⁻¹ | day 0–day 8 | |
| L. pennelli (Correll) D'Arcy (wild salt tolerant) | Root | | 0.5–0.8 μmol mL⁻¹ | 0.052–0.082 mg mL⁻¹ | day 0–day 8 | |
| 11 lines of San Marzano tomatoes | Fruits | At harvest | 132–201 mg 100 g⁻¹ | 1.32–2.01 mg g⁻¹ | ≠ lines | (Loiudice et al., 1995) |
| L. peruvianum | Fruits | At harvest | 9.8–10.1 mg 100 g⁻¹ FW | 0.098–0.101 mg g⁻¹ | ≠ lines | (Anan, Ito, & Monma, 1996) |
| L. esculentum | Fruits | At harvest | 52.4–107.7 mg 100 g⁻¹ FW | 0.524–1.077 mg g⁻¹ | ≠ lines | |
| L. pimpinellifolium | Fruits | At harvest | 34.2–49.7 mg 100 g⁻¹ FW | 0.342–0.497 mg g⁻¹ | ≠ lines | |
| L. hirsutum | Fruits | At harvest | 25.5 mg 100 g⁻¹ FW | 0.255 mg g⁻¹ | | |
| Lycopersicon esculentum Mill | Fruits | At harvest | 17.4 mg 100 g⁻¹ FW | 0.174 mg g⁻¹ | 2.60 mg g⁻¹ DW | (Zushi et al., 2005) |
| 61 commercial cultivars, wild species, and wild derivatives | Fruits | At harvest | 8.8–189.7 mg 100 g⁻¹ FW | 0.088–1.897 mg g⁻¹ | ≠ cultivars | (Saito et al., 2008) |
| Solanum lycopersicum Mill. “NDM051TM” | Fruits | At harvest | 40.3 mg 100 g⁻¹ FW | 0.403 mg g⁻¹ | | (Saito et al., 2008) |
| 12 varieties of Korean cherry tomato | Fruits | At harvest | 195.2–735 mg 100 g⁻¹ DW | 1.952–7.35 mg g⁻¹ | ≠ varieties | (Choi et al., 2014) |

(Continued)
Table 3. (Continued)

| Tomato variety * | Tissue* | Stage * | GABA content | GABA content (harmonized units) | Data comments | Reference |
|------------------|---------|---------|--------------|---------------------------------|---------------|-----------|
| Cherry tomato, variety Lycopersicon | Fruits | At harvest | 305.99 mg 100 g⁻¹ DW | 3.06 mg g⁻¹ | = varieties | Ahn & 김현룡, 2014 |
| * Solanum lycopersicum L., (varieties Rafito, Momotaro, and Medison) | Fruits | At harvest | 666.95–868.48 mg 100 g⁻¹ DW | 6.67–8.68 mg g⁻¹ | = varieties | Ahn, 2016 |
| * Solanum lycopersicum L., (House Momotaro cultivar) | Fruits | At harvest | 8.2–9 μmol g⁻¹ FW | 0.846–0.928 mg g⁻¹ | = lines | Mae et al., 2010 |
| * Solanum pennellii | Pericarp | At harvest | 0.2–0.8 μmol g⁻¹ FW | 0.021–0.082 mg g⁻¹ | = lines | Deewatthanawong & Watkins, 2010 |

*As named by authors

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* IG, Immature green; pMG, partially mature-green; MG, mature-green; B, breaker; LP, light pink; DP, dark pink; TR, table ripe
(Mori et al., 2013) reported the amount of GABA in nine selected varieties of aubergine (Solanum melongena L.). The results (23.3–38.1 mg 100 g⁻¹ FW) [0.23–0.38 mg g⁻¹] were very similar to those reported by (Horie, Ando, & Saito, 2013). The average content in the fruit was 24 mg 100 g⁻¹ FW [0.24 mg g⁻¹], and the difference among the varieties was not significant. Heat treatment at 60°C induced the accumulation of GABA in the fruit and doubled the contents of GABA after supplying glutamate to the fruit.

The variability of GABA levels was investigated in six cultivars of bitter melon (Momordica charantia L.) of different origins: Nikko and Peacock from Japan, Galaxy and Verde Buenas from Philippines and two native cultivars from China and Korea (Kim et al., 2009). The Philippines cultivar, Galaxy, contained the highest amount of GABA (19.3 μmol g⁻¹ DW [1.990 mg g⁻¹]) followed by the Chinese native (14.0 μmol g⁻¹ DW [1.444 mg g⁻¹]) which was around five times more than the other cultivars. The cultivars Peacock, the Korean native, Verde Buenas and Nikko contained as low as 3.5, 4.2, 4.8 and 5.2 μmol GABA g⁻¹ DW [0.361, 0.433, 0.495 and 0.536 mg g⁻¹], respectively. (Lee, 2016) also studied the GABA content of bitter melon and determined that it was rich in GABA, with a concentration of 283.8 mg 100 g⁻¹ DW [2.838 mg g⁻¹]. Courgette fruit (Cucurbita pepo) was found to have less GABA content in the exocarp, fluctuating from 26 to 40 μg g⁻¹ [0.026–0.040 mg g⁻¹] depending on variety. GABA content decreased during storage at 4°C in two varieties, by approximately 70% in Natura fruit (more tolerant to chilling) and 35% in Sinatra fruit (more sensitive) at 7 and 14 days (Palma, Carvajal, Jamilena, & Garrido, 2014). The floral nectar of Cucurbita pepo L was analyzed and showed a GABA content in male and female flowers of 734 ± 86.3 and 678.6 ± 94.1 pmol μL⁻¹ [75.69 ± 8.90 and 69.98 ± 9.70 mg mL⁻¹] respectively (Nepi et al., 2012).

Among cucurbits with inedible peel, studies on muskmelon (Cucumis melo L.) have been reported. Absolute concentration of GABA varied between 1 and 7 mM L⁻¹ of juice [0.103–0.722 mg mL⁻¹] depending on the location in the slice of melon fruit used (Cezanne cv.) (Biais et al., 2010). During plant growth (cv. Yipintianxia No. 208) leaves and roots behave differently with respect to GABA content. GABA in leaves remained constant over a period of 7 days (28.20–28.70 mg 100 g⁻¹ FW [0.282–0.287 mg g⁻¹]), whereas GABA content in roots increased from 27.6 to 50 mg 100 g⁻¹ FW [0.276–0.50 mg g⁻¹] (Hu et al., 2015).

Pumpkin is another widely cultivated vegetable used for human consumption. GABA was present in significant concentrations in the five cultivars of pumpkin seeds, ranging from 3.71 to 15.53 mg g⁻¹ (Qi, Yang, Wang, Xu, & Qu, 2012). (Watanabe et al., 2013) showed that pumpkin had a similar GABA content after freezing, 115 ± 31 mg 100 g⁻¹ [1.15 ± 0.31 mg g⁻¹].

2.2.4. Brassica vegetables

The levels of amino acids in broccoli (Brassica oleracea L. var italica) stems and florets have been analyzed (Murcia, Lopez-Ayerra, Martinez-Tome, & Garcia-Carmona, 2001). GABA content in raw broccoli stem was lower, 19 mg kg⁻¹ FW [0.019 mg g⁻¹] than in raw broccoli florets (31 mg kg⁻¹ FW [0.031 mg g⁻¹]). This data is similar to the data of (Oh et al., 2003) (77 nmol g⁻¹ DW [0.008 mg g⁻¹]). Powdered sprouts of broccoli had higher amounts of GABA, 30.7 mg 100 g⁻¹ [0.307 mg g⁻¹] (Nakamura et al., 2016). Postharvest treatments negatively affected the amount of GABA in broccoli. In the case of frozen (after blanching) broccoli florets, GABA decreased by 83.9 and 52.6% in frozen stems (Murcia et al., 2001). However, when bottling, GABA is one of the amino acids least affected (19.3% loss). Postharvest storage under CO₂ atmosphere increased GABA content from 27.4 μmol g⁻¹ DW [2.825 mg g⁻¹] (fresh harvested) to 211.8 μmol g⁻¹ DW [21.841 mg g⁻¹] after 7 days under an atmosphere of 20% CO₂ in N₂ (Hansen, Sorensen, & Cantwell, 2001).

(Park et al., 2014) identified moderate levels of GABA in different cabbage varieties. Quantification of GABA was made in 45 varieties of green cabbage (3.2–7.1 mg 100 g⁻¹ FW [0.032–0.071 mg g⁻¹]) and red cabbage (2.2–35.1 mg 100 g⁻¹ FW [0.022–0.351 mg g⁻¹]). Average contents were 1.66-fold higher in red cabbage, as opposed to the results obtained for...
kohlrabi (Brassica oleracea var. gongylodes) in which GABA was more abundant in green kohlrabi than in purple or pale green (Park et al., 2017). Using 1H NMR analysis (Kim et al., 2013) it was observed that Brassica rapa ssp. Pekinesis cultivars in Korea contained less GABA (below 500 μmol L⁻¹ [0.052 mg mL⁻¹]) than in China (700–2800 μmol L⁻¹ [0.072–0.289 mg mL⁻¹]).

(Na, Xiaofeng, & Liqian, 2013) observed that in leaves of fresh cabbage (Brassica oleracea var. capitata L.) GABA content in inner leaves (1.88 mg g⁻¹) was significantly higher than that in the outer leaves (1.02 mg g⁻¹). Postharvest treatments such as soaking or storing at low temperatures increased GABA concentration. GABA content in the Head-Type Kimchi cabbage leaves was higher than previously described (Seong, Chung, & Hwang, 2016). Kimchi cabbage leaves were divided into three portions, outer, mid and inner and the quantified GABA was 3.14 ± 0.06 mg 100 g⁻¹; 2.47 ± 0.15 mg 100 g⁻¹; 2.74 ± 0.09 mg 100 g⁻¹ wet basis [0.031 ± 0.0006; 0.025 ± 0.0015; 0.027 ± 0.0009 mg g⁻¹], respectively. Freeze-dried Chinese cabbage leaf and root were reported to contain 4690 and 7020 nmol g⁻¹ [0.484–0.724 mg g⁻¹] (Oh et al., 2003).

2.2.5. Leafy vegetables, herbs and edible flowers
Spinach (Spinacia oleracea) is an edible leaf vegetable with a high amount of GABA (414 nmol g⁻¹ DW [0.043 mg g⁻¹]; Oh et al., 2003)). GABA content was quantified in spinach grown in open fields and harvested at different intervals after sowing (DAS), showing that GABA concentration differed significantly depending on the harvesting day, 267 ± 29.3, 132.2 ± 15 and 260.7 ± 3.3 mg 100 g⁻¹ DM [2.67 ± 0.293; 1.32 ± 0.15; 2.61 ± 0.03 mg g⁻¹] at 79, 116, 145 DAS (Yoon et al., 2017). As in many other plants, GABA accumulated in spinach exposed to a variety of stresses, such as cold during development, cultivation in polder soil with high levels of NaCl (Shimomachi et al., 2008) or increase of UV-C radiation (Kobashigawa, Tamaya, & Shimomachi, 2011). Portulaca oleracea was found to contain a high concentration of GABA, 390 nmol g⁻¹ FW [0.040 mg g⁻¹] (Mudryj, Yu, & Aukema, 2014).

Mustard leaf (Brassica juncea (L.) Czern.) is part of a traditional fermented vegetable food (Kimchi) in Korea. In red mustard, the GABA content in flower buds was the highest (179.8 mg 100 g⁻¹ FW [1.798 mg g⁻¹]), whereas roots contained the lowest amount (1.77 mg 100 g⁻¹ FW [0.018 mg g⁻¹]). In green mustard, the GABA content in young leaves was the highest (97.76 mg 100 g⁻¹ FW [0.978 mg g⁻¹]), whereas seeds had the lowest (1.23 mg 100 g⁻¹ FW [0.012 mg g⁻¹]) (Kim, Lee, Kim et al., 2013).

2.2.6. Legume vegetables (fresh)
Legumes are considered to be an important dietary food with an excellent nutritional profile (Mudryj, Yu, & Aukema, 2014). They provide protein and fibre, as well as being a significant source of vitamins and minerals, such as iron, zinc, folate and magnesium. Among the amino acids, GABA is not very abundant in legume seeds although its concentration differs with the legume type. It is usually below a few milligrams per gram (Jeong et al., 2010; Li et al., 2010; Martinez-Villaluenga, Kuo, Lambein, Frias, & Vidal-Valverde, 2006; Pradeep, Malleshi, & Guha, 2011; Tiansawang, Luangpituksa, Varanyanond, & Hansawasdi, 2016).

Some studies related to amino acid metabolism and growth capacity in legumes have been reported (Bauer, Joy, & Urquhart, 1977; Camargos, Aguiar, Souza, Justino, & Azevedo, 2015; Dixon & Fowden, 1961). As in other types of vegetables, it has been shown that germination is the most sensitive growth stage when the concentration of GABA can be influenced (Nikmaram et al., 2017). Many methods have been tried to obtain sprouts with high GABA content. Such methods include varying pH, air flow (Li et al., 2010), temperature (Li et al., 2010; Mayer, Cherry, & Rhodes, 1990), irradiation (Antoniw & Sprent, 1978), hypoxia (Yang, Guo, & Zhenxin, 2013), salinity (Fougère, Le Rudulier, & Streeter, 1991), soaking during germination periods or the use of elicitors within the germination solution (Limon, Peñas, Martinez-Villaluenga, & Frias, 2014; Peñas et al., 2015). GABA content increases with fermentation. (Yeap et al., 2012) reported that 100 g of the nonfermented mung bean extract contained only 0.016 g [0.16 mg g⁻¹] of GABA, whereas the fermented mung bean extract showed an increased GABA concentration by 7.6-fold to 0.122 g 100 g⁻¹ [1.22 mg g⁻¹] of dried powder.
On the contrary, GABA decreased significantly after standard cooking methods. In germinated mung bean (0.807 g kg\(^{-1}\) DM [0.807 mg g\(^{-1}\)]), the remaining amounts of GABA were 0.063, 0.178, 0.218 and 0.184 mg g\(^{-1}\) after boiling, steaming, microwave cooking and open pan roasting processes, respectively (Tiansawang et al., 2016). Typical commercial products also showed very low GABA contents (Hermanussen, Gonder, Jakobs, Stegemann, & Hoffmann, 2010).

Data related to the most common legumes used as food dietary or forage crop are reported in Table 4.

2.2.7. Stem vegetables

Harvested fresh asparagus has a GABA content of 0.15 mg g\(^{-1}\) FW (Zhao & Jiang, 2007). This concentration is positively affected by post-harvest processes, such as soaking treatments in different conditions. Best results were obtained after soaking in citric acid-disodium hydrogen phosphate buffer of pH 7.0 or 100 μmol L\(^{-1}\) CaCl\(_2\) solutions for 2 h, resulting in an increase of GABA content by 73 or 62.23% over the control, respectively. Standard processing of green asparagus (Asparagus oficinalis, L.) for commercial purposes negatively affected the GABA content (Lopez et al., 1996). No substantial differences were found on the GABA contents of green asparagus, classified by commercial sizes according to the Spanish Quality Classification for processing vegetables (Fine (≤8 mm), Middle (9–11 mm), Thick (12–14 mm); Very thick (15–19 mm); Extra Thick ≥20 mm). Treatments like washing, blanching (5 min in 90°C water by gradual immersion) and canning (time elapsed from harvesting to obtain the processed product was between 18 and 24 h) decreased the amount of GABA to 1.39–1.67 mg g\(^{-1}\) DW, 0.62–1.39 mg g\(^{-1}\) DW and 0.37–0.84 mg g\(^{-1}\) DW respectively. Extra thick asparagus had the highest GABA content once canned.

To better understand their metabolism, isolated asparagus (Asparagus sprengeri Regel) mesophyll cells (Cholewa, Bown, Cholewinski, Shelp, & Snedden, 1997; Crawford, Bown, Breitkreuz, & Guinel, 1994) were studied. GABA content was reported in the range of 2.16–2.70 nmol of GABA/10\(^6\) cells [0.00022–0.00028 mg/10\(^6\) cells]).

GABA concentrations in artichoke heads of Cynara scolymus L. “Capuanella” were reported (Dosi, Daniele, Ferrara, Severino, & Maro, 2013). The amount of GABA was 1.140 mg 100 g\(^{-1}\) FW [0.011 mg g\(^{-1}\)], representing 0.015% of the total amino acid content.

2.2.8. Fungi, mosses and lichens

The kingdom Fungi is one of the most diverse groups of organisms and is generally recognized as comprising 1.5 million species, classified in five different phyla. Mushrooms generally are considered to be the spore-bearing fruiting body of higher fungi and most belong to the Basidiomycota. As they have been used as foods and food flavouring materials for centuries, their profile of volatile and non-volatile compounds has been widely studied (Kim et al., 2009; Oka, Tsuji, Ogawa, & Sasaoka, 1981; Rotzoll, Dunkel, & Hofmann, 2006) and references in Table 5). Data for GABA content in different species of culinary-medicinal mushrooms are summarized in Table 5. Concentration of GABA varies between species and strains. (Chen, Kung-Jui, Hsieh, Wang, & Mau, 2012) classified mushrooms into five levels depending on the amount of GABA (GABA content of >200 mg kg\(^{-1}\) DW, 100–200 mg kg\(^{-1}\), 10–100 mg kg\(^{-1}\), <10 mg kg\(^{-1}\), no detection; [>0.200, 0.100–0.200, 0.010–0.100, <0.010, mg g\(^{-1}\), no detection]). However, due to the variability of the reported data, this classification system is not commonly used.

Huitlacoche or cuitlacoche (Ustilago maydis) is an edible corn smut fungus consumed in Mexico, and it is becoming internationally known as a delicacy for its flavour. Its GABA concentration (0.75 mg g\(^{-1}\) DW) is much lower than most other reported fungi (Lizárraga-Guerra & López, 1996).
### Table 4. GABA content in legumes. First part includes legumes for typical human used. Second part, examples of commercial products with legumes. Third part, cultivated mainly as forage crops

| Legume               | Tissue//Stage*       | GABA content          | GABA content (harmonized units) | Data comments                  | Reference                                |
|---------------------|----------------------|-----------------------|----------------------------------|--------------------------------|------------------------------------------|
| Vigna radiata cv.   | Powdered sprouts     | 61.6 mg 100 g⁻¹ DW    | 0.616 mg g⁻¹                     |                                | (Nakamura et al., 2016)                 |
| Vigna radiata       | cv. Powedered sprouts| 61.6 mg 100 g⁻¹ DW    | 0.616 mg g⁻¹                     |                                |                                          |
| Vigna radiata L. Wilczek (6 cultivars) | Seed/sprout          | 9–18.5/20–27 mg 100 g⁻¹ DW | 0.09–0.185/0.20–0.27 mg g⁻¹ | = cultivars                   | (Jeong et al., 2010)                     |
| Vigna radiata       | Grain//soaking//sprout | 0.132/0.435/0.682 g kg⁻¹ DW | 0.132/0.435/0.682 mg g⁻¹ | Grain/soaking/12 h germ         | (Tiansawang et al., 2016)                |
| Vigna radiata       | Grain//soaking//sprout | 0.132/0.435/0.682 g kg⁻¹ DW | 0.132/0.435/0.682 mg g⁻¹ | Grain/soaking/12 h germ         | (Tiansawang et al., 2016)                |
| Vigna radiata       | Grain//soaking//sprout | 0.132/0.435/0.682 g kg⁻¹ DW | 0.132/0.435/0.682 mg g⁻¹ | Grain/soaking/12 h germ         | (Tiansawang et al., 2016)                |
| Vigna mungo         | Grain//soaking//sprout | 0.044/0.677/0.164 g kg⁻¹ DW | 0.044/0.677/0.164 mg g⁻¹ | Grain/soaking/12 h germ         | (Tiansawang et al., 2016)                |
| Vigna unguiculata cv California Blackeye | Suspension cells | 179–359 nmol g⁻¹ FW | 0.018–0.037 mg g⁻¹ | ≠ culture periods              | (Mayer et al., 1990)                     |
| Vicia faba L.       | seed/sprout// (cotyledon//embryo) | 1/1.25/1.15/1.5 mg g⁻¹ DW | 1/1.25/1.15/1.5 mg g⁻¹ | 5 days germ                    | (Yang et al., 2013)                      |
| Vicia faba L. (9 cultivars) | Seed/sprout         | 0–0.05/1.21–2.37 g kg⁻¹ DW | 0–0.05/1.21–2.37 mg g⁻¹ | –/⅓ day old; ≠ pH, T and air flow | (Li et al., 2010)                       |
| Phaseolus vulgaris cv Glamis | Nodules//Host cells | 7/16 µmol g⁻¹ | 0.722/1.650 mg g⁻¹ | At two irradiance levels 7/28 W/m² | (Antoniw & Sprent, 1978)                |
| Phaseolus vulgaris cv Glamis | Nodules//Host cells | 7/16 µmol g⁻¹ | 0.722/1.650 mg g⁻¹ | At two irradiance levels 7/28 W/m² | (Antoniw & Sprent, 1978)                |
| Phaseolus vulgaris var. Pinto | Sprout              | 0.57/0.72/0.79 mg g⁻¹ DW | 0.57/0.72/0.79 mg g⁻¹ | 4/6/8 days                     | (Limon et al., 2014)                     |
| Phaseolus aureus Roxb | Native//soaking//sprout//sprout | 20.6/385.0/644.5/781.0 nmol 100 mg⁻¹ | 0.021/0.397/0.665/0.805 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011)                   |
| Phaseolus mungo Roxb | Native//soaking//sprout//sprout | 11.1/349.4/312.2/385.5 nmol 100 mg⁻¹ | 0.011/0.360/0.322/0.398 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011)                   |
| Phaseolus acuminifolius, Jacq | Native//soaking//sprout//sprout | 20.7/531/1242.5/1401.7 nmol 100 mg⁻¹ | 0.021/0.548/1.281/1.445 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Butler & Bathurst, 1958)                |
| Lupinus angustifolius | Nodules              | 11/12 mg 100 g⁻¹ DW   | 0.11/0.12 mg g⁻¹                  | Free//Bound                     | (Larher, Goas, Le Rudulier, Gerard, & Hamelin, 1983) |
| Lupinus angustifolius | Nodules              | 4 µmol g⁻¹ DW         | 0.412 mg g⁻¹                     |                                |                                          |

(Continued)
| Legume                  | Tissue//Stage* | GABA content | GABA content (harmonized units) | Data comments     | Reference                  |
|------------------------|---------------|--------------|--------------------------------|-------------------|----------------------------|
| Lupinus angustifolius  | Seed//sprout  | 0.46/1.69 mg g⁻¹ DW | 0.46/1.69 mg g⁻¹ | 9 days germ       | (Martinez-Villaluenga et al., 2006) |
| L. var. zapaton        | Sprout        | 1.2–1.5 mg g⁻¹ DW | 1.2–1.5 mg g⁻¹ | Day 8             | (Peñas et al., 2015)        |
| Lens culinaris var.    | Seedlings     | 1.64/0.78/1.00/2.04/1.26 mg g⁻¹ DW | 1.64/0.78/1.00/2.04/1.26 mg g⁻¹ | 4 day old         | (Rozan, Kuo, & Lambein, 2001) |
| Castellana             | Sprout        | 1.2–1.5 mg g⁻¹ DW | 1.2–1.5 mg g⁻¹ | Day 8             | (Peñas et al., 2015)        |
| Lens culinaris, L.     | Native//soaking//sprout | 12.6/139.5/301.4/384.6 nmol 100 mg⁻¹ | 0.013/0.144/0.311/0.397 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011) |
| orientalis, L. ervoides, L. nigricans and L. adeimensis. | Nodules | 36 μmol g⁻¹ DW | 3.712 mg g⁻¹ | Day 5: Cotyledons/Root-shoot axis (1 d)/shoot shafts/root tips/ root tips | (Lawrence & Grant, 1963) |
| Pisum sativum L. var.  | Nodules       | 12/18 mg 100 g⁻¹ DW | 0.12/0.18 mg g⁻¹ | Free/Bound        | (Butler & Bathurst, 1958)    |
| Unica                  | Seedlings     | 491 μmol 100 seedlings⁻¹ | 50.63 mg 100 seedlings⁻¹ | Day 5, whole seedling | (Lawrence & Grant, 1963)    |
| Asmus sativum L. var.  | Nodules       | 435/1.8/35/18/6/0.2 μmol 100 seedlings⁻¹ | 44.86/0.19/3.61/1.86/0.62/0.02 mg 100 seedlings⁻¹ | Day 5: Cotyledons/Root-shoot axis (1 d)/shoot shafts/root tips/ root tips | (Mils & Joy, 1980) |
| Unica                  | Chloroplasts from leaf homogenates//Chloroplasts from ruptured protoplasts | 4/230 nmol mg⁻¹ Chl | 0.412/23.712 mg g⁻¹ Chl |                          | (Mils & Joy, 1980) |
| Asmus sativum L. cv.   | Native//soaking//sprout | 14.2/89.0/47.6/573.1 nmol 100 mg⁻¹ | 0.015/0.092/0.462/0.591 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011) |
| Little Marvel           | Nodules       | 10.9/312.4/290.0/367.7 nmol 100 mg⁻¹ | 0.011/0.322/0.299/0.379 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011) |
| Cicer arietinum         | Native//soaking//sprout | 14.2/89.0/47.6/573.1 nmol 100 mg⁻¹ | 0.015/0.092/0.462/0.591 mg g⁻¹ | Native/soaking/48 h germ/96 h germ | (Pradeep et al., 2011) |
| (Continued)             |               |              |                                |                   |                            |
## Table 4. (Continued)

| Legume               | Tissue//Stage* | GABA content | GABA content (harmonized units) | Data comments                  | Reference                          |
|----------------------|----------------|--------------|---------------------------------|--------------------------------|-----------------------------------|
| Primana lentils      | Commercial product  | 4 mg 100 g\(^{-1}\) | 0.04 mg g\(^{-1}\)              |                                | (Hermanussen et al., 2010)        |
| Lentils ’chef’       | Commercial product  | 5 mg 100 g\(^{-1}\) | 0.05 mg g\(^{-1}\)              |                                |                                   |
| Primana peas         | Commercial product  | 9 mg 100 g\(^{-1}\) | 0.09 mg g\(^{-1}\)              |                                |                                   |
| Dolichos biflorus    | Native//soaking//sprout | 16.9/63.5/162.7/241.0 nmol 100 mg\(^{-1}\) | 0.017/0.065/0.168/0.249 mg g\(^{-1}\) | Native//soaking//48 h germ/96 h germ | (Pradeep et al., 2011) |
| Trifolium repens/T. pratense/T. medium | Nodules | 1006 (2)/120 (12)/104 (-) mg 100 g\(^{-1}\) DW | 10.06 (0.02)/1.20 (0.12)/1.04 (-) mg g\(^{-1}\) | Bound GABA (free GABA) | (Butler & Bathurst, 1958) |
| Lotus uliginosus/L. Corniculatus | Nodules | 29 (-)/trace (-) mg 100 g\(^{-1}\) DW | 0.29 (-)/trace (-) mg g\(^{-1}\) | Bound GABA (free GABA) | (Butler & Bathurst, 1958) |
| Cytisus scoparius    | Nodules | 12 (8) mg 100 g\(^{-1}\) DW | 0.12 (0.08) mg g\(^{-1}\) | Bound GABA (free GABA) |                                   |
| Galega officinalis   | Nodules | 6 (13) mg 100 g\(^{-1}\) DW | 0.06 (0.13) mg g\(^{-1}\) | Bound GABA (free GABA) |                                   |
| Trifolium repens     | Effect nodules//(nelf nodules//roots//stems and petioles//leaves | 1.6/1.8/3.0/2.2/2.7 mg 100 g\(^{-1}\) DW | 0.016/0.018/0.03/0.02/0.027 mg g\(^{-1}\) | Free GABA |                                   |
| Medicago Sativa      | Nodules | 5/639 μmol g\(^{-1}\) DW | 0.516/65.89 mg g\(^{-1}\) | Free GABA/Bound GABA (2-month old plants) | (Larher et al., 1983) |
| Medicago Sativa      | Nodules (Cytosol Fractions) | 2700 nmol g\(^{-1}\) FW | 0.278 mg g\(^{-1}\) |                                   | (Ta, Mohamad, & Macdowall Fergus, 1986) |

*As named by authors.
Table 5. GABA content in fruting body and mycelia of different species of culinary-medicinal mushrooms. Multiple data for the same specie are for different strains. All presented data have been harmonized from mg kg\(^{-1}\) to mg g\(^{-1}\).

| Mushroom                  | Fruiting body (mg g\(^{-1}\) DW) | Mycelia (mg g\(^{-1}\) DW) | Reference |
|---------------------------|----------------------------------|-----------------------------|-----------|
| Agaricus bisporus         | 0.125; 0.36\(^a\)                |                             | Chen      |
| Agaricus blazei           | 0.360                             | 0.200                       | Chen      |
| Agaricus brasiliensis     | 1.845; 0.394; 0.590              | 0.039                       | Lo        |
| Agrocybe aegerita         | 0.822                             | 0.490                       | Lin       |
| Agrocybe cylindracea      | 0.730; 0.210                      | 0.123                       | Lo        |
| Agrocybe chauingi         | 0.239                             |                             | Lo        |
| Antrodia camphorata       |                                   | 0.038                       | Chen      |
| Antrodia salmonea         | 0.133                             |                             | Chen      |
| Armillaria mellea         |                                   | 0.034                       | Chen      |
| Auricularia fuscosequinea | 0.536                             |                             | Lo        |
| Auricularia mesenterica   | n.d.                              |                             | Chen      |
| Auricularia polytrichia   | 0.282                             |                             | Lo        |
| Boletus edulis            | 0.202; 0.110                      | 1.274                       | Lo        |
| Clitocybe maxima (cap)    | 0.017                             |                             | Chen      |
| Clitocybe maxima (stipe)  | 0.023                             |                             | Chen      |
| Coprinus comatus          | 1.092; 0.630                      | n.d.; 0.234; 0.230          | Cohen     |
| Cordyceps cicadae         |                                   | 0.255                       | Chen      |
| Cordyceps militaris       | 0.756                             | 0.071; 0.069; 0.180; 0.553; 0.494 | Cohen     |
| Coriolus versicolor       | 0.116                             |                             | Chen      |
| Cyathus striatus          | 0.037                             |                             | Lin       |
| Daedalia gibbosa          | 0.538                             |                             | Lin       |
| Flamulina velutipes       | 0.360; 0.230; 0.339               |                             | Cohen     |
| Fomes fomentarius         | 0.159                             |                             | Lin       |

(Continued)
Table 5. (Continued)

| Mushroom                      | Fruiting body (mg g⁻¹ DW) | Mycelia (mg g⁻¹ DW) |
|-------------------------------|---------------------------|---------------------|
| *Ganoderma sp.*               | 0.013; n.d.               | 0.250               |
| *Ganoderma lucidum*           | 0.017                     | 0.114; 0.095; 0.007 |
| *Ganoderma lucidum* (antler)  |                           | Lo                  |
| *Ganoderma lucidum* (baby Ling-chih) | 0.018                 | Lo                  |
| *Ganoderma lucidum* (regular) |                           | Lo                  |
| *Grifola frondosa*            |                           | Lo                  |
| *Hericium erinaceus*          |                           | 0.043               |
| *Hypsizygus marmoreus* (white) | 0.008                 | 0.012               |
| *Inonotus obliquus*           |                           | 0.012               |
| *Laetiporus sulphureus*       |                           | 0.018               |
| *Lentinus edodes*             |                           | 0.012               |
| *Marasmius crocatus*          |                           | 0.008               |
| *Marasmius cremnipes*         |                           | 0.008               |
| *Marasmius elodes*            |                           | 0.008               |
| *Phellinus linteus*           |                           | 0.018               |
| *Reaurotus crinitum*          |                           | 1.632               |
| *Reaurotus columbrius*        |                           | 1.107               |
| *Reaurotus cornucopiae*       |                           | 1.31                |

References:
- Cohen Chen Lin
- Lo
- Ramos-Ruiz et al., Cogent Food & Agriculture (2018), 4: 1534323

https://doi.org/10.1080/23311932.2018.1534323
| Mushroom                  | Fruiting body (mg g\(^{-1}\) DW) | Mycelia (mg g\(^{-1}\) DW) | Reference |
|---------------------------|----------------------------------|-----------------------------|-----------|
| Pleurotus cystidiosus     | 0.037                            | 2.553                       | Chen, Lin |
| Pleurotus dryinus         | 2.402                            |                             | Lin       |
| Pleurotus eryngii         | n.d.; 2.812                      |                             | Chen, Lin |
| Pleurotus eryngii (base)  | n.d.                             |                             | Chen      |
| Pleurotus eryngii (sporophore) | 0.025                          |                             | Chen      |
| Pleurotus ferulae         | 0.047                            | 0.062                       | Lo, Chen  |
| Pleurotus flavida         | 0.197                            |                             | Lin       |
| Pleurotus nebrodensis     | 1.057                            |                             | Lin       |
| Pleurotus ostreatus       | 1.305                            | 0.844                       | Cohen, Lin|
| Pleurotus ostreatus (Japan)| 0.006                           |                             | Chen      |
| Pleurotus ostreatus (Korea)| 0.024                           | 0.262                       | Lo, Chen  |
| Pleurotus ostreatus (Taiwan)| n.d.                           | 0.532                       | Lo, Chen  |
| Pleurotus pulmonarius     | 0.237; 1.321                     |                             | Lin       |
| Pleurotus salmoneastramineus | n.d.                            | 0.138                       | Lo, Chen  |
| Pleurotus smithii         | 1.994                            |                             | Lin       |
| Pleurotus tuber-regium    | 1.039                            |                             | Lin       |
| Termitomyces albuminosus  | 2.560                            |                             | Lo        |
| Trametes versicolor       | 0.100                            | 0.049; 0.146                | Cohen, Lin|
| Trametes zonata           | 0.125                            |                             | Lin       |
| Tremella fucoformis       | 0.687; 0.525; 0.372              |                             | Lo, Cohen |
| Tremella mesenterica\(^a\) | n.d.                             |                             | Lin       |
| Verpa bohemica            | 0.094                            |                             | Lin       |
| Volvariella volvacea      | 0.990                            |                             | Lo        |

\(^a\) n.d., not detected; \(^\#\) One-cell biomass. §, in mmol kg\(^{-1}\) in the original paper. References: Cohen: (Cohen et al., 2014); Chen: (Chen et al., 2012); Lin: (Lin et al., 2013); Lo: (Lo et al., 2012); Oh: (Oh et al., 2003); Okar (Oka et al., 1981); Tsai 7: (Tsai, 2007); Tsai 8: (Tsai, Tsai, & Mau, 2008).
Processing for commercial uses affect the chemical profile and, as in other food items, GABA content decreases in canned mushrooms (Chiang, Yen, & Mau, 2006). Considering the three types analyzed, canned mushrooms of Flammulina velutipes contained the highest amount of GABA (fruit body/broth; 25.8/18.7 μg g⁻¹ [0.026/0.019 mg g⁻¹]), whereas the concentrations of GABA in Agaricus bisporus (1.38/0.78 μg g⁻¹ [0.0014/0.0008 mg g⁻¹]) and Volvariella volvacea (1.31/0.34 μg g⁻¹ [0.0013/0.0003 mg g⁻¹]) were similar for fruit bodies and broth respectively. Drying processes also negatively affect GABA content. One example is reported by (Thomke, Rundgren, & Eriksson, 1980) using the white-rot fungus (Sporotrichum pulverulentum). The GABA content was 6.9 g per 16 g N (nitrogen) when the test material was dried in bulk, but 8.9 g and 1.8 g when material was dried by freeze plus oven or by fluid bed respectively.

Mushroom mycelia of Antrodia camphorata, Agaricus blazei, Hericium erinaceus and Phellinus linteus have been used to substitute 5% of wheat flour to make bread. After baking, mycelium-supplemented bread still contained substantial amounts of GABA (0.23–0.86 mg g⁻¹ DM) (Ulziijargal, Yang, Lin, Chen, & Mau, 2013).

(Bent & Morton, 1964) reported a study of the free and combined amino acids of the fungus Penicillium griseofulvum throughout its life cycle. GABA content of Penicillium griseofulvum, during growth in shaken culture, varied depending on the type and duration of the culture (7.3–25.3% of total free amino-N). After 45 h, the shaken culture showed levels of GABA of 4.9% (conidia) and 10.1% (sporogenous mycelium).

Pseudevernia furfuracea, a lichenized species of fungus that grows on the bark of firs and pines, contained 34.66 μmol g⁻¹ FW [3.574 mg g⁻¹] (Seher et al., 2013).

2.2.9. Algae and prokaryotes organisms

Marine algae comprises thousands of species that represent a considerable part of the littoral biomass. They are classified as green (Chlorophyta), brown (Phaeophyta) and red (Rhodophyta) algae on the basis of their nutrient and chemical compositions. Brown seaweeds are a very large group and, since ancient times, have been part of the diet in Asian countries. (Cao, Duan, Guo, Guo, & Zhao, 2014) reported the chemical analysis of 24 brown algae samples collected from different locations in China, all of them of the Sargassaceae family (Saccharina japonica, Sargassum pallidum, S. fusiforme, S. thunbergii and S. muticum). GABA was detected in some samples (33%), but generally in trace amounts (1.6–8.6 μg g⁻¹ [0.0016–0.0086 mg g⁻¹]).

Some examples of GABA content in green edible algae have been determined. Ulva lactuca (Seher et al., 2013) and green laver (Oh et al., 2003) have been analyzed showing an amount of GABA of 71.5 μmol g⁻¹ FW [3.574 mg g⁻¹] and 37 nmol g⁻¹ DW [0.004 mg g⁻¹], respectively. Chlorella vulgaris is an unicellular green algae that, under cultivation, produces GABA with the highest production rate of 1.90 μg L⁻¹ per day [1.9 × 10⁻⁶ mg mL⁻¹] under favourable conditions (Kim, Lim, Hong et al., 2016).

Due to its high GABA content, it is worth noting the data reported for the aquatic plants Nymphaea alba and Iris kaempferi, 787.76 μmol g⁻¹ FW [81.23 mg g⁻¹] and 738.14 μmol g⁻¹ FW [76.12 mg g⁻¹], respectively (Seher et al., 2013). (Lahdesmaki, 1968) reported that the amount of GABA in the leaves of Salvinia natans increases with age.

2.2.9.1. Prokaryotes organisms

Phytoplankton represents an important source of carbon and nitrogen in marine systems. (Kittredge, Simonsen, Roberts, & Jelinek, 1962) described for the first time that the dinoflagellate Gonyaulax polyedra had high concentrations of GABA, among other amino acids.
Sinking particles obtained in Breid Bay, Antarctica, at different depths, were analyzed for organic materials, stable carbon and nitrogen isotopes (Handa, Nakatsuka, Fukuchi, Hattori, & Hoshiai, 1992). The acid hydrolysates of these particles consisting of diatoms (mainly Thalassiosira Antarctica) had 15 types of protein amino acids with traces of GABA, β-Alanine and ornithine. The traces of these amino acids indicated that the sinking particles were fresh and that little microbial degradation had occurred.

The analysis made by (Nguyen & Rodger Harvey, 1997) on the contribution of the diatom Thalassiosira weissflogii, the cyanobacterium Synechococcus sp. and the dinoflagellate Prorocentrum minimum, to the amino acid and the particulate carbon and nitrogen pools during their microbially mediated degradation, gave similar results. In the oxic and anoxic dinoflagellate decay experiments, GABA plus β-Alanine reached a maximum of 3.6 and 5.6% respectively of the total hydrolysable amino acids and, thereafter, decayed to concentrations not significantly different from the initial concentrations (1.5%).

This same pattern was obtained in different samples from the Pacific Ocean, also suggesting the presence of microbes. High purity, hydrothermal fluids (300°C) sampled from natural and drilled vents in hydrothermal systems at Suiyo (Horiuchi et al., 2004), yielded different amounts of amino acids including GABA (1.2–6.9 nmol L⁻¹) [1.2 10⁻⁷–7.1 10⁻⁷ mg mL⁻¹] plus β-Alanine as minor constituents, in line with approximately 10⁴–10⁵ cell mL⁻¹ of microbes.

Particles in sea water can originate from a variety of sources including phytoplankton biomass, fragments and moulds of crustaceans, faecal pellets and exudates, resuspension of sediments, terrestrial inputs from rivers and even Aeolian transport. Biochemical and transformation processes occur in these sinking particles throughout the water column, ending as sediments, where they continue their metabolic degradation. Examples of processes will be discussed in the section regarding GABA in soils.

2.3. GABA in pulses
According to the Food and Agriculture Organization (FAO), pulses are defined as “Leguminosae crops harvested exclusively for their grain, including dry beans, peas and lentils”. Pulses are categorized into 11 groups as follows: dry beans, dry brood beans, dry peas, chickepeas, black-eyed peas, pigeon peas, lentils, bambara groundnut, vetch, lupins and other “minor” pulses. It is difficult to differentiate between fresh and dried seeds within literature on pulses, including metabolite profile during development. Therefore, within this review the information related to seed leguminosae, either fresh or dry, has been included in the section on legume vegetables.

2.4. GABA in oil seeds and oil fruits
2.4.1. Oil seeds
Soybean or soya bean is a legume classified as an oilseed due to its high oil content. Soybean accounts for more than a half of the overall world oilseed production. Soybean is a very versatile crop with many different applications from human food to industrial uses. It has been recognized for its healthy properties, being the focus of multiple research projects. GABA content in soybean has been well studied, including the influence of culture conditions during development, post-harvest treatments and processing.

The GABA content of dried soybeans was reported to be 211 μg g⁻¹ (0.211 mg g⁻¹) of soybeans (Zazzeroni et al., 2009) and it was found to be higher for powdered sprouts, 1.16 mg g⁻¹ (Nakamura et al., 2016). Similar to the observations for other seeds, soybean germination caused a significant increase of GABA. GABA content increased around four-fold from 0.25 to 0.9 mg g⁻¹ DW in Glycine max var. Jutro after 4 days of germination compared to var. Merit, which took 6 days of germination to reach 1.09 mg of GABA g⁻¹ DW (initial GABA content, 0.26 mg g⁻¹ DW) (Martínez-Villaluenga et al., 2006). (Tiansawang et al., 2016) obtained the best results after 6 h of incubation, from 0.1222 g kg⁻¹
The influence of germination in isolated germs was also evaluated. GABA content increased considerably as germination progressed, from 26.5 mg 100 g\(^{-1}\) [0.265 mg g\(^{-1}\)] in ungerminated soy seeds to 718.0 mg 100 g\(^{-1}\) [7.180 mg g\(^{-1}\)] after 24 h of germination. The total GABA content of whole soybeans (var. Daepung) was 5.79 mg 100 g\(^{-1}\) [0.058 mg g\(^{-1}\)] (Kim et al., 2013).

(Abe & Takeya, 2005) reported the quantitative differences in free amino acids and GABA in the cotyledon of immature seeds harvested at 35 days after flowering (DAF) of six vegetative-type soybean (Edamame) and two grain-type soybean. The concentration of GABA varied greatly among cultivars. Immature seeds of two vegetative-type soybean cultivars, Shirayama-dadacha and Wase-shirayama, had the highest content of GABA at 15 DAF with over 50 mg 100 g\(^{-1}\) FW [0.50 mg g\(^{-1}\)], and it remained high until 35 DAF, after which it decreased until 50 DAF.

Growth conditions during germination can have important effects on the composition of secondary metabolites of nutritional importance. GABA was shown to accumulate in high concentrations under stressed germination conditions. (Xing, Jun, Hau, & Liang, 2007) showed that the amount of GABA in soybean roots after germination under salinity stress (150 mM NaCl) increased to 11.3 \(\mu\)mol g\(^{-1}\) FW [1.165 mg g\(^{-1}\)] after 2 weeks (GABA content after standard growth was 0.61 \(\mu\)mol g\(^{-1}\) FW [0.063 mg g\(^{-1}\)]). Similar results were obtained after germination under hypoxia stress. GABA content in embryos of soybean sprouts increased from 0.65 mg kg\(^{-1}\) DW to 1.63 g kg\(^{-1}\) DW [0.65 to 1.63 mg g\(^{-1}\)] and in cotyledons increased to 2.61 g kg\(^{-1}\) DW [2.61 mg g\(^{-1}\)] compared to 0.86 g kg\(^{-1}\) DW [0.86 mg g\(^{-1}\)] under no-hypoxia conditions (Guo, Yang, Chen, Song, & Zhenxin, 2012). GABA content in leaves, roots and nodules also changed after 3 h of hypoxia during germination, increasing from 0.35, 0.11 and 1.27 \(\mu\)mol g\(^{-1}\) FW [0.036, 0.011 and 0.131 mg g\(^{-1}\)] to 0.90, 0.34 and 3.03 \(\mu\)mol g\(^{-1}\) FW [0.093, 0.035 and 0.312 mg g\(^{-1}\)], respectively (Serraj, Barry, & Sinclair Thomas, 2002). Drought stress also resulted in an increase in GABA concentration of about 230%. Similar changes in amino acid composition and accumulation of GABA have been observed previously in soybean leaves (with a low content of GABA, 0.05–0.35 \(\mu\)mol g\(^{-1}\) FW [0.05–0.35 mg g\(^{-1}\)]) in response to hypoxia, cold or mechanical stress (Ramputh & Bown, 1996; Shelp et al., 1999; Wallace, Secor, & Schrader, 1984).

Processing treatments also modify GABA concentration. Drying of immature seeds of vegetable soybean (Glycine max L. Merrill) at a maximum temperature of 40\(^\circ\)C increased the GABA content more than 5 times. Untreated seeds contained 79.6 mg of GABA 100 g\(^{-1}\) DW [0.796 mg g\(^{-1}\)] and heat-dried seeds accumulated 447.5 mg 100 g\(^{-1}\) DW [4.475 mg g\(^{-1}\)] (Takahashi, Sasuma, & Abe, 2013). Cooking processes had a negative influence on the GABA content of germinated soy beans. After 6 h of germination, GABA content was of 0.498 g kg\(^{-1}\) DW [0.498 mg g\(^{-1}\)], which decreased after boiling, steaming, microwave cooking and open pan roasting to 0.204, 0.407, 0.191 and 0.306 g kg\(^{-1}\) DW [0.204, 0.407, 0.191 and 0.306 mg g\(^{-1}\)], respectively (Tiansawang et al., 2016).

The nutritional evaluation of sesame seeds and sprouts has also been reported. GABA content of untreated Sesamum indicum seeds was very low, 24.12 \(\mu\)g g\(^{-1}\) DW [0.024 mg g\(^{-1}\)]. As germination progressed an increase of GABA was found, almost three times higher than in seeds 5 days after seeding, 95.28 \(\mu\)g g\(^{-1}\) DW [0.953 mg g\(^{-1}\)] (Liu, Guo, Zhu, & Liu, 2011). The same behaviour was reported by (Tiansawang et al., 2016), who found that the initial amount of GABA, 90.8 \(\mu\)g g\(^{-1}\) [0.091 mg g\(^{-1}\)] increased to 165 \(\mu\)g g\(^{-1}\) [0.165 mg g\(^{-1}\)] after 6 h of germination. (Bor et al., 2009) observed 150 \(\mu\)g g\(^{-1}\) FW [0.150 mg g\(^{-1}\)] of GABA in sesame seedlings.

The influence of post-harvest processing treatments in sesame seeds on GABA content is very similar to that described for soybean seeds. Temperature treatments induced GABA enrichment with a maximum GABA content of 0.84 \(\mu\)mol g\(^{-1}\) [0.087 mg g\(^{-1}\)] when the seeds were heated at 100\(^\circ\)C (GABA content of raw seeds was 0.06 \(\mu\)mol g\(^{-1}\) [0.006 mg g\(^{-1}\)]). Moreover, when water was added to sesame seeds, heating treatment increased GABA production to a maximum of 4.2 \(\mu\)mol g\(^{-1}\) [0.433 mg g\(^{-1}\)] when the seeds were heated at 60\(^\circ\)C (Katsuno et al., 2015). On the contrary,
cooking decrease GABA content of germinated sesame seeds. The amount of GABA in germinated sesame was $0.165 \text{ g kg}^{-1}$ DW [$0.165 \text{ mg g}^{-1}$], which decreased after boiling, steaming, microwave cooking and open pan roasting to $0.072, 0.073, 0.158$ and $0.093 \text{ g kg}^{-1}$ DW [$0.072, 0.073, 0.158$ and $0.093 \text{ mg g}^{-1}$] respectively (Tiansawang et al., 2016).

Other oil seeds or tissues of oil plants have been analyzed to determine the concentration of GABA. Some examples of GABA content are reported: Mustard seed ($Brassica juncea$ (L.) Czern.), $1.23 \text{ mg 100 g}^{-1}$ FW [$0.012 \text{ mg g}^{-1}$] (Kim, Lim, Kim et al., 2013); Conophor Nut ($Tetracarpidium conophorum$), $0.5 \text{ mmol (relative amount, (Ogunsua, 1988))}$; incubated excised cotyledons of germinated sunflower seed ($Helianthus annuus$ L.), $0.39 \text{ mmol g}^{-1} \text{ FW}$ [$0.040 \text{ mg g}^{-1}$] (Arunugam, Tung, Chinnappa, & Reid, 1997); roots of $Brassica napus$ L. cv. Capitol, $494 \text{ nmol g}^{-1} \text{ FW}$ [$0.051 \text{ mg g}^{-1}$] (Beuve et al., 2004).

GABA content of seed oils have also been reported, that is sunflower oil ($0.4-0.7 \text{ ng g}^{-1}$ [$4 \times 10^{-7}$-$0.7 \times 10^{-7} \text{ mg g}^{-1}$]), corn oil ($0.5-0.7 \text{ ng g}^{-1}$ [$5 \times 10^{-7}$-$0.7 \times 10^{-7} \text{ mg g}^{-1}$]), soybean oil ($0.37-0.62 \text{ ng g}^{-1}$ [$3.7 \times 10^{-7}$-$6.2 \times 10^{-7} \text{ mg g}^{-1}$]) (Sánchez-Hernández, Marina, & Crego, 2011).

2.4.2. Oil trees

The main focus of the studies performed with olives was to determine the chemical composition related to fatty acids, vitamins and volatile components. There is very little information related to the amino acid profile. (Rosati et al., 2014) reported that olive ($Olea europaea$ L.) of Leccino cultivars had larger amounts of GABA than Frantoio cultivars.

GABA content is much lower in olive oils than in seed oils. Hojiblanca extra virgin olive oil contained $0.10-0.12 \text{ ng g}^{-1}$ [$0.0001-0.00012 \text{ mg g}^{-1}$] and Arbequina extra virgin olive oil contained $0.06-0.14 \text{ ng g}^{-1}$ [$0.00006-0.00014 \text{ mg g}^{-1}$] (Sánchez-Hernández et al., 2011).

2.5. GABA in cereals

Cereals are the edible seeds or grains of the grass family, Gramineae, including corn, barley, oats, triticale, millet, sorghum and rice. On a worldwide basis, wheat and rice are the most important crops, accounting for over 50% of the world’s cereal production. Cereals are basic foods, and are an important source of energy, carbohydrates, proteins and fibres, as well as containing a range of micronutrients such as vitamin E, some of the B vitamins, magnesium and zinc. They are also an important source of GABA compared to other vegetables (Oh et al., 2003). Many studies are available reporting GABA content in cereals (Tables 6 and 7) and nearly half of them focused on rice ((Cho & Lim, 2016; Patil & Khan, 2011), references in Table 7).

Considering the data reported, it was observed that brown rice, barley and corn had higher concentrations of GABA compared to other cereal grains. Nevertheless, there is great variability dependent on many factors including the cultivar (Frank, Reichardt, Shu, & Engel, 2012; Kihara, Okada, Iimure, & Ito, 2007; Ko et al., 2011; Nagota et al., 2012; Roohinejad et al., 2009; Saikusa, Horino, & Mori, 1994), soaking condition (Banchuen, Thammarutwasik, Oraikul, Wuttijummong, & Sirivongpaisal, 2008; Komatsuzaki et al., 2007; Oh, 2003), germination conditions (Reggiani, Cantu, Brambilla, & Bertani, 1988; Pradeep et al., 2011; Paucar-Menacho, Luz, Duenas, Frias, & Martinez-Villaluenga, 2017), stress pre-treatments (Caceres, Penas, Martinez-Villaluenga, Amigo, & Frias, 2017; Choi et al., 2014) and post-harvest treatments (Mazzucotelli, Tartari, Cattivelli, & Forlani, 2006).

Soaking generally increases the GABA content (Homma, Morohashi, Yoshii, Hosokawa, & Miura, 2006) and similar results have been reported for germination (Morita, Miyake, Maeda, & Van Hung, 2013; Morita, Park, & Maeda, 2013; Polthum & Ahromrit, 2014, van Hung, Maeda, Yamamoto, & Morita, 2012; Yang, Peng Wang, Elbaloula, & Zhenxin, 2016). Again, soaking and germination conditions and time influenced the final GABA concentration. Grain fermentation also increased the GABA content (Hayat et al., 2015).
| Cereal (1) | Tissue/Stage (1) | GABA content | GABA content (mg g⁻¹) | Data comments | Reference |
|------------|------------------|---------------|------------------------|---------------|-----------|
| Adlay Seed (Coixlachryma-jobi L.) | non-germinat./germinat | 29.70/102.7 mg 100 g⁻¹ | 0.297/1.027 | 60 h germinat. | (Xu et al., 2017) |
| Barley | Seed/sprout | 190/326 nmol g⁻¹ DW | 0.020/0.034 | | (Oh et al., 2003) |
| 43 Barley varieties (Canada, Germany, Australia, New Zealand and Japan) | non-germinat./germinat | 10–12/25.7–89.4 mg 100 g⁻¹ DM | 0.10–0.12/0.26–0.89 | | (Kihara et al., 2007) |
| 20 cultivars and 20 breeding lines barley samples | Cultivar/breeding line | 2.7–24.5/4.3–41.7 mg 100 g⁻¹ | 0.027–0.245/0.043–0.417 | | (Nogata et al., 2012) |
| Frost resistant barley (H vulgare L cv Nure); Frost-sensitive barley (H vulgare cv. Tremois) | Seedlings | 0.023; 0.020 μmol g⁻¹ FW | 0.002; 0.002 | 8 day germinat | *(Mazzucotelli et al., 2006) |
| Buckwheat | Non-germinat. grain/germinat grain | 12.4/28.7 mg 100 g⁻¹ DM | 0.124/0.287 | 24 h germinat | (Morita, Miyake et al., 2013) |
| (Fagopyrum esculentum Moench) | Seed/sprout | 2.5/79 mg 100 g⁻¹ DW | 0.025/0.79 | 7 days after seeding | (Kim, Kim, & Park, 2004) |
| Buckwheat | Milled | 9; 3; 87; 310; 89 mg 100 g⁻¹ DM | 0.009; 0.003; 0.87; 3.10; 0.89 | Grain gradually milled from the inner to the outer layers | (Morita, Miyake et al., 2013) |
| Fagopyrum esculentum cv. | Powdered sprouts | 144.7 mg 100 g⁻¹ DW | 1.447 | | (Nakamura et al., 2016) |
| Corn | Seed | 199 nmol g⁻¹ DW | 0.021 | | (Oh et al., 2003) |
| Five corn isonuclear inbred lines | Seed | 65.59–871.96 μg g⁻¹ | 0.066–0.872 | | (Culea et al., 2015) |
| 2 Thai waxy corn KKU-KND (purple seed); KKU-SLE (white seed) | Non-germinat./germinat | 2.68; 1.58/10.45; 10.20–5.94; 7.78 mg 100 g⁻¹ DM | 0.027; 0.016/0.104; 0.102–0.059; 0.078 | 24 h–48 h germinat. | *(Polthum & Ahromrit, 2014) |
| 4 small ear waxy corn | Seed/sprout/seedling | 0.016–0.03/0.020–0.028/0.145–0.231 mg 100 g⁻¹ | 0.0002–0.0003/0.0002–0.0003/0.0003/0.0002–0.0003 | | *(Chalorcharoenying et al., 2017) |
| 3 waxy corn | Seed/sprout/seedling | 0.021–0.038/0.033–0.053/0.209–0.224 mg 100 g⁻¹ | 0.0002–0.0004/0.0003–0.0004/0.0004–0.0002 | | *(Chalorcharoenying et al., 2017) |
| Cereal (1)                  | Tissue/Stage (1)               | GABA content (mg g⁻¹) | GABA content (mg g⁻¹) | Data comments                                      | Reference                                      |
|-----------------------------|--------------------------------|------------------------|------------------------|----------------------------------------------------|-----------------------------------------------|
| 3 field corn                | Seed/sprout/seedling           | 0.038–0.066/0.031–0.038/0.150–0.232 mg 100 g⁻¹ | 0.0004–0.0007/0.0003–0.0004/0.0015–0.0023 | (Chalorcharoenying et al., 2017)                   |
| 3 sweet corn                | Seed/sprout/seedling           | 0.028–0.035/0.027–0.090/0.092–0.184 mg 100 g⁻¹ | 0.0003–0.0003/0.0003–0.0009/0.0009–0.0018 | (Chalorcharoenying et al., 2017)                   |
| Corn                        | Root                           | 0.37 μg g⁻¹ FW         | 0.0004                 | Best germinat conditions 26°C for 63 h and 28°C for 42 h | (Fan et al., 1986)                           |
| Kiwicha (Amaranthus caudatus) | Non-germinat./germinat         | 2.6/9.47–75.69 mg 100 g⁻¹ DM | 0.0026/0.0095–0.0076   | (Maria Paucar-Menacho et al., 2017)                |
| Eleusine coracana; Panicum sumatrense | Native/germinated     | 21.4; 32.2/83.8; 77.2–256.5; 84.6–361.8; 55.4 nmol 100 mg⁻¹ DM | 0.022; 0.033/0.086; 0.080–0.265; 0.087–0.373; 0.057 | (Prodeep et al., 2011)                         |
| 2 foxtail millet and 2 proso millet cultivars | Non-germinat./germinat                        | 236.0–335.5/336.5–347.4 μg g⁻¹ | 0.236–0.335/0.337–0.347 | Max GABA concentration at different germinat. times | (Ko et al., 2011)                            |
| Kodo millet (Paspalum scrobiculatum) | Non-germinat./germinat         | 9.36/47.43 mg 100 g⁻¹ | 0.094/0.474            | (Sharma, Saxena, & Riar, 2017)                     |
| Avena sativa L.             | Native oat                     | 57.1 μg g⁻¹            | 0.057                  | (Cai et al., 2014)                                 |
| Oat                         | Non-germinat./germinat         | 0.076/0.109 μg g⁻¹ DW   | 0.00008/0.00011        | (Khang, Vasiljevic, & Xuan, 2016)                  |
| Sorghum vulgare             | Native/germinated              | 24.9/88.7–68.9–49.0 nmol 100 mg⁻¹ DM | 0.026/0.091–0.071–0.051 | 0 h—24 h—96 h germinat                             | (Prodeep et al., 2011)                         |
| Sudanese Sorghum cultivar   | Non-germinat./germinat         | 65/300 μg g⁻¹           | 0.065/0.300            | 3 day germinat                                     | (Yang et al., 2016)                           |
| 2 sorghum cultivars         | Non-germinat./germinat         | 250.5; 353.7/44.0; 410.0 μg g⁻¹ | 0.250; 0.354/0.444; 0.410 | Max GABA concentration at different germinat. times | (Ko et al., 2011)                            |
| 3 Wheat cultivars           | Green wheat kernels            | 65.4–79.3 mg 100 g⁻¹ FW | 0.654–0.793            | 23–26 maduration days                              | (Kim et al., 2007)                            |
| Wheat (cv Banks)            | Non-germinat. grain/germinat grain | 5.2/7.9 mg 100 g⁻¹ DM | 0.052/0.079            | 24 h germinat                                      | (Morita, Miyake et al., 2013)                  |

(Continued)
| Cereal (1) | Tissue//Stage (1) | GABA content | GABA content (mg g\(^{-1}\)) | Data comments | Reference |
|------------|------------------|--------------|-----------------------------|--------------|----------|
| Frost resistant wheat (T. aestivum cv Cheyenne); Frost sensitive wheat (T. aestivum cv Chinese Spring) | Seedlings | 0.018; 0.096 μmol g\(^{-1}\) FW | 0.002; 0.010 | 8 day germinat | *(Mazzucotelli et al., 2006)* |
| Waxy wheat (Uraramochi (Nohrin-mochi 163)) | Milled seed/milled sprouts | 84/155 mg kg\(^{-1}\) DW | 0.084/0.155 | Germin 48 h | *(van Hung et al., 2012)* |
| Wheat (cv Banks) | Leaves | 9 μmol g\(^{-1}\) DW | 0.928 | | *(Naidu, Paleg, Aspinall, Jennings, & Jones, 1991)* |

(1) As described in reference; *Reference includes stress treatments.
Table 7. GABA content in rice

| Cereal (1) | Tissue//Stage (1) | GABA content | GABA content | Data comments | Reference |
|------------|------------------|--------------|--------------|---------------|-----------|
| 35 Malaysian brown rice varieties | Grain | 0.01–0.1 mg g\(^{-1}\) | 0.01–0.1 | | (Roohinejad et al., 2009) |
| Yunam brown rice cultivars | Grain | 6.63–8.38 mg 100 g\(^{-1}\) | 0.066–0.084 | | (Zeng et al., 2010) |
| 2 Oryza sativa ssp. indica rice mutant | Grain | 3.46–4.09 mg 100 g\(^{-1}\) | 0.035–0.041 | | (Zhang, Hu, Tang, Zhao, & Wu, 2005) |
| 32 Thai rice varieties | Grain | 7.60–29.46 mg 100 g\(^{-1}\) | 0.076–0.295 | | (Kittibunchakul, Thiyajai, Suttisomsanee, & Sanlivarangkna, 2017) |
| 5 Pakistani brown rice (basmati super, 385–2000, Irri-6, −9) | Brown rice/polished | 4.1–6.58/0.32–0.47 mg 100 g\(^{-1}\) | 0.041–0.066/0.003–0.005 | | (Hayat et al., 2014) |
| Oryza sativa L. cv. Arborio | Root | 0.96 μmol g\(^{-1}\) FW | 0.099 | | *(Aurisano, Bertani, & Reggiani, 1995) |
| Oryza sativa cv Arborio | Excised rice root | 0.54 μmol g\(^{-1}\) FW | 0.056 | | *(Reggiani et al., 1988) |
| Korean pigmented rice | Germinat | 293.0 μg g\(^{-1}\) | 0.293 | Soaked 18°C, 20 h, Germinat 30°C, 24 h. Data for red rice | (An, Ahn, Lee, & Lee, 2010) |
| Brown rice | Non-germinat./germin | 170/850 nmol g\(^{-1}\) FW | 0.018/0.088 | | *(Oh, 2003) |
| Brown rice Giant Embryo; Brown rice Normal Embryo | Non-germinat./germin | 1.67; 1.58/35.86; 17.65 mg 100 g\(^{-1}\) | 0.017; 0.016/0.359; 0.176 | 2 day germinat | (Choi et al., 2006) |
| Brown rice | Non-germinat./germin | 1.20/3.05 mg 100 g\(^{-1}\) | 0.012/0.030 | | *(Choi, Park, Park, & Kim, 2004) |
| 2 large germ cultivars Oryza sativa (rice) L. ssp. Japonica | Non-germinat./germin | 7.3–14/10.1–15 mg 100 g\(^{-1}\) | 0.073–0.14/0.101–0.15 | | *(Komatsuzaki et al., 2007) |
| 3 normal germ cultivars Oryza sativa (rice) L. ssp. Japonica | Non-germinat./germin | 2.5–4.3/10 mg 100 g\(^{-1}\) | 0.025–0.043/0.10 | | *(Komatsuzaki et al., 2007) |
| 21 rice varieties | Non-germinat./germin | 3.96/17.87–9.91–1.36 mg 100 g\(^{-1}\) DM | 0.040/0.179–0.099–0.014 | Germinat. 24, 36, 48 h | (Karladee & Suriyong, 2012) |

(Continued)
| Cereal (1) | Tissue//Stage (1) | GABA content | GABA content (mg g$^{-1}$) | Data comments | Reference |
|-----------|------------------|---------------|-----------------------------|---------------|-----------|
| 5 Thai brown rice cultivars | Non-germinat./germin | 0.45–1.9/7.11–40.17 mg 100 g$^{-1}$ DM | 0.0045–0.019/0.071–0.402 | (Khwanchai, Chinprahost, Pichyangkura, & Chawanichsiri, 2014) |
| Polish Thai rice | Non-germinat./germin | n.d./0.74–6.33 mg g$^{-1}$ | n.d./0.74–6.33 | 30°C, 15 days every 3 days | (Jannoey et al., 2010) |
| Brown rice | Non-germinat./germin | 2.10/23.31 mg 100 g$^{-1}$ | 0.021/0.233 | *(Cheevitsopon & Noomhorm, 2011) |
| Oryza sativa L. | Non-germinat./germin rough rice part; hull; brown rice; sprout | 15.34; 1.7; 13; n.d./31.79; 3.34; 26.84; 6.04 mg 100 g$^{-1}$ | 0.153; 0.017; 0.13; n.d./0.318; 0.033; 0.268; 0.060 | (Kim et al., 2012) |
| Rough rice of Oryza sativa L. | Non-germinat/germinat brown rice/germinated rough rice/germinated rough rice powder | 23.8/68.4/115/15 mg 100 g$^{-1}$ FW | 0.238/0.684/1.15/0.15 | (Moongngarm & Saetung, 2010) |
| Sangyod Maung Phatthalung rice | Non-germinat./soaked/germin | 2.64/8.36/44.53 mg 100 g$^{-1}$ | 0.026/0.084/0.445 | Soaking solution: citrate buffer pH 3.0, 5 h, 30°C. Germin 36 h. * (Banchuen et al., 2008) |
| 3 ecuatorian Brown Rice cultivars | Non-germinat./soaked/germin | 4.34–5.7/16.9/102.26–124.43 mg 100 g$^{-1}$ DW | 0.043–0.057/0.080–0.167/1.023–1.244 | Soaking: 28°C; 24 h; germin: 28°C 96 h | *(Caceres, Martinez-Villaluenga, Amigo, & Frias, 2014) |
| Ecuatorian Brown Rice cultivar (Oryza sativa L. indica) | Non-germinat./soaked/germin | 1.07/34.84/99.03 mg 100 g$^{-1}$ DW | 0.011/0.348/0.990 | (Seed freeze-dried) Soaking: 28°C; 24 h; germin: 28°C 96 h | *(Caceres et al., 2017) |
| Ecuatorian Brown Rice cultivar (Oryza sativa L. indica) | Non-germinat./soaked/germin | 1.07/12.75/49.85 mg 100 g$^{-1}$ DW | 0.011/0.127/0.498 | (Seed sun dried) Soaking: 28°C; 24 h; germin: 28°C 96 h | *(Caceres et al., 2017) |
| 10 Brown Rice cultivars | Germ(soak germ) | 4–70/16–540 mg 100 g$^{-1}$ DW | 0.04–0.70/0.16–5.40 | 4 h, 40°C | (Saikusa et al., 1994) |
| Cereal (1) | Tissue//Stage (1) | GABA content (mg g\(^{-1}\)) | Data comments | Reference |
|------------|------------------|-------------------------------|---------------|-----------|
| 6 Thai rice varieties | Germ/soak germ | 107.5–186.2/135.5–555.1 mg kg\(^{-1}\) | 0.107–0.186/0.135–0.555 | Soak 4 h 40°C | (Varanyanond, Tungtrakul, Surojanametakul, Watanasiritham, & Wang, 2005) |
| Brown rice | Germin by soak/germin by moist | 12.81/29.03 mg 100 g\(^{-1}\) | 0.128/0.290 | Soak 12 h 30°C + germinat 24 h 25 °C/moisture 30°C + germinat 40 h 25°C | (Cao, Jia, Han, Liu, & Zhang, 2015) |
| Brown rice | Seed/Germ/sprouts/ | 123/718/389 nmol g\(^{-1}\) DW | 0.013/0.074/0.040 | | (Oh et al., 2003) |
| 2 glutinous rice | Seed/sprout/seedling | 0.021–0.026/0.053–0.068/0.034–0.110 mg 100 g\(^{-1}\) | 0.0002–0.0003/0.0005–0.0007/0.0003–0.0011 | | (Chalorcharoenying et al., 2017) |
| Rice | Seed/sprout/seedling | 0.064/0.085/0.056 mg 100 g\(^{-1}\) | 0.0006/0.0008/0.0006 | | (Chalorcharoenying et al., 2017) |
| Thai waxy paddy rice | Cultivar/breeding line | n.d./60/220 mg 100 g\(^{-1}\) embryo FW | n.d./0.60/2.20 | Soak 50 h; germin. 60 h | (Maisont & Narkrugsa, 2010) |
| 5 Pakistani brown rice (basmati super; 385–2000, Irri-6, −9) | Seed/germinat./ferment. | 47–65/115–935/1032–1089 mg kg\(^{-1}\) | 0.047–0.065/0.115–0.935/1.032–1.089 | | (Hayat et al., 2015) |
| Brown rice (Oryza sativa L.) | Milled | 27.71/22.48/20.87/17.64 μg g\(^{-1}\) DW | 0.028/0.022/0.021/0.018 | Milling time: 1.5 min; 2 min; 3 min; 4.5 min | (Iwaki & Kitada, 2007) |
| Brown rice | Milled | 6 mg 100 g\(^{-1}\) DW | 0.06 | | *(Sasagawa et al., 2006) |

(1) As described in reference; *Reference includes stress or processing treatments; n.d.: not detected.
Data of GABA content in cereals other than rice and data related to rice are shown in Tables 6 and 7 respectively.

2.6. GABA in teas, coffee, herbal infusions, cocoa and carobs

2.6.1. Teas

Tea is one of the most widely consumed beverages in the world made from the leaves and buds of *Camellia sinensis* (L.). Tea contains many chemical components such as amino acids, polyphenols (catechins and flavonoids), polysaccharides, volatile oils, vitamins, minerals and alkaloids (Syu, Lin, Huang, & Lin, 2008). Amino acids account for approximately 1–4% of the dry weight of fresh tea leaves, which mainly comprise theanine, glutamic acid (Glu), Asp, Arg and GABA (Zhao et al., 2013). As in other vegetables, the amino acid profile differs among species and cultivars, incubation under stress conditions (Sawai, Yamaguchi, Miyama, & Yoshitomi, 2003; Tsushida & Murai, 1987) or fermentation (Jeng, Chen, Fang, Chien-Wei Hou, & Yuh-Shuen, 2007) Table 8 details some of the data reported in the literature.

2.6.2. Herbal infusions

Information about the free amino acid pool and the role of these substances in non-*Camellia* teas is not as well studied. (Bi et al., 2016) studied 33 non-*Camellia* teas collected in China. GABA was detected in all teas except tea from *Sarcandra glabrate*. The GABA content in teas from *Ampelopsis grossedentata* (2.26 mg g⁻¹), *Isodon serra* (1.82 mg g⁻¹) and *Hibiscus sabdariffa* (1.03 mg g⁻¹) were the highest, much higher than that in green tea (0.28 mg g⁻¹).

The GABA content of some extracts was also studied (Sahin, Eulenburg, Kreis, Villmann, & Pischetsrieder, 2016) to identify specific allosteric GABAAR modulators. Reported results of the amount of GABA in 1 mg mL⁻¹ plant extracts were as follows: Sage leaves: 0.33 μg mL⁻¹ [0.00033 mg mL⁻¹], Lavender flowers: 0.22 μg mL⁻¹ [0.00022 mg mL⁻¹], *Sideritis condensata*: 0.38 μg mL⁻¹ [0.00038 mg mL⁻¹], Chamomile flowers: 0.81 μg mL⁻¹ [0.00081 mg mL⁻¹], *S. sipylea*: 0.23 μg mL⁻¹ [0.00023 mg mL⁻¹], *S. arguta*: 0.21 μg mL⁻¹ [0.00021 mg mL⁻¹], *S. stricta*: 0.45 μg mL⁻¹ [0.00041 mg mL⁻¹], lemon balm leaves: 0.61 μg mL⁻¹ [0.00061 mg mL⁻¹]. The concentrations were all higher than in green tea leaves, 0.14 μg mL⁻¹ [0.00014 mg mL⁻¹].

A study about the composition of free amino acids in 19 species of botanical plants was reported (Carratu, Boniglia, Giammarioli, Mosca, & Sanzini, 2008). GABA was detected in almost all the extracts of dried plants (from 5 to 629 mg 100 g⁻¹ FW [0.05–6.29 mg g⁻¹]). GABA was one of the major amino acids observed in the following 13 extracts: *Camellia sinensis, Coleus forskohii, Echinacea angustifolia, Echinacea pallida, Echinacea purpurea, Ginkgo biloba, Glycine max, G. simplicifolia, Hypericum perforatum, Panax ginseng, Passiflora incarnate, Serenoa repens, Sutherlandia frutescens and Valeriana officinalis*. Two examples are *Valeriana officinalis* and *Panax ginseng* with a GABA content in roots of 57 and 198 mg 100 g⁻¹ FW [0.57–1.98 mg g⁻¹] and in the extracts of 85 and 322 mg 100 g⁻¹ FW [0.85–3.22 mg g⁻¹], respectively.

The GABA content of Asian ginseng (*Panax ginseng* C.A. Meyer) was studied in more detail (Kuo, Ikekami, & Lambein, 2003). The seeds and some parts of the plants (one to three years old) were analyzed. GABA concentrations increased dramatically after germination and reached its maximum in 70% ethanol extracts of the 3-year-old plants: Seed 0.051 mg g⁻¹; 1 year whole plant: 1.175 mg g⁻¹; 2 years root and stem plus leaves, 0.972 and 2.284 mg g⁻¹, respectively and 3 year root, stem and leaves plus buds 1.778, 2.335 and 2.774 mg g⁻¹ of GABA respectively.

Processing also changed the amino acid profile of *Panax ginseng*. GABA content of White Ginseng (0.876 mg g⁻¹ DW) decreased to 0.659 mg g⁻¹ DW after steaming at 100°C (Red Ginseng) and to 0.161 mg g⁻¹ DW after steaming at 120°C (Cho et al., 2008).
| Tea* | GABA content | GABA content (harmonized units) | Data comments | Reference |
|------|--------------|-------------------------------|---------------|-----------|
| Camellia sinensis cv. Yabukita (Leaves) | 0.86 μmol g⁻¹ | 0.089 mg g⁻¹ | Aerobic and anaerobic incubation after feeding 15N-Glutamic acid increased GABA | (Tsushida & Murai, 1987) |
| Camellia sinensis cv., Leaves/leaves extract | 4/28 mg 100 g⁻¹ FW | 0.04/0.28 mg g⁻¹ | | (Carratu et al., 2008) |
| Camellia sinensis cv. Yabukit; Fresh leaf/stem | 0.03/0.09 mg g⁻¹ DW | 0.03/0.09 mg g⁻¹ | Anaerobic incubation increased GABA content | (Sawai et al., 2001) |
| 1st leaf/6th leaf/stem bark/stem wood/root/bark/root-wood/root-roots/pericarp/cotyledons/sap | —/—/—/—/—/—/—/—/— | —/—/—/—/—/—/—/—/— | | (Selvendran & Selvendran, 1973) |
| 28 Black Teas | 0.07–0.55 mg g⁻¹ DW | 0.07–0.55 mg g⁻¹ | | (Horanni & Engelhardt, 2013) |
| Ceylon Black Teas, “Silver Tips”; “White Tea” | 63–444; 91–803 mg kg⁻¹ | 0.063–0.444; 0.091–0.803 mg g⁻¹ | | (Carvalho et al., 2014) |
| Sri Lanka, “Black Tea” | 81–129 mg kg⁻¹ | 0.081–0.129 mg g⁻¹ | | |
| Japan, “Black Tea” | 311–415 mg kg⁻¹ | 0.311–0.415 mg g⁻¹ | | (Zhao et al., 2011) |
| China, Black Tea | 0.08 mg g⁻¹ | 0.08 mg g⁻¹ | | (Bi et al., 2016) |
| China, 3 Black Tea | 1.18–2.42 nmol g⁻¹ | 0.0001–0.0002 mg g⁻¹ | | (Zhao et al., 2013) |
| 28 Green Teas | 16.94 ± 8.46 mg 100 g⁻¹ DW | 0.169 ± 0.085 mg g⁻¹ | | (Wang, Tsai, Lin, & Ou, 2006) |
| 23 Green Teas | 0.05–0.87 mg g⁻¹ DW | 0.05–0.87 mg g⁻¹ | | (Horanni & Engelhardt, 2013) |
| Green Tea, leaves | 0.14 mg g⁻¹ | 0.14 mg g⁻¹ | | (Sahin et al., 2016) |
| Sri Lanka, “Green Tea” | 13–48 mg kg⁻¹ | 0.013–0.048 mg g⁻¹ | | (Carvalho et al., 2014) |
| Taiwan, Green Tea | 0.5 μM | 0.00005 mg mL⁻¹ | GABA content increase with Temperature and decrease with infusion times | (Hsieh & Chen, 2007) |
| Taiwan, “Green Tea” | 169.4 ± 84.6 mg kg⁻¹ | 0.169 ± 0.085 mg g⁻¹ | | (Wang et al., 2006) |
| China, 3 Green Teas | 0.49–1.51 nmol g⁻¹ | 0.0001–0.0002 mg g⁻¹ | | (Zhao et al., 2013) |
| China, Green Tea | 0.28 mg g⁻¹ | 0.28 mg g⁻¹ | | (Bi et al., 2016) |

(Continued)
Table 8. (Continued)

| Tea*          | GABA content (harmonized units) | Data comments                                      | Reference                                |
|--------------|---------------------------------|---------------------------------------------------|------------------------------------------|
| China, “Green Tea” | 19–105 mg kg⁻¹ | 0.019–0.105 mg g⁻¹ | GABA content increase with temperature and decrease with infusion times | (Syu et al., 2008) |
| Japan, “Green Tea” | 138–204 mg kg⁻¹ | 0.138–0.204 mg g⁻¹ |                                            |                          |
| Japan, Green Tea | 2.4 μM                         | 0.00025 mg mL⁻¹ | GABA content increase with temperature and decrease with infusion times | (Hsieh & Chen, 2007) |
| Taiwan, Red Tea | 5.2 μM                         | 0.00054 mg mL⁻¹ | GABA content increase with temperature and decrease with infusion times | (Hsieh & Chen, 2007) |
| 9 White Teas  | 0.24–2.07 mg g⁻¹ DW            | 0.24–2.07 mg g⁻¹ |                                           | (Horanni & Engelhardt, 2013) |
| 4 Oolong Teas | 0.09–0.97 mg g⁻¹ DW            | 0.09–0.97 mg g⁻¹ |                                           |                          |
| 3 Pu-erh Teas | 0.01–0.02 mg g⁻¹ DW            | 0.01–0.02 mg g⁻¹ |                                           |                          |
| China, Pu-erh Tea | 0.51 mg/g mg g⁻¹              | 0.51 mg/g mg g⁻¹ |                                           | (Bi et al., 2016)       |
| Pu-erh Tea/Fresh leaves | 4.9/1.27 mg g⁻¹ | 4.9/1.27 mg g⁻¹ | Fermentation increased GABA content | (Jeng et al., 2007) |
| 28 GABA Tea   | 180.97 ± 51.43 mg 100 g⁻¹ DW   | 1.810 ± 0.514 mg g⁻¹ |                                           | (Wang et al., 2006)    |
| Japan, Gaboron Tea | 1.37 mg g⁻¹                  | 1.37 mg g⁻¹ |                                           | (Ishikawa et al., 2009) |
| China, “Fudingdabaicha”, normal tea cultivar | 0.28 ± 0.02 mg g⁻¹ DW | 0.28 ± 0.02 mg g⁻¹ |                                           | (Li et al., 2016) |
| China, ‘White leaf No.1; “Xiaoxueya”, temperature-sensitive albino mutants | 0.39 ± 0.02/0.49 ± 0.07 mg g⁻¹ DW | 0.39 ± 0.02/0.49 ± 0.07 mg g⁻¹ |                                           |                          |

*As described in reference

GABA: γ-Aminobutyric acid
2.6.3. Coffee and cocoa beans

Untreated seeds of Arabica green coffee beans (Coffea arabica L.) contained 30–310 nmol of GABA per seed [0.003–0.032 mg] (Bytof, Knopp, Schieberle, Teutsch, & Selmar, 2005). In order to produce tradable standard green coffee, beans are usually dried, leading to a GABA accumulation during the process. Unwashed Arabica beans produced by drying processes had a higher GABA content (1009–2619 nmol seed⁻¹ [0.104–0.270 mg]) than washed Arabica beans (89–264 nmol seed⁻¹ [0.009–0.027 mg]) resulting from a less stressful wet processing method. (Kramer, Breitenstein, Kleinwächter, & Selmar, 2010) reported that GABA accumulation in coffee beans could be associated to the drought stress induced by the drying process.

GABA was detected in C. arabica L. (arabica) green coffee from Burundi, Colombia and Guatemala in different ratios. Interestingly, lower levels of GABA were observed in speciality beans compared to commercial-grade green coffee beans (Kwon et al., 2015).

Little information is available in literature regarding GABA content in cocoa. (Marseglia, Palla, & Caligiani, 2014) provide an overview on the GABA content in 39 fermented and dried cocoa beans from different geographical origins (13 from Africa, 20 from Central/South America, 4 from Asia and 2 from Oceania). Results showed that cocoa beans are an excellent source of GABA and its content is extremely variable as a function of the geographical origin. Cocoa beans from Africa showed a GABA content ranging from 35 to 93.9 mg 100 g⁻¹ [0.35–0.939 mg g⁻¹]; cocoa beans from America had a GABA concentration from 31.7 (minimum found in Grenada beans) to 101.2 mg 100 g⁻¹ [0.317 to 1.012 mg g⁻¹]. The maximum was measured in Ecuador beans. Cocoa beans from Asia and Oceania had a GABA content in the ranges of 47–95 and 45–68 mg 100 g⁻¹ [0.47–0.95 and 0.45–0.68 mg g⁻¹], respectively.

Concentrations of free amino acids in cacao tissues depend on the ontogenic stage of the somatic embryos and the culture conditions (Niemenak, Saare-Surminski, Rohsius, Ndoumou, & Lieberei, 2008). The contribution of GABA to the total free amino acids in embryogenic callus is substantial compared to non-embryogenic callus and further developmental stages of cacao somatic embryos.

2.7. GABA in hops

Studies related to the activity of hops (Humulus lupulus L.) have been published. Although some of them relate to GABAergic functions (Moir, 2000; Zanoli & Zavatti, 2008), most do not provide any data on the GABA content in hops. (Sahin et al., 2016) reported that extracts of 1 mg mL⁻¹ of hop cones contains 0.44 μgm mL⁻¹ [0.00044 mg mL⁻¹] of GABA.

2.8. GABA in spices

Spices have a long history of both culinary uses and of providing health benefits (Tapsell et al., 2006). Nevertheless, quantitative GABA contents in the different species have not been extensively studied. GABA content of Curcuma sp. varies depending on the species. In Curcuma aromatica Salisb. from India the GABA concentration was 0.04 μg mg⁻¹ [0.04 mg g⁻¹] but Curcuma longa L., both from Korea and Myanmar contain more than 1 μg mg⁻¹ [1 mg g⁻¹] of GABA, (1.11 and 1.31 μg mg⁻¹ [1.11–1.31 mg g⁻¹], respectively (Jung et al., 2012)). It was also reported that the concentration of GABA in ethanol extracts from Zingiber officinale Rosc. from Korea reached 1.12 μg mg⁻¹ [1.12 mg g⁻¹]. GABA content in Zingiber sp. was also identified by (Anju, Moothedath, & Shree, 2014).

2.9. GABA in sugar plants

Metabolomic studies on sugar beets are not common (Kazimierczak et al., 2014) and the amino acid content has not been determined. (Sekiyama, Okazaki, Kikuchi, & Ikeda, 2017) demonstrated that GABA could be found in early growth stages in leaves of sugar beets (Beta vulgaris L). As a pool of amino acids, GABA with Orn, Pro, Thr Iso, Val, Leu, Ala, His, Lys and Phe, was shown to increase in
roots of chicory during plant development from 27.16 nmol mg\(^{-1}\) DW [2.801 mg g\(^{-1}\)] at day 21 to 49.81 nmol mg\(^{-1}\) [2.166 mg g\(^{-1}\)] at day 56 (Druart, Goupil, Dewaele, Boutin, & Rambour, 2000).

2.10. GABA in miscellaneous plants
This section collects some examples of the presence of GABA in plants that are not included in the previous groups. Examples of GABA content for pollen and floral nectar have also been included here. As discussed throughout the review, GABA content differs among species, tissues and development stages (Table 9). Values are in similar ranges than those reported in other sections.

Reported data for pollen samples also showed high variability among species.

3. GABA in animals
GABA is widely distributed in nature independently of the type of organisms, species and even phylum. In animals, it seems that GABA plays multiple roles and functions considering the location of GABA receptors in nearly all tissues.

In vertebrates, GABA is present at significantly high levels in the brain and central nervous system, and its functions as an inhibitory neurotransmitter are well recognized (Otsuka, Obata, Miyata, & Tanaka, 1971; Waagepetersen, Sonnewald, & Schousboe, 2002). GABA exerts its biological effects through the activation of GABA receptors, the GABA\(_A\) ionotropic receptors, which are ligand-gated ion channels, and GABA\(_B\) metabotropic receptors, which are coupled to G proteins (Chebib & Johnston, 1999; Palacios, Wamsley, & Kuhar, 1981; Ramesh, Tyerman, Gilliham, & Bo, 2017; Watanabe et al., 2002). These receptors are found in a wide range of peripheral tissues (Ong & David, 1990; Tanaka, 1985), including parts of the peripheral nervous system, male and female reproductive system (Erdö, Riesz, Kárpáti, & Szporny, 1984; Geigerseder et al., 2003; Riesz & Erdö, 1985; Ritta, Calamera, & Bas, 1998), enteric system (Auteri, Zizzo, & Serio, 2015; Krantis, 2000; Zhou & Galligan, 2000), respiratory system (Chapman, Hey, Rizzo, & Bolser, 1993; Tohda et al., 1998), salivary glands (Shida et al., 1995), liver (Minuk, 1992), kidney (Auteri et al., 2015) and heart sinus node (Matsuyama, Saito, Shuntoh, Taniyama, & Tanaka, 1993) among others.

This paper will not focus on the analysis of tissues with GABA receptors, but will review the tissues in which endogenous GABA has been quantified.

3.1. GABA in mammals
GABA was discovered in 1950 in the brain (Awapara et al., 1950; Roberts & Frankel, 1950; Udenfriend, 1950) and soon after identified as a key neurotransmitter. Since then, evidence has been discovered of its functional importance in many peripheral tissues (Gerber & Hare, 1980; Krantis, 2000; Louzan, Gallardo, & Tramezzani, 1986; Micholik & Maria, 1992) and in all studied species (Gabriel, Halasy, Fekete, Eckert, & Benedeczky, 1990; Galvez Rojas et al., 2015; Robertson, Auclair, Ménard, Grillier, & Dubuc, 2007; Shi, Liang, Song, Yang, & Gao, 2012).

Due to the significant amount of information retrieved, this section describes the results measured in rodents, mammals different than livestock and human tissues. Studies on livestock are described in a separate section.

3.1.1. GABA in rodents
Due to their similarity to humans genetic, biological and behavioural characteristics, rats and mice are used as models for medical testing. The information related to GABA content in different tissues/systems of rats, guinea pigs and mice are included in Table 10. GABA is present not only in the nervous system, but also in peripheral tissues, cardiovascular, digestive, endocrine, lymphoid, muscular, ocular, reproductive and respiratory systems. The concentration of GABA in mammalian organs varies considerably. It is particularly high in the brain, but, by contrast, is low in most peripheral tissues (about 1% compared to brain). Exceptions are the female genital tract and...
Table 9. GABA content in pollen, floral nectar and several tissues of miscellaneous plants not included in other sections

| Plant/product          | Tissue                                    | GABA content (harmonized units) | Data comments                              | Reference                                      |
|------------------------|-------------------------------------------|---------------------------------|--------------------------------------------|------------------------------------------------|
| Bee-pollen             | Pollen                                    | 0.35 mg g⁻¹                    |                                            | (Paramás, González, Cordón Marcos, García-Villanova, & Sánchez, 2006) |
| Cistus ladanifer       | Pollen                                    | 0.7 mg g⁻¹                     |                                            | (Paramás et al., 2006)                         |
| Sweet corn             | Pollen                                    | 4.26 ± 0.46 μmol g⁻¹ pollen    |                                            | (Hollister & Mullin, 1999)                     |
| Squash                 | Pollen                                    | 7.98 ± 1.14 μmol g⁻¹ pollen    |                                            | (Hollister & Mullin, 1999)                     |
| Sunflower              | Pollen                                    | 0.28 ± 0.02 μmol g⁻¹ pollen    |                                            | (Hollister & Mullin, 1999)                     |
| Goldenrod              | Pollen                                    | 0.82 ± 0.12 μmol g⁻¹ pollen    |                                            | (Hollister & Mullin, 1999)                     |
| Arabidopsis            | Pollen/leaves/tubes                       | 270 μM                         |                                            | (Palanivelu et al., 2003)                      |
| Arabidopsis            | Stigma/style/ovule/ovary wall/pistil      | 0.20/0.09 μmol g⁻¹             |                                            | (Palanivelu et al., 2003)                      |
| Phryganic (East Mediterranean garrigue) community | Floral nectar                                      | 0.021/0.009 mg g⁻¹             | Flowers                                     | (Palanivelu et al., 2003)                      |
| Cucurbita pepo L       | Floral nectar                              | 734 ± 86.3/78.6 ± 94.1 pm µL⁻¹ | Male/female                                | (Nepi et al., 2012)                            |
| Tobacco                | Leaves                                    | 0.025/0.02/0.046 mg N 100 g⁻¹ DW | Flue-curing: 0h/2 h/4h/7 h/96 h           | (Yoshida, 1961)                                |
| Tobacco (Nicotiana tabacum) | Seedlings                              | 1.3 ± 0.3 mg N 100 g⁻¹ DW      |                                            | (Noguchi & Tamaki, 1962)                       |
| Tobacco (Nicotiana tabacum) | Shoots/roots                          | 6.9-7 nmol g⁻¹ FW              |                                            | (McLean et al., 2003)                          |
| Sutherlandia frutescens (L) | Aerial part                       | 0.48-1.32 mg g⁻¹               |                                            | (Mncwangi & Viljoen, 2012)                     |
| Lessertia (Sutherlandia frutescens L.) | Leaves extracts; seed extracts          | 7.29/3.48/1.69 mg g⁻¹          | in vitro leaf extract/field leaf extract/seed extract | (Shaik, Singh, & Nicholas, 2011) |

(Continued)
| Plant/product                          | Tissue                   | GABA content | GABA content (harmonized units) | Data comments          | Reference                                      |
|--------------------------------------|--------------------------|--------------|---------------------------------|------------------------|-----------------------------------------------|
| Sutherlandia frutescens (L.)         |                          | 0.23–0.85 mg g\(^{-1}\) | 0.23–0.85 mg g\(^{-1}\)         | Commercial samples     | (van Wyk & Albrecht, 2008)                   |
| Rye grass (Lolium perenne L.)        | Rye grass juice          | 0.45 mg mL\(^{-1}\) grass juice | 0.45 mg mL\(^{-1}\)            |                        | (Synge, 1951)                                |
| Tall fescue                          | Herbage                  | 318–546 mg kg\(^{-1}\) DM | 0.318–0.546 mg g\(^{-1}\)       |                        | (Kogan et al., 2008)                         |
| Acanthopanax sessiliflorus           | Aerial part              | 4.49 mg g\(^{-1}\)          | 4.49 mg g\(^{-1}\)             |                        | (Lee et al., 2015)                           |
| Crataegus pinnatifida                | Fruit                    | 10.59 mg g\(^{-1}\)         | 10.59 mg g\(^{-1}\)            |                        | (Lee, Cha, Lee, Cha, & Lee, 2015)            |
| Aloe species                         |                          | 7.99/90.15/71.0 μmol g\(^{-1}\) DW | 0.824/9.296/7.322 mg g\(^{-1}\) | Aloe arborescens/A. vera/ saponaria         | (Kim et al., 2013)                           |
| Scots pine (Pinus sylvestris L.)     | Needles                  | 0.15–0.6 μmol g\(^{-1}\) DW | 0.015/0.062 mg g\(^{-1}\)       |                        | (Raitio & Sarjala, 2000)                     |
| Datura-Metel                         | Cultured anthers         | 31.05/31.85–35.50–155.51/276.43 μmol g\(^{-1}\) DW | 3.202/3.284–3.661–16.036/ 28.505 mg g\(^{-1}\) | Induction phase/ embryogenesis (3 phases)/ young plantlet | (Songwan, 1978)                              |
| Eucalyptus globulus (ssp. Globulus and Nitens) | Leaves | 50–100/10 μg cm\(^{-2}\) | 0.050–0.100/0.010 mg cm\(^{-2}\) | Upper surface/lower surface | (Steinbauer, Davies, Gaertner, & Deridj, 2009) |
| Animal            | System          | GABA content (harmonized units) | Reference                                   |
|-------------------|-----------------|---------------------------------|--------------------------------------------|
| Rat               | Brain-CNS       | 86 μg g⁻¹ WW                    | (Awapara et al., 1950)                     |
| Rat               | Brain-CNS       | 1.85 μg g⁻¹ FW                  | (Fan et al., 1956)                         |
| Rat               | Brain-CNS       | 2.33 nmol g⁻¹                  | (Tsujii & Nakajima, 1976)                  |
| Rat               | Brain-CNS       | 2.33/1.72/0.19 nmol g⁻¹         | (Sarhan, Seiler, Grove, & Birk, 1979)      |
| Rat               | Brain-CNS       | 801 ± 39 nmol g⁻¹               | (Goodyer, Mills, & Scriver, 1982)          |
| Rat (male S-P)    | Brain-CNS       | 1.2–2.1 μmol g⁻¹               | (Lowry, Houck, & Mark Wightman, 1982)      |
| Rat               | Brain-CNS       | 48.26/3.10 mmol mg⁻¹ protein   | (Hamel, Krause, & Roberts, 1981)           |
| Rat               | Brain-CNS       | 4976.5/219.67 μg g⁻¹ protein   | (Cattabeni, Marchetti, De Angelis, & Rizzoti, 1980) |
| Rat               | Brain-CNS       | 177.5/513.2/238 μg g⁻¹         | (Zecca, Zambotti, Zonta, & Monteleone, 1980) |
| Animal                        | System         | GABA content (harmonized units) | Tissue                                                                 | Reference                                                                 |
|-------------------------------|----------------|---------------------------------|------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Rat (Albino Wistar)           | Brain-CNS      | 120.32/170 μg g⁻¹               | Brainstem/frontal cortex                                               | (Aburawi, Elhwuegi, Ahmed, Saad, & Attia, 2003)                           |
| Rat (male S-P)                | Brain-CNS      | 154 μg g⁻¹                       | Hippocampus                                                            | (Harvey, Jonker, Brand, Heenop, & Stein, 2002)                            |
| Rat (male S-P)                | Brain-CNS      | 241/540/173/254 μg g⁻¹           | Hippocampus/hypothalamus/brainstem/frontal cortex                      | (Clarke, O'Mahony, Malone, & Dinan, 2007)                                 |
| Rat (male S-P)                | Brain-CNS      | 264.6/956.3/197.6/207.1 μg g⁻¹   | Hippocampus/hypothalamus/brainstem/frontal cortex                      | (Li et al., 2005)                                                        |
| Rat (Wistar)                  | Brain-CNS      | 240/307/189 μg g⁻¹               | Hippocampus/hypothalamus/brainstem/frontal cortex                      | (Acosta, 1998)                                                           |
| Rat (Wistar)                  | Brain-CNS      | 104.8/101.88 μg mg⁻¹/ protein    | Hippocampus/prefrontal cortex                                           | (Mao et al., 2011)                                                       |
| Rat (Wistar)                  | Brain-CNS      | 329.3/241.84/354.59 μg g⁻¹       | Hippocampus/Thalamus/prefrontal cortex                                  | (de Freitas Silva, Ferraz, & Ribeiro, 2009)                               |
| Rat (Wistar, 22d)             | Brain-CNS      | 250/300/50 μg g⁻¹                | Hippocampus/hypothalamus/frontal cortex                                 | (Leret et al., 2004)                                                     |
| Rat (male, hooded Lister)     | Brain-CNS      | 0.2 pmol 20 μL⁻¹                 | Ventral hippocampal extracellular GABA                                  | (Rowley, Martin, & Marsden, 1995)                                        |
| Rat (male S-P)                | Brain-CNS      | 292/435 203/2.79 μg g⁻¹          | Decapitation: Stratum/Substantia Nigra                                 | (Saller & Czupryna, 1989)                                                |
| Rat (male S-P)                | Brain-CNS      | 0.03 ng 5μL⁻¹                    | Striatal microdialysates                                               | (Chen, Jin, Baker, Parent, & Dovichi, 2001)                               |
| Rat (male S-P)                | Brain-CNS      | 70.9 nM                          | Striatal microdialysates                                               | (Sauvinet et al., 2003)                                                  |
| Animal          | System       | GABA content | GABA content (harmonized units) | Tissue                                   | Reference                                                                 |
|-----------------|--------------|--------------|---------------------------------|------------------------------------------|---------------------------------------------------------------------------|
| Rat (male Wistar) | Brain-CNS    | 0.31 pmol 15 μL⁻¹ | 0.0021 μg mL⁻¹                  | Striatal microdialysis sample           | (Petteri & Skujins, 2001)                                                 |
| Rat (male S-P)  | Brain-CNS    | 307/114/244/141 nM | 0.032/0.012/0.025/0.014 μg mL⁻¹ | Transverse microdialysis: Cortex/Hippocampus/Septum/Neostriatum          | (Bianchi, Della Corte, & Tipton, 1999)                                    |
| Rat (male S-P)  | Brain-CNS    | 29/25/31 nM     | 0.003/0.002/6/0.003 μg mL⁻¹     | Vertical microdialysis: Neostriatum/Globus Pallidus/Substantia Nigra reticulata | (Bianchi et al., 1999)                                                    |
| Rat (male S-P)  | Brain-CNS    | 109/22 fmol (min mg)⁻¹ w.t. | 0.011/0.002 μg g⁻¹ min⁻¹      | Extracellular levels of GABA monitored in vitro by perfusion of rat neostriatal/substantia nigra slices | (Bianchi et al., 1999)                                                    |
| Rat             | Cardiovascular | 0.62 nmol mg⁻¹ protein | 61.93 μg g⁻¹                  | Aorta                                    | (Hamel et al., 1981)                                                      |
| Rat             | Cardiovascular | 5.4 nmol g⁻¹     | 0.557 μg g⁻¹                  | Heart                                    | (Tsuji & Nakajima, 1978)                                                  |
| Rat (male S-P)  | Cardiovascular | 580 pmol mL⁻¹    | 0.06 μg mL⁻¹                  | Plasma                                   | (Gerber & Hare, 1980)                                                     |
| Rat (albino male) | Cardiovascular | 800 ± 58 pmol mL⁻¹ | 0.082 ± 0.006 μg mL⁻¹          | Blood from cardiac puncture (50 % was found in plasma)                     | (Ferkany, Smith, Seifert, Caprili, & Enna, 1978)                           |
| Rat (male S-P)  | Cardiovascular | 8 pmol mg⁻¹ WW   | 0.825 μg g⁻¹                  | Cardiac ventricular tissue              | (Gerber & Hare, 1980)                                                     |
| Rat             | Digestive    | 0.008-0.632/0.496/0.190-5.04 mmol kg⁻¹ WW | 0.825-65.17/51.15/19.59-519.72 μg g⁻¹ | Pancreas/Acini/Islets of Langerhan  | (Michalik & Maria, 1992)                                                  |
| Rat             | Digestive    | 2.51/18.9/1.97 mmol kg⁻¹ DW | 259.04/1948.97/203.15 μg g⁻¹ | Pancreas/Islets of Langerhan/exocrine acini | (Okada, Taniguchi, & Shimada, 1976)                                      |
| Animal          | System     | GABA content (harmonized units) | GABA content (harmonized units) | Tissue                                      | Reference                                      |
|-----------------|------------|---------------------------------|---------------------------------|---------------------------------------------|-----------------------------------------------|
| Rat             | Digestive  | 21.8–87 nmol g⁻¹                | 2.248–8.971 μg g⁻¹              | Liver                                       | (Minuk, 1992)                                 |
| Rat             | Digestive  | 32.7/67.0 nmol g⁻¹              | 3.370/6.909 μg g⁻¹              | Liver/Small intestine                       | (Tsuji & Nakajima, 1978)                      |
| Rat (male S-P)  | Digestive  | 0.55 ± 0.06 nmol kg⁻¹ DW        | 6.10⁻⁵ ± 6.10⁻⁶ μg g⁻¹          | Duodenum                                    | (Taniguchi, Osaya, Okada, & Baba, 1982)      |
| Rat             | Endocrine  | 21.3 nmol g⁻¹                   | 2.196 μg g⁻¹                    | Kidney                                      | (Tsuji & Nakajima, 1978)                      |
| Rat (male S-P)  | Endocrine  | 3.95 ± 5.3/19.6/26.7/43.6/37.8 nmol g⁻¹ WW | 4.07 ± 0.55/2.02/2.75/4.50/3.90 μg g⁻¹ | Whole kidney/superficial renal cortex/mid-renal cortex/juxtamedullary renal cortex/renal | (Goodyer et al., 1982)                         |
| Rat             | Endocrine  | 35 pmol mg⁻¹ WW                 | 3.609 μg g⁻¹                    | Adrenal                                     | (Gerber & Hare, 1980)                        |
| Rat             | Endocrine  | 34 ± 8/27 ± 4 μmol kg⁻¹ WW      | 3.51 ± 0.41/2.78 ± 0.41 μg g⁻¹  | Adrenal/thyroid                             | (Okada, Taniguchi, & Baba, 1982)             |
| Rat             | Lymphoid   | 3.4 nmol g⁻¹                    | 0.351 μg g⁻¹                    | Spleen                                      | (Tsuji & Nakajima, 1978)                     |
| Rat (male S-P)  | Lymphoid   | 38/18 pmol mg⁻¹ WW              | 3.919/1.856 μg g⁻¹              | Thymus/spleen                               | (Gerber & Hare, 1980)                        |
| Rat             | Muscular   | 0.7 nmol g⁻¹                    | 0.072 μg g⁻¹                    | Muscle                                      | (Tsuji & Nakajima, 1978)                     |
| Rat             | Ocular     | 1.55 ± 0.014 μmol g⁻¹ FW        | 15.84 ± 1.444 μg g⁻¹            | Retina                                      | (Ponsantes-Morales, Klethi, Ledig, & Mandel, 1972) |
| Rat             | Ocular     | 20 nmol kg⁻¹ FW                 | 2062.4 μg g⁻¹                   | Retinal layers                              | (Ross, Parli, & Godfrey, 1989)               |
| Animal | System     | GABA content (harmonized units) | GABA content (harmonized units) | Tissue                      | Reference                                      |
|--------|------------|---------------------------------|---------------------------------|-----------------------------|------------------------------------------------|
| Rat    | Ocular     | 3.21/0.10/0.05/0.22 μmol g⁻¹ DW | 331.01/10.31/5.16/22.69 μg g⁻¹ | Retina/lens/iris-ciliary body/cornea | (Heinämäki, Muhonen, & Piha, 1986)            |
| Rat    | Ocular     | 0.0/0.0/0.034 nmol kg⁻¹ H₂O    | 0.0/0.0/3.506 μg g⁻¹            | plasma/anterior aqueous/ lens water | (Reddy, 1967)                                 |
| Rat    | Ocular     | 0.15 μmol 5 mL⁻¹               | 3.094 μg ml⁻¹                   | Vitreous                    | (Heinämäki et al., 1986)                      |
| Rat    | Reproductive | 710 ± 55 μmol kg⁻¹ protein    | 73.21 ± 5.67 μg g⁻¹ protein     | Ovary                       | (Okada et al., 1982)                         |
| Rat    | Reproductive | 29.8 ± 7.6 nmol g⁻¹ WW       | 3.073 ± 0.784 μg ml⁻¹           | Uterus                      | (Erdo, 1984)                                 |
| Rat    | Reproductive | 4438 ± 220/584 ± 72 nmol g⁻¹ WW | 457.65 ± 22.69/ 60.22 ± 7.42 μg g⁻¹ | Oviduct/ovary              | (Erdo, Rosdy, & Szpony, 1982)                |
| Rat    | Reproductive | 46.02 ± 3.65/1.01 ± 0.09 nmol mg⁻¹ protein | 47.45 ± 376/104.1 ± 9.3 μg g⁻¹ protein | Oviduct/ovary              | (Apud et al., 1984)                         |
| Rat    | Reproductive | 5.030.04/0.027 μmol g⁻¹ FW     | 518.69/4.12/2.78 μg g⁻¹         | Oviduct/ovary/uterus        | (Martin Del Rio, 1981)                      |
| Rat    | Reproductive | 3500–7000/50–100/80/150 nmol mg⁻¹ protein | 3.6 10⁻²/7.2 10⁻⁵/5.2 10⁻⁵/ 1.0 10⁻⁵/8.2 10⁻⁵/1.5 10⁻⁵ μg g⁻¹ protein | Oviduct/ovary/uterus/vagina | (Louzan et al., 1986)                        |
| Rat    | Reproductive | 30 ng μL⁻¹                   | 30 μg ml⁻¹                      | Fluid of the ovarian bursa  | (Louzan et al., 1986)                        |
| Rat    | Reproductive | 0.6 nmol g⁻¹                 | 0.062 μg g⁻¹                     | Testis                      | (Tsuiji & Nakajima, 1978)                     |
| Rat (male S-P) | Reproductive | 6 pmol mg⁻¹ WW             | 0.619 μg g⁻¹                     | Testis                      | (Gerber & Hare, 1980)                        |
| Rat    | Reproductive | 0.019/0.02/traces μmol g⁻¹ FW | 0.959/2.062/traces μg g⁻¹       | Seminal vesicles/ducturs deferens/Epididymis | (Martin Del Rio, 1981)                      |
| Animal     | System          | GABA content | GABA content (harmonized units) | Tissue          | Reference                                      |
|------------|-----------------|--------------|---------------------------------|-----------------|-----------------------------------------------|
| Rat        | Respiratory     | 7.3          | 0.753 μg g⁻¹                   | Lung            | (Tsuji & Nakajima, 1978)                      |
| Rat (male S-P) | Respiratory  | 15 pmol mg⁻¹ WW | 1.547 μg g⁻¹               | Lung            | (Gerber & Hare, 1980)                        |
| Guinea pig | Brain-CNS       | 100 μg g⁻¹ WW | 100 μg g⁻¹                    | Brain           | (Awapara et al., 1950)                       |
| Guinea pig | Digestive       | 17.5 ± 3.1 nmol g⁻¹ WW | 1.805 ± 0.320 μg g⁻¹ | Tenia coli     | (Jessen, Mirsky, Dennison, & Burnstock, 1979) |
| Guinea pig | Digestive       | 43.5/79.2/69.7/64.7/66.4/65.8/63.6 nmol g⁻¹ WW | 4.48/8.17/7.19/6.67/6.85/6.78/6.56 μg g⁻¹ | Duodenum/jejenum/ileum/Appendix/Asc colon/Trans colon/Desc colon | (Miki, Taniyama, Tanaka, & Tobe, 1983) |
| Guinea pig | Digestive       | 18.3/34.6/43.2/77.3 nmol g⁻¹ WW | 1.89/3.57/4.45/7.97 μg g⁻¹ | Gallbladder: Neck/upper body/lower body/base | (Saito, Taniyama, & Tanaka, 1985) |
| Guinea pig | Respiratory     | 0.082 ± 0.014/0.026 ± 0.004 pmol mg⁻¹ | 0.008 ± 0.001/0.003 ± 0.0004 μg g⁻¹ | Eluted from airway rings: with the epithelium intact/with the epithelium denuded | (Gallos et al., 2013) |
| Guinea pig | Urinary         | 34/17.9/12.6/11.5 nmol g⁻¹ WW | 3.51/1.84/1.30/1.19 μg g⁻¹ | Urinary bladder: Upper body/Lower body/Bse/Trigone | (Kusunoki, Taniyama, & Tanaka, 1984) |
| Mouse      | Brain-CNS       | 5 55 mg 100 g⁻¹ WW | 550 μg g⁻¹                   | Brain           | (Roberts & Frankel, 1950)                    |
| Mouse      | Brain-CNS       | 1.41–1.50/1.70–1.66/1.15–1.11/1.35–1.43 pmol g⁻¹ | 165.4–154.7/175.3–171.2/118.6–114.5/139.2–147.5 μg g⁻¹ | Cerebral cortex/corpus striatum/cerebellum/hippocampus (data depending on technique) | (Bernasconi, Bittiger, Heid, & Martin, 1980) |
| Mouse      | Cardiovascular  | 548 ± 61 pmol mL⁻¹ | 0.056 ± 0.006 μg mL⁻¹ | Blood from cardiac puncture                  | (Ferkany et al., 1978) |

(Continued)
| Animal | System | GABA content | GABA content (harmonized units) | Tissue | Reference |
|--------|--------|--------------|---------------------------------|--------|-----------|
| Mouse  | Digestive | 0.004 nmol g⁻¹ WW | 0.0004 µg g⁻¹ | Pancreas | (Drummond & Phillips, 1974) |
| Mouse  | Digestive | 0.004/0.560-0.827 mmol kg⁻¹ WW | 0.412/57.74–85.28 µg g⁻¹ | Pancreas/Islets of Langerhans | (Michalik & Maria, 1992) |
| Mouse  | Digestive | 15 nmol g⁻¹ | 1.547 µg g⁻¹ | Liver | (Minuk, 1992) |
| Mouse  | Ocular | 16.7 ± 0.7/13.6 ± 0.3 mmol kg⁻¹ protein | 1722 ± 72/1402 ± 31 µg g⁻¹ protein | 90 days old: light-adapted retina/dark-adapted retina | (Cohen, McDaniel, & Orr, 1973) |
pancreatic islets, where considerably higher amounts have been found. The difficulties in measuring GABA and the different techniques used are the main reasons for discrepancies.

3.1.2. GABA in humans
Medical and pharmacological effects of GABA have been widely studied due to its numerous physiological functions and positive effects on metabolic disorders. However, abnormal GABA levels do not always result in an illness. Considering different tissues, one of the most common analysis is the measurement of the amount of GABA in plasma. It seems that there are no marked effects on plasma GABA concentrations due to gender, exercise, diet, season, time of day or menstrual cycle (Petty, 1994). GABA levels in other tissues are summarized in Table 11, including results from in vivo analysis (Goddard, Mason, & Almai et al., 2001; Terpstra, Ugurbil, & Gruetter, 2002).

3.1.3. GABA in other mammals
Several studies have been performed to obtain information on amino acids and related compounds from tissues of different mammals. Reported results demonstrated a similar pattern to that shown previously, brain and ocular tissues contain higher concentrations of GABA, although it is distributed in several other organs of mammals. Table 12 shows GABA content in different tissues from cats, dogs and monkeys.

3.2. GABA in livestock
Consumer demand and regulatory requirements for food items of high quality and nutritional properties are constantly increasing. A wide number of methods and breeding programs have been developed to maintain healthy livestock and improve production, yield and quality, from adapted feeding diets to controlled facilities and regular health inspections. Within these procedures, many controls evaluate livestock performance and evolution of plasma metabolites during development. Amino acid profiles, besides the nutritional properties, are of crucial importance due to their particular contribution to the taste. Free amino acids are classified into four categories (saccharinity, amino acids with sulphide, fragrant amino acids and essential amino acids.) However non-protein amino acids are not considered and GABA is not usually quantified (Bermúdez, Franco, Carballo, Sentandreu, & Lorenzo, 2014; Iida et al., 2016; Lim, Jo, Seo, & Nam, 2014; Lisa, Spragins Jeffrey, Reyzer Michelle, Norris Jeremy, & Caprioli Richard, 2014; Mullen et al., 2000; Soriano-Santos, 2000; Subbaraj, Brad Kim, Fraser, & Farouk, 2016).

In recent years, along with the increasing knowledge of its functional properties, GABA has become part of the diet of livestock (Li et al., 2015; Tang & Chen, 2016; Wang, Wang, Liu, Liu, & Ferguson, 2013; Zhang, Zou, Li, Dong, & Zhao, 2011; Zhigang, Sheikahmodi, & Li, 2013). The final objective is to obtain feeding material with good nutritional and sensory properties improving the life quality of the animals.

Table 13 summarizes some data related to GABA content in livestock. Although most of the results are not from tissues included in human diets, they provide evidence of the natural occurrence of GABA in these different animals. Data for muscles show a GABA content of more than 120 μg g⁻¹ in Longissimus lumborum muscle of swine. GABA distribution is similar to that described previously for humans and other mammals.

Food items produced by different type of animals, such as eggs, milk or honey, also show remarkable GABA content without any processing steps. It is interesting that even human milk for baby nutrition contains 0.01 μg mL⁻¹ GABA. Data are shown in Table 14.

3.3. GABA in other animals
For species that could be part of the human diet, there has been a growing interest in studying their biochemistry, physiology and nutritional characteristics. These studies focus on both physical characteristics and chemical composition (mineral fatty acid and amino acid profile). Nevertheless,
### Table 11. GABA content in humans

| System    | GABA content (harmonized units) | Tissue                                                                 | Reference                                                                 |
|-----------|----------------------------------|------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Brain-CNS | 60/75/77/70/62/103/86/62/65/32 μg g⁻¹ FW | Pons/temporal lobe/frontal lobe/parietal lobe/occipital lobe/caudate nucleus/cerebellum/medulla/gray matter/white matter | (Awapara et al., 1950)                                                   |
| Brain-CNS | 0.208 ± 0.091/4.65 ± 1.92 nmol mL⁻¹ | CSF: free GABA/conjugated GABA                                           | (Manyam & Tremblay, 1984)                                                |
| Brain-CNS | 0.019 to 0.022 μg mL⁻¹            | CSF samples (patients suffering from tuberculosis meningitis and septic meningitis) | (Khuhawar & Rajper, 2003)                                                |
| Brain-CNS | 0.025 ± 0.009/0.025 ± 0.008 μg mL⁻¹ | CSF 20 normal volunteers/19 neurologically normal controls              | (Hare & Bala Manyam, 1980)                                               |
| Brain-CNS | 77.34 ± 14.37 μg g⁻¹              | Occipital lobe in vivo                                                  | (Terpstra et al., 2002)                                                  |
| Brain-CNS | 156.74–254.71 μg g⁻¹ brain        | Occipital in vivo                                                       | (Goddard et al., 2001)                                                  |
| Cardiovascular | 0.013 ± 0.001 μg mL⁻¹            | Plasma (female+ male)                                                  | (Bjork et al., 2001)                                                   |
| Cardiovascular | 0.020/0.023 μg mL⁻¹              | Plasma: Female/Male                                                     | (Petty, 1994)                                                           |
| Cardiovascular | 90.74 μg mL⁻¹                   | Plasma dialysate                                                        | (Páez, Rada, & Hernández, 2000)                                         |
| Cardiovascular | 0.089 ± 0.007 μg mL⁻¹            | Blood from the antecubital vein (less than 30% was found in plasma)     | (Ferkany et al., 1978)                                                  |
| Digestive | 73.01/662.03 μg g⁻¹              | Human insulinoma: non-tumor region/tumor region                         | (Michalik & Maria, 1992)                                                |
| Digestive | 289.77/2629.56 μg g⁻¹             | Human insulinoma: non-tumor region/tumor region                         | (Okada et al., 1976)                                                   |
| Digestive | 23.72/15.47/35.06/259.86 μg g⁻¹ protein | Mucosa/Circular muscle/Longitudinal muscle/Auerbach’s plexus              | (Miki et al., 1983)                                                   |
| Digestive | 25.99 μg g⁻¹                     | Liver                                                                   | (Minuk, 1992)                                                           |

(Continued)
| System      | GABA content (harmonized units) | Tissue                                      | Reference                                                                 |
|------------|----------------------------------|---------------------------------------------|----------------------------------------------------------------------------|
| Endocrine  | 0.3–2.9 mg 100 g⁻¹               | 3–29 μg g⁻¹                                 | Kidney _children with different disease (Zachmann, Tocci, & Nyhan, 1966)  |
| Ocular     | 1.90–3.82 μmol 100 mL⁻¹          | 1.96–3.94 μg mL⁻¹                           | Aqueous humor (Durham, 1970)                                               |
| Reproductive | 177 ± 54 nmol g⁻¹             | 18.25 ± 5.57 μg g⁻¹                         | Oviduct (Erdö, László, Szporny, & Zsolnai, 1983)                          |
| Reproductive | 214 ± 66 nmol g⁻¹             | 22.07 ± 6.81 μg g⁻¹                         | Ovary (Erdö Sándor & Adam, 1984)                                           |
| Reproductive | 0.036 nmol/10⁶ cells          | 0.0037 μg 10⁶ cells⁻¹                       | Spermatozoa (Ritta et al., 1998)                                           |
| Reproductive | 15.21 nmol mL⁻¹              | 1.568 μg mL⁻¹                               | Seminal plasma (Tsuiji & Nakajima, 1978)                                   |
| Milk       | 117.7 nM                        | 0.012 μg mL⁻¹                               | Milk (7 samples) (Limon et al., 2014)                                     |
| Animal | System | GABA content | GABA content (harmonized units) | Tissue | Reference |
|--------|--------|--------------|---------------------------------|--------|-----------|
| Cat    | Brain-CNS | 23.4 mg 100 g⁻¹ WW | 234 μg g⁻¹ | Brain | Tallan, Moore, & Stein, (1954) |
| Cat    | Brain-CNS | 0.2/0.9/2.7/6.3/6.0/6.6/6.25 mM | 20.62/92.83/278.4/649.6/618.72/680.59/257.80 μg mL⁻¹ | Spinal ganglion cells/spinal mononeurons/large cells ventral part of Deiters’ nucleus/large cells dorsal part of Deiters’ nucleus/cerebellar nuclei cells/cerebellar Purkinje cells/cerebral Betz cells | Otsuka et al., (1971) |
| Cat    | Brain-CNS | 5.8 ± 1.5/1.5 ± 0.5 mM | 898.10 ± 154.68/154.68 ± 51.56 μg mL⁻¹ | Purkinje cells/Motoneurons | Obata, (1969) |
| Cat    | Cardiovascular | <0.02 mg 100 g⁻¹ WW | <0.2 μg g⁻¹ | Plasma | Tallan et al., (1954) |
| Cat    | Cardiovascular | 899 ± 204 pmol mL⁻¹ | 0.093 ± 0.021 μg mL⁻¹ | Blood from the cephalic vein | Ferkany et al., (1978) |
| Cat    | Digestive | 0.68 mmol kg⁻¹ WW | 70.122 μg g⁻¹ | Pancreas | Ferkany et al., (1978) |
| Cat    | Digestive | 9.7 nmol g⁻¹ | 10.003 μg g⁻¹ | Liver | Michalik & Maria, (1992) |
| Cat    | Digestive | 1.0/0.7 mg 100 g⁻¹ WW | 10/7 μg g⁻¹ | Liver/Pancreas | Minuk, (1992) |
| Cat    | Digestive | 29.2/26.6/27.8/31.0/33.8/35.9/36.6 nmol g⁻¹ WW | 3.013/2.743/2.867/3.197/3.485/3.774 μg g⁻¹ | Duodenum/jejumun/Ileum/Appendix/Asc colon/Trans colon/Desc colon | Tallan et al., (1954) |
| Cat    | Digestive | 0.14/0.19/0.24/0.60 nmol mg⁻¹ protein | 14.44/19.59/24.75/44.35 μg g⁻¹ | Mucosa/Circular muscle/Longitudinal muscle/Auerbach's plexus | Miki et al., (1983) |
| Cat    | Digestive | 1.09 ± 0.13 mmol kg⁻¹ DW | 112.40 ± 13.41 μg g⁻¹ | Transcolon | Taniguchi et al., (1982) |
| Cat    | Endocrine | 0.5 mg 100 g⁻¹ WW | 5 μg g⁻¹ | Kidney _children with different disease | Tallan et al., (1954) |
| Cat    | Urinary | <0.1 mg 100 g⁻¹ WW | <1 μg g⁻¹ | Gastrocnemius | Tallan et al., (1954) |
| Dog    | Cardiovascular | <0.1 μg g⁻¹ FW | <0.1 μg g⁻¹ | Heart | Fan et al., (1986) |
| Dog    | Cardiovascular | 6.30 ± 89 pmol mL⁻¹ | 0.065 ± 0.009 μg mL⁻¹ | Blood from the cephalic vein | Ferkany et al., (1978) |
| Dog    | Digestive | 0.43 mmol kg⁻¹ WW | 44.342 μg g⁻¹ | Pancreas | Michalik & Maria, (1992) |
| Monkey | Cardiovascular | 1122 ± 84 pmol mL⁻¹ | 0.116 ± 0.009 μg mL⁻¹ | (Macaca mulatt): Blood from the sural vein | Ferkany et al., (1978) |
| Monkey | Ocular | 0.799/3.34 mmol kg⁻¹ H₂O | 82.39/344.42 μg g⁻¹ | Lens water: Cynamolgus/Vervet | Reddy, (1967) |
| Animal       | Group       | Tissue            | GABA content | (harmonized units) | Data comments                                      | Reference |
|--------------|-------------|-------------------|---------------|-------------------|----------------------------------------------------|-----------|
| Beef         | Bovine      | Brain-CNS         | 60            | μg g⁻¹ WW          | 69                                                 | Brain     |
| Cow          | Bovine      | Cardiovascular    | 23.6          | mmol L⁻¹          | 2433.63 μg mL⁻¹                                   | Serum (early lactating dairy cows) |
| Calf         | Bovine      | Ocular            | Not quantified|                   | -                                                  | GABA detected in calf lens |
| Sheep        | Sheep       | Cardiovascular    | 1332 ± 313 pmol mL⁻¹ | 0.137 ± 0.032 μg mL⁻¹ | Blood                                             |
| Swine        | Sweat       | Muscle            | 12.08         | mg 100 mg⁻¹       | 120.8 μg g⁻¹                                       | Longissimus lumborum muscle |
| Broiler      | Poultry     | Cardiovascular    | 865           | nmol mL⁻¹         | 89.199 μg mL⁻¹                                     | Serum     |
| Broiler      | Poultry     | Cardiovascular    | 810/792       | nmol mL⁻¹         | 83.53/81.67 μg mL⁻¹                               | Plasma: days 28/35 |
| Chicken      | Poultry     | Ocular            | 3.02 ± 0.192  | μmol g⁻¹ FW       | 311.42 ± 19.80 μg g⁻¹                             | Retina    |
| Cherry Valley Duck | Poultry | Cardiovascular | 13.17/0.27 | nmol mL⁻¹ _μmol g⁻¹ | 1.36/27.84 μg mL⁻¹/mg g⁻¹ | Day 42 with heat stress (30°C): Breast muscle |
| Cherry Valley Duck | Poultry | Digestive        | 0.59          | μmol g⁻¹          | 60.84 μg g⁻¹                                       | Day 42 with heat stress (30°C): Liver |

(Continued)
| Animal   | Group        | Tissue       | GABA content | (harmonized units) | Data comments                              | Reference                                      |
|----------|--------------|--------------|--------------|--------------------|--------------------------------------------|------------------------------------------------|
| Horse    | Equine       | Brain-CNS    | 48.5 - 53.6  | ng mL\(^{-1}\)     | 0.048 - 0.054 ng mL\(^{-1}\)               | (Knych, Steinmetz, & McKemie, 2015)           |
| Horse    | Equine       | Cardiovascular | 55.7/23.9/57.7/39.2/24.7 | ng mL\(^{-1}\) | 0.056/0.024/0.058/0.039 ng mL\(^{-1}\) | Wctphalan/Pony/ Lusitano/ Oldenburg/ Holsteiner (Knych et al., 2015) |
| Horse    | Equine       | Cardiovascular | 35.0 - 55.8  | ng mL\(^{-1}\)     | 0.035/0.056 ng mL\(^{-1}\)                | 16 exercised Thoroughbred horses: Plasma (Knych et al., 2015) |
| Rabbit   | Other farmed | Brain-CNS    | 38           | μ g\(^{-1}\) WW    | 38 μ g\(^{-1}\)                            | Brain (Awapara et al., 1950)                  |
| Rabbit   | Other farmed | Brain-CNS    | 100.67/3.76  | nmol mg\(^{-1}\) protein | 10,381.1/387.73 μ g\(^{-1}\) protein | Brain tissue/Pia-arachnoid vessels (Hamel et al., 1981) |
| Rabbit   | Other farmed | Brain-CNS    | 1.902        | nmol g\(^{-1}\)    | 0.196 μ g\(^{-1}\)                        | Brain (Tsui & Nakajima, 1978)                |
| Rabbit   | Other farmed | Cardiovascular | 0.45/1.76/0.80/0.96 | nmol mg\(^{-1}\) protein | 46.40/181.49/82.51/98.99 μ g\(^{-1}\) protein | Aorta/Vena caval/ Femoral artery/ Mesenteric artery (Hamel et al., 1981) |
| Rabbit   | Other farmed | Cardiovascular | 3            | nmol g\(^{-1}\)   | 0.309 μ g\(^{-1}\)                       | Heart (Tsui & Nakajima, 1978)               |
| Rabbit   | Other farmed | Cardiovascular | 560 ± 93     | pmol mL\(^{-1}\)   | 0.058 ± 0.009 pmol mL\(^{-1}\)            | Blood from the marginal ear vein (Ferkany et al., 1978) |
| Rabbit   | Other farmed | Digestive    | 0.014/0.003  | μ mol kg\(^{-1}\) WW | 1.44/0.309 μ g\(^{-1}\)               | Pancreas (tail)/ Pancreas (body) (Michalk & Maria, 1992) |
| Rabbit   | Other farmed | Digestive    | 14/3         | pmol mg\(^{-1}\) WW | 1.44/0.309 μ g\(^{-1}\)               | Pancreas (tail)/ Pancreas (body) (Gerber & Hare, 1980) |
| Rabbit   | Other farmed | Digestive    | 42.3         | nmol g\(^{-1}\)   | 4.362 μ g\(^{-1}\)                      | Liver (Minuk, 1992)                          |
| Rabbit   | Other farmed | Digestive    | 42.6/97.8    | nmol g\(^{-1}\)   | 4.393/10.085 μ g\(^{-1}\)              | Liver/Small intestine (Tsui & Nakajima, 1978) |

Table 13. (Continued)
| Animal | Group          | Tissue    | GABA content | (harmonized units) | Data comments | Reference                     |
|--------|----------------|-----------|---------------|--------------------|---------------|--------------------------------|
| Rabbit | Other farmed   | Endocrine | 42.8          | nmol g\(^{-1}\)    | 4.413         | Kidney (Tsuji & Nakajima, 1978) |
| Rabbit | Other farmed   | Endocrine | 42.2/10.55    | μg g\(^{-1}\) protein | 42.2/10.55 | Adrenal/thyroid (Haber, Kuriyama, & Roberts, 1970) |
| Rabbit | Other farmed   | Lymphoid  | 3             | nmol g\(^{-1}\)    | 0.309         | Spleen (Tsuji & Nakajima, 1978) |
| Rabbit | Other farmed   | Muscle    | 16.4          | nmol g\(^{-1}\)    | 1.691         | Muscle (Tsuji & Nakajima, 1978) |
| Rabbit | Other farmed   | Ocular    | traces        | mmol kg\(^{-1}\) water in lens | traces | Lens (no detected as mg/100 g of lens) (Reddy & Kinsey, 1962) |
| Rabbit | Other farmed   | Reproductive | 0.11 ± 0.04 | μmol g\(^{-1}\) | 11.343 ± 4.125 | Oviduct (Erdö et al., 1984) |
| Rabbit | Other farmed   | Reproductive | 16.3 ± 5.3 | nmol g\(^{-1}\) WW | 1.681 ± 0.546 | Uterus (Erdö, 1984) |
| Rabbit | Other farmed   | Respiratory | 15           | nmol g\(^{-1}\)    | 1.547         | Lung (Tsuji & Nakajima, 1978) |
as previously mentioned, GABA has not always been measured or considered in these reports (Alam, Karim, Chakrabortty, Amin, & Hasan, 2016; Bechtel & Oliveira, 2006; Mohanty et al., 2014; Wu, 2013). Table 15 provides a summary of GABA content in other animals not covered in other sections. They are grouped in two main categories, vertebrates and invertebrates. Within these examples several could be included in the food category.

GABA is present in numerous invertebrates (Kittredge et al., 1962), acting as an inhibitory transmitter in central and peripheral nervous systems (Lunt, 1991). In many insect species, there are ionotropic GABA receptors distributed throughout the nervous system (Hosie, Sattelle, Aronstein, & Ffrench-Constant, 1997; Lummis, 1990), confirming the widespread existence of GABA.

These receptors have become the target of numerous commercial insecticides and plants use this pathway as defence against invertebrate pests (Bown et al., 2006). Table 15 shows some examples of GABA content in insects.

### 4. GABA in products for human diet

Consumer preferences towards healthier lifestyles and safe and nutritional food products are the main drivers for producers to offer best-quality products. Studies with the aim of understanding and evaluating the real composition and functional claims of conventional products in our diets have become common (Diana et al., 2014; Hermanussen et al., 2010). The food industry increasingly develops the functionality of traditional products, trying to improve their properties and to add health claims.

Considering the interest of GABA as a functional food ingredient, many efforts have been made to improve the GABA content during food manufacturing, not only by just adding GABA but also by using ingredients with high GABA content or “in-situ producers of GABA” (Dhakal et al., 2012; Kook & Cho, 2013; Poojary et al., 2017; Quilez & Diana, 2017).

It has been widely reported that the food industry is taking advantage of the different species of microorganisms that are able to produce GABA from glutamate in one step (Bach et al., 2009; Choi et al., 2006; Hayakawa, Ueno, Kawamura, Taniguchi, & Oda, 1997; Hudec et al., 2015; Pietruszko & Fowden, 1961; Reed, 1950; Yang et al., 2008; Yokoyama, Hiramatsu, & Hayakawa, 2002). These microorganisms are included during food production or processing and produced GABA maintained within the foodstuff, fortifying the final product. The fermented products usually have higher GABA concentrations than standard products.
| Animal | Classification | System | GABA content (harmonized units) | Data comments | Reference |
|--------|----------------|--------|---------------------------------|--------------|-----------|
| Pigeon | Ave            | Brain-CNS | 110 μg g\(^{-1}\) WW | 278.62 ± 21.65/232.02 ± 12.37 | (Awapara et al., 1950) |
| Frog   | Amphibia       | Ocular | 2.70 ± 0.21/2.25 ± 0.12 μmol g\(^{-1}\) DW | 27.84 ± 21.65/23.20 ± 12.37 | (Starr, 1973) |
| Rana Pipiens | Amphibia | Ocular/Nervous system | 5.64/12.5/8.74 μmol g\(^{-1}\) DW | 581/1289.00/901.27 | (Graham, Baxter, & Lolley, 1970) |
| Rana Pipiens | Amphibia | Nervous system | 6.99/21.1/24.1 μmol g\(^{-1}\) DW | 720.81/2175.83/2485.19 | (Graham et al., 1970) |
| Rana temporaria | Amphibia | Nervous system | 1.77 ± 0.12/2.75 ± 0.14/3.95 ± 0.36 μmol g\(^{-1}\) DW | 185.62 ± 21.65/232.02 ± 24.75/303.17 ± 37.19 | (Osborne, 1971) |
| Petromyzon marinus and Lampetra fluviatilis | Fish | Cerebellum | 0.97 ± 0.06/0.59 ± 0.03 μmol g\(^{-1}\) WW | 100.03 ± 6.19 | (Robertson et al., 2007) |
| Ictalurus nebulosis | Fish | Brockman body | 121.0 μmol mL\(^{-1}\) | 0.012 μg g\(^{-1}\) WW | (Gerber & Hare, 1980) |
| Scyllium canicula | Fish | Endocrine system | 25 μg g\(^{-1}\) | 25 μg g\(^{-1}\) | (Osborne, 1971) |
| Carassius auratus | Fish | Ocular | 3.15 ± 0.35/1.65 ± 0.21 μmol g\(^{-1}\) DW | 324.83 ± 36.09/170.15 ± 21.65 | (Osborne, 1971) |
| Carassius auratus | Fish | Retina | 1.96 ± 0.11/1.2 ± 0.08 μmol g\(^{-1}\) DW | 202.11 ± 14.6/146.43 ± 8.25 | (Starr, 1973) |

(Continued)
| Animal                      | Classification | System                | GABA content          | GABA content (harmonized units) | Data comments                                                                 | Reference                                      |
|-----------------------------|----------------|-----------------------|-----------------------|---------------------------------|--------------------------------------------------------------------------------|------------------------------------------------|
| Spodoptera littoralis Boisduval | Arthropod-Insect | Larve-hemolymph       | 63–351 μmol 100 mL⁻¹ | 64.96–361.95 μg mL⁻¹            | GABA in the haemolymph of the second, third, fourth and sixth instar larvae   | (Boctor & Salem, 1973)                        |
| Locusta migratoria          | Arthropod-Insect | Nervous system        | 16.8 μg g⁻¹ WW        | 16.8 μg g⁻¹                      | Brain and ventral nerve-cord                                                 | (Osborne, 1971)                               |
| Cockroach                   | Arthropod-Insect | Nervous system        | 60 μmol g⁻¹ weight tissue h⁻¹ | 6187.2 μg g⁻¹                   | Formed GABA in central ganglia                                               | (Baxter & Torralba, 1975)                      |
| Musca domestica             | Arthropod-Insect | Head                  | 0.100/0.138 μg head⁻¹ | 0.100/0.138 μg head⁻¹            | Female/male                                                                   | (Shi et al., 2012)                            |
| Plutella xylostella         | Arthropod-Insect | Head                  | 0.00375 μg head⁻¹     | 0.00375 μg head⁻¹                |                                                                                | (Shi et al., 2012)                            |
| Lumbricus terrestris L      | Annelida        | Nervous system        | <0.2/<0.2/<0.2 μg g⁻¹ WW | <0.2/<0.2/<0.2 μg g⁻¹            | Nerve cord/ supræesophag. + subesophag. ganglia + periesophag. connectives/ supræesophag. Ganglion | (Koidl, 1974)                                 |
| Lumbricus terrestris        | Annelida        | Nervous system        | 1.2 μg g⁻¹ WW          | 1.2 μg g⁻¹                       | Cerebral and subpharyng. ganglia, circumoesophag. commissures                 | (Osborne, 1971)                               |
| Hirudo medicinalis          | Annelida        | Nervous system        | <0.2 μg g⁻¹ WW         | <0.2 μg g⁻¹                      | Nerve cord                                                                    | (Koidl, 1974)                                 |
| Aphodite aculeata           | Annelida        | Nervous system        | 0.6 μg g⁻¹ WW          | 0.6 μg g⁻¹                       | Ventral nerve-cord                                                            | (Osborne, 1971)                               |
| Helix aspersa               | Molusca         | Nervous system        | 0.7 μg g⁻¹ WW          | 0.7 μg g⁻¹                       | Circumoesophag. ganglia mass                                                 | (Osborne, 1971)                               |
| Buccinum undatum            | Molusca         | Nervous system        | 0.9 μg g⁻¹ WW          | 0.9 μg g⁻¹                       | Circumoesophag. ganglia mass                                                 | (Osborne, 1971)                               |
| Animal                      | Classification  | System                    | GABA content (harmonized units) | Data comments                                                                 | Reference                       |
|-----------------------------|-----------------|---------------------------|---------------------------------|-------------------------------------------------------------------------------|---------------------------------|
| Elodone cirhosa             | Molusca         | Nervous system            | 1.3 μg g⁻¹ WW                   | Optic ganglia                                                                 | (Osborne, 1971)                 |
| Lobster                     | Arthropod-Crustac. | Nervous system           | 9–14/130/480/26,600/1011 μg g⁻¹ DW | Sensory nerve/mixed nerve/CNS ganglia and connectives/motor inhibitory bundles/CNS ganglia alone | (Kravitz, Kuffler, & Potter, 1963) |
| Lobster (Homarus americanus) | Arthropod-Crustac. | Nervous system           | n.d./1.2–2.4 μmol 100 mm⁻¹ fibre | Isolated axons from the meropodite region: Motor/inhibitory                  | (Kravitz et al., 1963)          |
| Lobster (Homarus americanus) | Arthropod-Crustac. | Nervous system           | 0.012–0.026/0.11–0.37 μmol 100 mm⁻¹ fibre | Isolated axons from the opener muscle surface: Motor/inhibitory             | (Kravitz et al., 1963)          |
| Nephrops norvegicus         | Arthropod-Crustac. | Nervous system           | 13.6 μg g⁻¹ WW                   | Brain and ventral nerve-cord                                                  | (Osborne, 1971)                 |
| Crab                        | Arthropod-Crustac. | Nervous system           | 625/127/19/10,000 μg g⁻¹ DW      | CNS connective tissue sheath removed/Mixed nerve/Sensory nerve/Motor inhibitory bundles | (Kravitz et al., 1963)          |
| Carcinus maenas             | Arthropod-Crustac. | Nervous system           | 21.3 μg g⁻¹ WW                   | Brain and ventral nerve-cord                                                  | (Osborne, 1971)                 |
| Astacus                     | Arthropod-Crustac. | Nervous system           | 86.6/99.0 μg g⁻¹ WW               | Nerve cord/ supraesophag. ganglion                                            | (Koidl, 1974)                   |
| Orconectes immunis          | Arthropod-Crustac. | Nervous system           | 113–153 μg g⁻¹                   | Ventral nerve cord                                                            | (Lin & Cohen, 1973)             |
| Animal                     | Classification      | System             | GABA content (harmonized units) | GABA content (harmonized units) | Data comments                  | Reference                        |
|----------------------------|---------------------|--------------------|---------------------------------|---------------------------------|--------------------------------|----------------------------------|
| *Orconectes immunis* Hagen | Arthropod-Crustac.  | Nervous system     | 1.10 ± 0.15/1.49 ± 0.34         | 113.43 ± 15.47/153.65 ± 35.06  | µg g⁻¹ WW                      | (Lin & Cohen, 1973)              |
| *Orconectes immunis* Hagen | Arthropod-Crustac.  | Hemolymph          | 0.002/0.002                      | 0.026/0.206                     | µg mL⁻¹                        | Female/Male                      |
| *Litopenaeus vannamei*     | Arthropod-Crustac.  | Body               | 0.1                             | 100                              | µg g⁻¹                         | Whole body                       |
| *Holothuria scabra*       | Echinoderm          | Whole body         | 4.67/n.d.                       | 4.67/n.d.                       | µg g⁻¹                         | Whole body/body wall             |
| *Echinus esculentus*       | Echinoderm          | Nervous system     | 0.9                             | 0.9                              | µg g⁻¹ WW                      | Radial nerve-cord (ectoneural tissue) |
| *Asterias rubens*          | Echinoderm          | Nervous system     | 1.1                             | 1.1                              | µg g⁻¹ WW                      | Radial nerve-cord (ectoneural and hyponeural tissue) |
| *Ciona intestinalis*       | Tunicata            | Nervous system     | 3                               | 3                                | µg g⁻¹ WW                      | Cerebral ganglion                |

WW: wet weight; n.d.: not detected
Table 16 shows the GABA levels in different examples of usual foodstuff like cheese, yoghurt, flour or bread; fermented food like Kimchi or Tempeh, very common in Asian countries and with high content of GABA; new developments mostly based on fermentation processes with GABA-producer starters and commercial processed products.

5. GABA in the environment
In the past, studies about the role of nitrogen in soil to sustain crop production in agricultural systems have been focused on inorganic nitrogen dynamics. The ability of numerous crop species to take up organic nitrogen from the free amino acids pool has increased the interest in the organic chemical composition of soils (Amelung, Zhang, & Flach, 2006; Bol, Ostle, Petzke, Chenu, & Balesdent, 2008; Friedel & Scheller, 2002; Mittner, Kindler, Knicker, Richnow, & Matthias, 2009; Scheller & Raupp, 2005).

Amino acids are widely present in soils (approximately 20–30% of total nitrogen) either in a free or a polymeric state (e.g. protein–humic complexes and peptides). The majority of amino acids are in a polymeric state and only 0.04–0.5% of the total weight is free amino acids. Most amino acids in the soil are derived from plant residues and root exudation but also from dry and wet deposition, microbial activity and animal inputs. The final level of amino acids in soil is influenced by many parameters from the soil matrix to the local environment, including plant life, external human intervention or microbial communities (Jones, Owen, & Farrar, 2002; Vieublé Gonod, Jones, & Chenu, 2005). Amino acid concentrations ranged from 3.9 to 16.5 g kg$^{-1}$ [3.9–16.5 mg g$^{-1}$] soil and correlated with the organic C and N contents at the sites (Amelung et al., 2006). The most abundant amino acids in soils were Glu, Gly, Asp, Arg and Ala.

In sediments, the amino acid composition may be altered with an increased turnover of proteins (Dauwe, Middelburg Jack, Peter, & Heip Carlo, 1999). In fact, the chemical composition of the sediments is considered to be a maturity indicator to estimate the relative degradation state of the organic matter. In order to understand compositional changes and evolution of oceanic and deep-sea sediments, many studies of analysis of the water column at different depths have been reported (Goutx et al., 2007; Ittekkot, Deuser, & Degens, 1984). Specifically, the examinations of non-protein amino acids like GABA and β-Alanine in sea particles are used as long-term signs of organic degradation and chemical evolution of sediments. As an example, GABA and β-Alanine, degradation products of Asp and Glu, tend to accumulate in older sediments and their relative molar concentration is lowest in the surface sediments and highest in the bottom sediments (Gupta & Kawahata, 2003a, 2003b). Surface waters or surface sediments have no GABA or very low levels (Müller, Suess, & AndréUngerer, 1986; Zhao, Shan, Tang, & Zhang, 2015). Examples of concentrations of GABA in sediments and soils are shown in Table 17.

Concentrations of free and combined amino acids in atmospheric particles have also been investigated. (Zhang & Anastasio, 2003) reported that the average concentrations of combined amino compounds (proteins and peptides) were generally four to five times higher than those of free amino compounds (amino acids and alkyl amines). GABA accounted for only 1% of the free amino acids in the atmospheric fine particles but 7% in the water fog. A different result was obtained by (Filippo et al., 2014) who did not detect GABA as a combined amino acid. Data are included at the end of Table 17.

6. Conclusions
Reviewed literature shows the great attention GABA has attracted over the last several decades due to its ubiquity in life. GABA occurs naturally in plants, animals and microorganisms, having diverse physiological functions and great potential health related benefits. Extensive data demonstrates that GABA content is usually higher in plants than in animals and its concentration is in the range of mg g$^{-1}$ depending on plant matrix, development stage and postharvest and processing conditions. GABA is present in almost all types of fruits and vegetables investigated, including wheat and rice as the worldwide most important crops, and in several food crops like tomato,
| Product                  | Processing features | GABA content | GABA content (harmonized units) | Data comments                                                                 | Reference                                      |
|-------------------------|---------------------|--------------|---------------------------------|-------------------------------------------------------------------------------|-----------------------------------------------|
| Pork loin               | Dry aged            | 12.08/23.09 mg 100 g⁻¹ | 0.121/0.231 mg g⁻¹ | Longissimus lumbarum muscles; Control/left halves of the carcasses aged at 2 ± 1°C, RH: 80%, 40 d | (Lee et al., 2016)                           |
| Flour                   | –                   | 7/19/12/3/27/4/0/12/15/18/24/78 mg kg⁻¹ | 0.007/0.019/0.012/0.003/0.027/0.040/0.012/0.012/0.015/0.018/0.024/0.078 mg g⁻¹ | Common wheat/durum wheat/rye/spelt/oat/buckwheat/Rice/Amaranth/millet/chickpea/soy/quinoa | (Coda, Rizzello, & Gobbetti, 2010)            |
| Cheese (commercial)     | –                   | 0.260/0.32/0.77 mg kg⁻¹ | 0.0003/0.0003/0.0008 mg g⁻¹ | Vento d’Estate/Mozzarella/Crescenza                                            | (Siragusa et al., 2007)                       |
| Cheese (commercial)     | –                   | 289/290/290/330/391 mg kg⁻¹ | 0.289/0.290/0.290/0.330/0.391 mg g⁻¹ | Pecorino Marchigiano/Pecorino del Reino/Pecorino Leccese/Pecorino Umbrali/Pecorino di Filiano | (Siragusa et al., 2007)                       |
| Cheese (13 Italian commercial) | – | 4–100 mg kg⁻¹ | 0.004–0.100 mg g⁻¹ | Parmigiano Reggiano, Baricato San Martino, Ubriaco di Roboso, Caciocavallo, Gorgonzola, Canestrato Pugliese, Caciotta di Urbino, Pecorino del Tarantino, Pecorino Piemontese, Flor di Capra, Caprino di Cavapese, Caprino di Valsassina, and Capritilla | (Siragusa et al., 2007)                       |
| 34 Cheeses (commercial) | –                   | 330 ± 50 mg kg⁻¹ | 0.330 ± 0.050 mg g⁻¹ | Average data                                                                  | (Diana, Tres, Quilez, Llombart, & Rafecas, 2014) |
| Cheese (commercial)     | –                   | n.d./177.0/7.1/n.d./n.d./48/4.2 μg g⁻¹ | n.d./0.177/0.007/n.d./n.d./0.048/0.004 mg g⁻¹ | Camembert/Gouda/Blue/Cream/Emmental/Cheddar/Edam                              | (Nomura, Kimoto, Someya, Furukawa, & Suzuki, 1998) |
| Cheese (commercial)     | –                   | 0.3–19.4 mg g⁻¹ | 0.3–19.4 mg g⁻¹ | Cheddar                                                                        | (Laleye, Simard, Gosselin, Lee, & Giroux, 1987) |

(Continued)
| Product | Processing features | GABA content (harmonized units) | Data comments | Reference |
|---------|---------------------|---------------------------------|---------------|-----------|
| Cheese (commercial) Goat's milk | Semi-ripened/Fresh | 0.93/0.9 g kg\(^{-1}\) | Babia-Laciana. Curd/ripening 15 days/ripen 60 days | (Diana, Tes, Quilez, Llombart, & Rafecas, 2014) |
| Cheese Goat's milk | 3.1/19.1/33.1/71.7 mg 100 g\(^{-1}\) | TS 0.031/0.191/0.331/0.717 mg g\(^{-1}\) | Murcia al Vino. Ripening day 2/ day 60/ day 60 | (Franco, Prieto, Bernardo, Prieto, & Carballo, 2003) |
| Cheese Goat's milk + Plant coagulant | | 7.02/56.1 mg g\(^{-1}\) TS 7.02/56.1 mg g\(^{-1}\) | Babia-Laciana: Curd/ripening 15 days/ripen 30 days/ripen 60 days | (Abellan et al., 2012) |
| Cheese Goat's milk + Animal rennet | | 9.6/52.9 mg g\(^{-1}\) TS 9.6/52.9 mg g\(^{-1}\) | Murcia al Vino: Ripening day 2/ day 60 | (Abellan et al., 2012) |
| Cheese Goat's milk | | 0.11/1.38/2.01 μmol g\(^{-1}\) | Teleme: 1 day/before cold room/ripen 60 days/ripen 180 days | (Diana, Tes, Quilez, Llombart, & Rafecas, 2014) |
| Cheese Ewe's milk | | 0.98 g kg\(^{-1}\) 0.98 mg g\(^{-1}\) | Ripened | (Diana, Tes, Quilez, Llombart, & Rafecas, 2014) |
| Cheese Ewe's milk | | 0.22/1.58/2.51 μmol g\(^{-1}\) | | (Mallatou, Pappa, & Boumba, 2004) |
| Cheese Ewe's milk | | 3.6/4.5/13.7/2.01 μmol g\(^{-1}\) | | (Mallatou, Pappa, & Boumba, 2004) |
| Cheese Ewe's milk | | 0.51/2.03/6.12/100 μg g\(^{-1}\) DW 0.51/2.03/6.12/100 μg g\(^{-1}\) | | (Manca et al., 2015) |
| Cheese Ewe's milk | | 0.23/1/6/0.25/9 mg g\(^{-1}\) | | (Manca et al., 2015) |
| Cheese Sheep's milk + 3 \(≠\) starter culture | | 0.21/0.23/6/0.25/9 mg g\(^{-1}\) | | (Manca et al., 2015) |

Continued
| Product                  | Processing features                                    | GABA content | GABA content (harmonized units) | Data comments                                    | Reference                                                                 |
|-------------------------|--------------------------------------------------------|--------------|---------------------------------|-------------------------------------------------|---------------------------------------------------------------------------|
| Cheese                  | Cow’s milk + 3 × starter culture                       | 2.4–8.3/3.5–10.3/5.7–16.2/24.4–36.4 mg 100 g⁻¹ DW | 0.024–0.083/0.037–0.103/0.011–0.062/0.124–0.364 mg g⁻¹ | Telemé: 1 day/before cold room/ripen 60 days/ripen 180 days              | (Pappa & Sotirakoglou, 2008)                                             |
| Cheese                  | Bovine milk (pasteurized)                              | 0.238/1.536/0.020 µmol g⁻¹                        | 0.025/0.158/0.002 mg g⁻¹                         | Mahon: 0 day/ripen 120 days/ripen 210 days                                | (García-Palmer, Serra, Palou, & Gianotti, 1997)                           |
| Cheese                  | Bovine milk (raw)                                      | 0.238/1.615/0.578 µmol g⁻¹                        | 0.025/0.167/0.060 mg g⁻¹                         | Mahon: 0 day/ripen 120 days/ripen 210 days                                | (García-Palmer, Serra, Palou, & Gianotti, 1997)                           |
| Cheese                  | Cow’s milk (raw)                                       | 3.72/49.77/37.4 mg 100 g⁻¹ TS                      | 0.037/0.498/0.374 mg g⁻¹                         | 0 day/ripen 60 days/ripen 90 days                                      | (Prieto, Franco, Josefa, Bernardo, & Carballo, 2002)                      |
| Milk beverage           | Pasteurized cow’s milk + fermentation till pH 4.4       | 36.9–43.8 mg L⁻¹                                   | 0.037–0.044 mg mL⁻¹                             | Depending on starter culture. GABA increase with storage                 | (Servili et al., 2011)                                                   |
| Milk beverage           | Fresh low-fat milk + lactic fermentation                | n.d./64.0 mg 100 g⁻¹                              | n.d./0.640 mg g⁻¹                               | Control/Lactic fermentation                                              | (Chen, Tsai, & Pan, 2007)                                                 |
| Fermented goat Milk     | Goat milk + lactic bacteria                            | 28 mg kg⁻¹                                         | 0.028 mg g⁻¹                                    |                                                                                | (Minervini, Bilancia, Siragusa, Gobbetti, & Caponio, 2009)               |
| Yogurt                  | + Germinated Brown rice                               | 0.35/0.59 µL⁻¹                                     | 0.00035/0.00059 mg mL⁻¹                        | Supplemented 1%/2%                                                        | (Kim, Ahn, Lim, Jhoo, & Kim, 2009)                                       |
| Yogurt                  | rice milk + GABA producing strain                     | 1.29/137.17 µg g⁻¹ DW                             | 0.0013/0.137 mg g⁻¹                             | Yogurt: Traditional/rice milk + GABA producing strain                    | (Park & Oh, 2005)                                                        |
| Yogurt                  | Germinated soya milk + lactic bac                      | 1.5/42.46 µg g⁻¹ DW                               | 0.0015/0.425 mg g⁻¹                             | Yogurt: Traditional/germinated soya milk + lactic bac                     | (Park & Suk-Heung, 2007)                                                 |
| Strawberry beverages    | Strawberry pure + fermentation                        | 1.89/5.99/6.73/5.12 mg L⁻¹                         | 0.002/0.006/0.007/0.005 mg mL⁻¹                | Control/Glucanobacter japonicus/Gluconobacter oxydans/Acetobacter malorum | (Ordóñez et al., 2015)                                                   |
| Commercial orange juice | Orange juice + ferment + pasteur                      | 187/167/126 mg L⁻¹                                 | 0.187/0.167/0.126 mg mL⁻¹                       | Orange juice/+ fermentat/+ ferment + pasteur                              | (Cerrillo et al., 2015)                                                  |
| Black raspberry beverages| Black raspberry uice + fermentation                   | n.d./1.2–1.6/13–15 mg mL⁻¹                        | n.d./1.2–1.6/13–15 mg mL⁻¹                      | Control/+ lactic acid fermentation 2 days/ferment 15 days                | (Kim, Lee, Ji, Lee, & Hwang, 2009)                                       |

(Continued)
| Product            | Processing features          | GABA content (harmonized units) | Data comments                                          | Reference                                      |
|--------------------|------------------------------|---------------------------------|-------------------------------------------------------|------------------------------------------------|
| Soy milk           | Soy milk + fermentation      | 93.9/198.4/361.1 mg 100 g⁻¹     | 0.939/1.984/3.611 mg g⁻¹                                | (Tsai, Lin, Pan, & Chen, 2006)                |
| Chinese rice wine  | Lactic ferment + Long storage| 126/137/143 mg mL⁻¹            | 126/137/143 mg mL⁻¹                                    | (Liu, Bobin, Zhou, Chen, & Halyun, 2015)      |
| Chinese yellow wine| Glutinous rice + yeast       | 10.1 ± 0.3 μg mL⁻¹             | 0.0101 ± 0.0003 mg mL⁻¹                                | (Lu et al., 2015)                             |
| Rice vinegar       | -                            | 100 mg L⁻¹                     | 0.1 mg mL⁻¹                                           | (Chen & Chen, 2009)                          |
| Beer               | -                            | 7.7–40.5 mg L⁻¹                | 0.008/0.040 mg mL⁻¹                                    | (Kutlán & Molnár-Perl, 2003)                 |
| Mung bean          | Mung bean + fermentation     | 0.016/0.122 g 100 g⁻¹ DW       | 0.16/1.22 mg g⁻¹                                       | (Yeap et al., 2012)                          |
| Rice flour         | + fermentation               | 36.82 mg 100 g⁻¹ DM            | 0.368 mg g⁻¹                                          | (Kradangar & Songsiriratpong, 2015)          |
| Commercial wheat   | Dough + fermentation         | 1.2/1.74 mg 100 g⁻¹ DW         | 0.0012/0.0017 mg g⁻¹                                   | (Collar, Mascaros, Prieto, & Debarber, 1991) |
| Bread              | Bread + fermented grains      | 2.20–2.45 μg g⁻¹ DW            | 0.0022/0.0024 mg g⁻¹                                   | (Chen, Ulziijargal, & Mau, 2016)             |
| Bread              | Bread + fermented rice       | 60.71 ± 7.21/79.92 ± 0.58 mg kg⁻¹ | 0.061 ± 0.007/0.080 ± 0.0006 mg g⁻¹                  | (Tseng, Yang, Chen, & Mau, 2011)             |
| Bread              | Several flours and yeast     | 11/88/504 mg kg⁻¹              | 0.011/0.088/0.504 mg g⁻¹                               | (Coda et al., 2010)                          |
| Commercial breads  | + L Brevis                   | 1.57–3.95/2.01–8.4/24.2 mg 100 g⁻¹ | 0.016–0.039/0.020–0.084/0.242 mg g⁻¹                  | (Diana, Rafecas, & Quilez, 2014)             |

(Continued)
| Product                | Processing features                                      | GABA content | GABA content (harmonized units) | Data comments                               | Reference                           |
|------------------------|----------------------------------------------------------|---------------|---------------------------------|---------------------------------------------|-------------------------------------|
| Breakfast cereals      | Recipe + glutamic acid decarboxylase                     | 33–219 ppm    | 33–219 ppm                      | Glutamic acid decarboxylase (Yersinia intermedia, GADyers) | (Joye, Lamberts, Brijs, & Delcour, 2011) |
| Noodles                | Brown rice/Rice brown                                    | 2751.6–4176.7/5522.0–9617.8 nmol 20 g⁻¹ | 0.014–0.021/0.028–0.050 mg g⁻¹ | Raw and cooked                             | (Kong & Lee, 2010)                  |
| Pu-ehr tea             | Fresh leaves/fermented                                   | 1270/4900 μg g⁻¹ | 1.270/4.900 mg g⁻¹              |                                             | (Jeng et al., 2007)                  |
| Kimchi                 | 40 h fermentation + 28 days storage                      | 20 mg 100 g⁻¹  | 0.2 mg g⁻¹                       | Constant GABA content during storage        | (Oh et al., 2008)                   |
| Japanese fermented fish| Long fermented                                           | 1.4–1.5 mg g⁻¹ | 1.4–1.5 mg g⁻¹                   | Aji-no-susu (4–12 months)                   | (Kuda et al., 2009)                 |
| Chinese fermented food |                                                          | 32.64/133.13 mg 100 g⁻¹ DM | 0.326/1.331 mg g⁻¹            | Sufu, soybean based: Control/48 h ferment   | (Ma, Cheng, Yin, Wang, & Lite, 2013) |
| Chorizo                | Fermented sausage                                        | 0.88/2.13 mg g⁻¹ DW | 0.88/2.13 mg g⁻¹                | 70 days ferment: Traditional/Industrial   | (Mateo, Dominguez, Aguirrezabala, & Zumalacarregui, 1996) |
| Nham                   | Thai sausage + GABA producing strains                    | 3962 mg kg⁻¹  | 3.962 mg g⁻¹                     | Thai fermented sausage                      | (Kantachote, Ratanaburee, Sukhoom, Sumpradit, & Asavarungpipop, 2016) |
| Commercial Japanese foodstuff |                                                          | 15.53/3.27/1.37/129.01/12.66 mg g⁻¹ | 15.53/3.27/1.37/129.01/12.66 mg g⁻¹ | Tempeh/Ukogi/Gabarun tea/GABA catechin puras/Pre-tio | (Ishikawa et al., 2009) |
| Commercial German foodstuff |                                                          | 18–25/23–39/4–8 mg 100 g⁻¹ | 0.18–0.25/0.23–0.39/0.04–0.08 mg g⁻¹ | Ravioli/spaguetti/noodles                   | (Hermanussen et al., 2010) |
| Commercial German foodstuff |                                                          | 11/17–23/3 mg 100 g⁻¹ | 0.11/0.17–0.23/0.03 mg g⁻¹ | Mc Donald cheeseburger/pizza/Lidi herbal baguette | (Hermanussen et al., 2010) |
| Commercial German foodstuff |                                                          | 9/4–5/3 mg 100 g⁻¹ | 0.09/0.04–0.05/0.03 mg g⁻¹ | Peas/lentils/rice pot                       | (Hermanussen et al., 2010) |
| Commercial German foodstuff |                                                          | 2/26 mg 100 g⁻¹ | 0.02/0.26 mg g⁻¹                | Chicken cordonbleu/Curry sausage            | (Hermanussen et al., 2010) |
| Sample                  | Place                          | GABA content | GABA content (harmonized units) | Data comments                  | Reference                      |
|-------------------------|--------------------------------|--------------|---------------------------------|--------------------------------|--------------------------------|
| Fen soil                | Weak intensity                 | Weak intensity |                                |                                | (Bremner, 1950)                |
| Clay loam soil          | Weak intensity                 | Weak intensity |                                |                                |                                |
| Peat soil               | Weak intensity                 | Weak intensity |                                |                                |                                |
| Chernozem soil          | Weak intensity                 | Weak intensity |                                |                                |                                |
| Agricultural soil        | Shanghai, China                | 0.624–0.631/0.194–0.624 | ng N g⁻¹ dry soil              |                                |                                |
| Arable cultivated soil  | loam                           | 15/58         | μg N kg⁻¹ soil                  | 0.015/0.058                    | Before/after hydrolysis         |
| Arable cultivated soil  | sand                           | -/83          | μg N kg⁻¹ soil                  | -/0.083                        | Before/after hydrolysis         |
| Arable cultivated soil  | clay loam                      | 8/18          | μg N kg⁻¹ soil                  | 0.008/0.038                    | Before/after hydrolysis         |
| Pine forest soil        |                                | 359/519       | μg N kg⁻¹ soil                  | 0.359/0.519                    | Before/after hydrolysis         |
| Forest soil with deciduous trees |                | 1042/1670     | μg N kg⁻¹ soil                  | 1.042/1.670                    | Before/after hydrolysis         |
| Soil of a sub-alpine grassland | Snowy Mountains, Australia   | 3%            | Of total amino N pool           | 3%                             | Humic umbrosol                  |
| Oa horizons collected beneath Pinus muri sat | J u g Hand le Reserve, northern California | 127 (787)/n.d. (n.d.) | nM | 0.013 (0.081)/n.d. (n.d.) | μg mL⁻¹ | Fresh samples: fertile-slightly acid soil/infertile-acidic soil (after hydrolysis) |

(Continued)
| Sample | Place | GABA content | GABA content (harmonized units) | Data comments | Reference |
|--------|-------|--------------|---------------------------------|---------------|-----------|
| Oa horizons collected beneath Cupressus pygmaea | Jug Handle Reserve, northern California | 140 (115)/213 (30) nM | 0.014 (0.012)/0.022 (0.003) µg mL⁻¹ | Fresh samples: fertile-slightly acid soil/infertile-acidic soil (after hydrolysis) | |
| Intertidal zone salt-marsh soil | La Pérouse Bay, Manitoba, Canada | 1.6/5.4 µM | 0.165/0.557 µg mL⁻¹ | >2ºC/2ºC | (Henry & Jefferies, 2002) |
| Supratidal zone salt-marsh soil | La Pérouse Bay, Manitoba, Canada | 0.9/0.5 µM | 0.093/0.051 µg mL⁻¹ | >2ºC/2ºC | |
| Sub-Surface of Semi-Permafrost environment | Hokkaido, altitude 207 m | 5/0.1/0.3 nmol g⁻¹ | 0.516/0.010/0.031 µg g⁻¹ | Depth: 0-5/5-10/175-200 cm (water extract aa) | (Takano, Gupta, Kawahata, Kobayashi, & Marumo, 2005) |
| Squeeze sediments of interstitial waters | Costa Rica Rift, Panama basin | 10.8% Of total aa (molar %) | 10.8% Of total aa (molar %) | Two holes at 3.5 m depth | (Kawahata & Ishizuka, 1993) |
| Filtered Interstitial waters | Costa Rica Rift, Panama basin | 0% Of total aa (molar %) | 0% Of total aa (molar %) | Two holes at 3.5 m depth | |
| Surface sediments | Haihe River Basin, China | <1 % Molar (total hydrolyzable aa) | <1 % Molar (total hydrolyzable aa) | | (Zhao et al., 2015) |
| Sediment trap material | Antarctic, Drake passage | 0.21/0.23 µmol g⁻¹ | 21.655/23.718 µg g⁻¹ | Depth: 965/2540 m | (Müller et al., 1986) |
| Subantarctic surface waters (6 m) | South Atlantic | 0% Of total aa (molar %) | 0% Of total aa (molar %) | Particle size 75-150 um | |
| Antarctic Surface waters (6 m) | South Atlantic | 0% Of total aa (molar %) | 0% Of total aa (molar %) | Particle size >75 um | |
| Antarctic Surface waters | Drake passage | 0.12 µmol g⁻¹ | 12.374 µg g⁻¹ | Particle size >75 um | |
| Sea water | East of Gotland, Baltic sea | 0.9-3.4/traces Of total aa (molar %) | 0.9-3.4/traces Of total aa (molar %) | Depth: 1-4.5 m/65-150 m | (Mopper & Lindroth, 1982) |

(Continued)
| Sample                  | Place            | GABA content | GABA content | Data comments                              | Reference                                                                 |
|------------------------|------------------|--------------|--------------|--------------------------------------------|---------------------------------------------------------------------------|
| Sea water              | Pacific Ocean    | 0.1%/0.7%    | Of total aa (molar %) 0.1%/0.7% | depth: 15 m/650 m                                | (Sheridan, Lee, Wakeham, & Bishop, 2002)                                  |
| Sea water              | California       | 3.8/2.0/4.7/0.1/0.7/1.3/0.7/0.9 nmol L⁻¹ | 0.0004/0.0002/0.0005/0.00001/0.0001/0.0001 | Depth, trapped with chloroform: 30/50/400/500/700/900/1400/2000 m | (Lee & Cronin, 1984) (Lee, Wakeham, & Farrington, 1983)                  |
| Sea water              | Panama Basin     | 1.42/1.86 μg m⁻³ | 1.42 10⁻⁶/1.86 10⁻⁶ μg mL⁻¹ | Depth: 1267 m, particles <53 um: Free/Combined (Lipid fraction) |                                                                          |
| Sea water              | Panama Basin     | 150.2 μg m⁻³ | 1.50 10⁻⁶ μg mL⁻¹ | Depth: 1267 m, particles <53 um: Combined (non-lipid fraction) |                                                                          |
| Groundwater            | Carolina slate belt | 3.8–11 nmol L⁻¹ | 0.0004/0.0011 μg mL⁻¹ | Fractured-rock aquifer                       | (Shen, Chapelle, Strom, & Benner, 2015)                                   |
| Surface water          | Carolina slate belt | 17–33 nmol L⁻¹ | 0.0018/0.0034 μg mL⁻¹ | Fractured-rock aquifer                       |                                                                          |
| Bacterial dissolved organic matter | Carolina slate belt | 4.1 ± 3.1 nmol L⁻¹ | 0.0004 ± 0.0003 μg mL⁻¹ | Fractured-rock aquifer                       |                                                                          |
| Samples of urban dust | Rome             | 0.02–0.4 ng m⁻³ | 0.02 10⁻⁶ 0.4 10⁻⁴ μg mL⁻¹ | Winter_ 2013 (free)                          | (Di Filippo et al., 2016)                                                 |
| Samples of urban dust | Rome             | n.d.–0.52 ng m⁻³ | n.d.–0.52 10⁻⁵ μg mL⁻¹ | Summer_ 2013 (free)                          |                                                                          |
| Atmospheric fine particles (≤2.5 um) | Davis California | 4/42 pmol m⁻³ | 4.12 10⁻⁹/4.33 10⁻⁹ μg mL⁻¹ | Free/Combined                               | (Zhang & Anastasio, 2003)                                                 |
| Wintertime fog waters  | Davis California | 47/70 pmol m⁻³ | 4.85 10⁻⁹/7.22 10⁻⁹ μg mL⁻¹ | Free/Combined                               |                                                                          |

n.d.: not detected
potato, asparagus or spinachs, GABA contents are above 1 mg g⁻¹. In animals, GABA was found at significantly high levels in the brain and central nervous system and some specific peripheral tissues like the pancreas, female reproductive tissues and retina. In the other peripheral tissues, GABA was also present in less abundant levels in the range of μg g⁻¹.

GABA is an important molecule naturally present in considerable amounts in many feed and food matrices from vegetable and animal origin. A healthy diet based on plant products (cereals, vegetables and fruits) following the WHO food-based dietary guidelines (FBGD, adapted to different countries and graphically represented in several food guide pyramids) or/and the Healthy Eating Plate,⁶ will provide a considerable amount of GABA as a natural nutrient. Additionally, considering its potential health benefits, many efforts are being allocated to developed new technological processes for GABA enhancement in traditional foodstuff or avoiding losses after processing treatments. Of particular relevance is the use of microorganisms such as yeast fungi or lactic acid bacteria with the ability of producing GABA within the food matrix. GABA research has been intensified in recent years in parallel with the interest of the food industry in its roles as a health-related compound. The increased tendency of consumers to support functional food will contribute to maintain this research into GABA and its physiological roles.

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Notes
1. In Europe and the United States, GABA is considered a “food constituent” and a “dietary supplement,” respectively. In China, GABA is listed in the Chinese Pharmacopoeia [National Drug Standards, Drug Standards No W5-10,001-(HD-0871)-2002].
2. Replacing Annex I to Regulation(EC) No 396/2005 of the European Parliament of 23 February 2005 on maximum residue levels of pesticides in or on food and feed of plant and animal origin.
3. Excluding brassica roots and brassica baby leaf crops.
4. Harvard Health Publishing and Harvard School of Public Health.

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