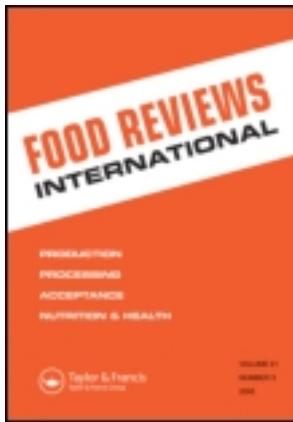


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Food Reviews International

Publication details, including instructions for authors and subscription information:
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Version of record first published: 06 Feb 2007

To cite this article: Catherine Vermeulen, Laurence Gijs & Sonia Collin (2005): Sensorial Contribution and Formation Pathways of Thiols in Foods: A Review, Food Reviews International, 21:1, 69-137

To link to this article: <http://dx.doi.org/10.1081/FRI-200040601>

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Sensorial Contribution and Formation Pathways of Thiols in Foods: A Review

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Since the mid-1990s, more than 300 publications have been devoted to the organoleptic relevance of thiols in foods (meats, wines, fruits). The available data about their physicochemical and sensorial properties, occurrence in foods, and potential formation pathways are compiled in this article.

Keywords Sulfur compounds, Thiols, Flavor, Aroma, Odor threshold, Catty, Blackcurrant, Food occurrence

Introduction

Flavors are certainly one of the most important determinants of food quality and acceptance (Mestress et al., 2000). In a few cases, the presence of a single compound (character impact substance) is sufficient to impart the typical note of the matrix (Buettner and Schieberle, 1999). More frequently, however, several compounds are needed to mimic the overall aroma. GC olfactometry (AEDA, CHARM) is probably the most useful way to find those key flavors. Unfortunately, the quality of the results depends strongly on the representativity of the analyzed extract (Bouchilloux et al., 1998b; Buettner and Schieberle, 2001; Darriet et al., 1993; Manning and Price, 1977). Extraction of thiols without artefacts is very difficult, especially when all chemical families are needed at the same time. By means of either efficient extraction procedures specific to thiols or isotopic dilution, it is possible to determine thiol concentrations accurately and to compare them with sensory thresholds

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(Manning and Price, 1977). Unfortunately, commercial thiols with sufficient olfactory purity for sensory threshold determination are usually unavailable for such experiments (Meilgaard, 1975). Too often neglected, moreover, especially when GC olfactometry is used, are the interactions of thiols with the matrix and their qualitative or quantitative synergistic effects with other odorants (Bezman et al., 2001; Marais and Swart, 1999). For example, 3-mercaptopropanol, known for its typical grapefruit flavor, surprisingly boosts the "red fruit" character when present in wine (Blanchard et al., 1999), whereas 4-mercaptopropanone, famous for its catty or blackcurrant odor, enhances the "citrus fruit" note in grapefruit juice (Buettner and Schieberle, 2001; Gora and Brud, 1983).

Among chemicals, sulfur-containing molecules and especially thiols are probably the most famous key flavors in many foods and beverages. They are often characterized by sensorial thresholds as low as the ppt level. In some cases, thiols are described by fruity notes, highly desired by the consumers. For instance, 4-mercaptopropanone appears to be crucial in white wines where the Sauvignon typicity (boxtree/blackcurrant aroma) is required. However, their occurrence is not recommended when exhaling pungent and objectionable odors (Mestres et al., 2000). Surprisingly, a few of them are considered as pleasant in some foods and damaging in others. For example, 3-methyl-2-butene-1-thiol is essential for the coffee flavor acceptance, but it is the worst enemy in beer. This article aims to compile all current data on their physical, chemical, and sensorial properties, their occurrence in foods, and formation pathways.

Physical and Chemical Properties

By definition, thiols are sulfur compounds possessing a SH functional group in their chemical structure. Because of the high polarisability of their sulfur atom (Blanchard, 2000), they are more acidic (pK_a : 9–12) than their corresponding alcohols (pK_a : 15). This property is often used in chemical syntheses involving a nucleophilic attack of the sulfur atom. In this kind of reaction, it is common to add a base such as piperidine in order to obtain the S^- form, which is much more nucleophilic than the SH one.

Thiols usually exhibit very strong antioxidant activity [free radical trapping (Naim et al., 1993, 1994), quinone or H_2O_2 reduction (Bandaranayake and Wickramasinghe, 1996; Negishi and Ozawa, 2000)]. They are easily oxidizable and convert quickly to disulfide forms (Ferreira et al., 2003; Haye et al., 1977; Hofmann et al., 1996; Mestress et al., 1997, 2000; Mottram and Madruga, 1995; Mottram and Whitfield, 1994). This phenomenon can be catalyzed by cupric ions (Fig. 1a). The resulting disulfides can be hydrolyzed to their corresponding thiols (Guth et al., 1995; Rauhut, 1993). In the absence of water, they are split to thiyl radicals and converted to thiols by other antioxidants (Guth et al., 1995). This well-known interchange reaction, between protein sulfhydryl groups (cysteine residue) and disulfides for instance (Fig. 1b; Adams et al., 2001; Axelsson and Mannervik, 1975; Bel Rhlid et al., 1999b; Bücking and Steinhart, 2002; Chen and Schofield, 1995; Friedman, 1994; Lavigne and Dubourdieu, 1996; Morel et al., 2000; Mottram and Madruga, 1995; Mottram et al., 1996, 1998; Nedjma, 1997; van Seeventer et al., 2001) is pH dependent (a higher pH involving greater disulfide loss) and temperature dependent (a higher temperature increasing interchanges). In the latter case, heat denaturation of proteins probably maximizes availability of



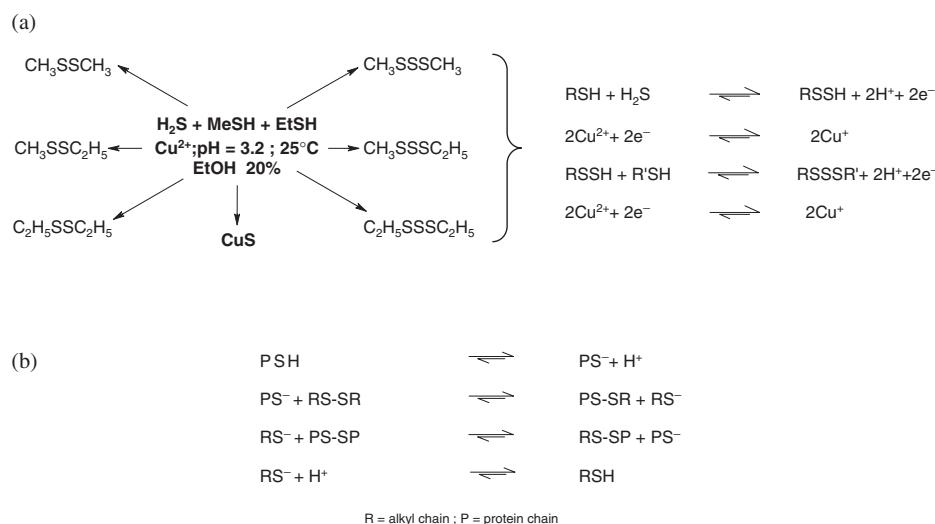


Figure 1. Thiol oxidation (a) and interchange reactions with proteins (b).

sulphydryl groups (Adams et al., 2001; Morel et al., 2000). Yet, although thiols are suspected of being thermally unstable (Blank et al., 1992; Hofmann, et al., 1996; Lin et al., 2002; Maga, 1976; Mottram et al., 1998; Vermeulen and Collin, 2002b), food processing such as pasteurization does not always alter the thiol content (Bezman et al., 2001).

This type of interchange reaction with yeast cell-wall mannoproteins can induce organoleptic evolution in fermented beverages [e.g., thiol trapping by lees in wines (Lavigne and Dubourdieu, 1996; Maujean, 2001; Tominga et al., 2003b) or H_2S removal during secondary fermentation in beer]. In living cells, glutathione with its SH moiety is also able to form mixed disulfides with proteins (Axelsson and Mannervik, 1975).

Some strong antioxidants (e.g., 2-furylthiol) can also sometimes act as prooxidants by promoting Fenton reactions after ferric ion reduction (Blank et al., 2002).

Thiols are also known to bind to metals such as Cu (Bouchilloux et al., 1998b, 1999; Darriet et al., 1993, 2001a, 2001b; Hatzimiditriou et al., 1996; Lavigne et al., 1993, 1998; Naim et al., 1997; Nedjma, 1997; Rauhut, 1993; Rigaud et al., 1986; Walker, 1995), Ag (Walker, 1995), Zn (Walker, 1995), Pb (Walker, 1995), and Hg (Darriet et al., 1995; Manning and Price, 1977; Mestres et al., 1997). This type of reaction has been used many times to extract thiols selectively from a complex matrix (e.g., reversible combination with *p*-hydroxymercuribenzoate) (Bouchilloux et al., 1996; Darriet et al., 1995; Dubourdieu and Darriet, 1993; Lavigne et al., 1993, 1998; Mestres et al., 1997; Tominaga, 1998; Tominaga and Dubourdieu, 1997; Tominaga et al., 1998b, 2003b). This thiol propensity to react with metallic ions also explains why the spraying on vine of antifungal agents containing Cu^{++} is unsuitable, especially when Sauvignon typicity is required (Darriet et al., 2001a).

Like other powerful nucleophiles (Edwards and Wedzicha, 1997; Heusinger and Mosandl, 1984; Naim et al., 1993, 1994; van Seeventer et al., 2001; Vermeulen and



Collin, 2002b), thiols can degrade unsaturated carbonyls (e.g., mesityl oxide), lactones (e.g., aflatoxins), and halogenous toxicants (Badings et al., 1976; Friedman, 1994; Takabe et al., 1970). More recent studies suggest that thiols could also be used as additives for prevention of browning in foods and beverages. For instance, fortification of orange juice and other foods with cysteine (Naim et al., 1993, 1994, 1998; Negishi and Ozawa, 2000; Voldrich et al., 1995), glutathione (Naim et al., 1997, 1998; Voldrich et al., 1995), or *N*-acetyl-cysteine (Naim et al., 1998; Voldrich et al., 1995) has proved an appropriate means of preventing Maillard reactions and browning, where thiols enter into competition with amino groups for carbohydrate reactivity (Edwards and Wedzicha, 1997; Friedman, 1994). Nevertheless, the fact that these three compounds can be a source of objectionable flavor must be taken into account (Mestres et al., 2000; Naim et al., 1997). Likewise, thiols are prone to react with polyphenols and quinones (Blanchard, 2000; Darriet et al., 2001b; Dubourdieu, 1995; Nedjma, 1997), and this explains why consumption of raw apple, pear, and prune containing significant amounts of polyphenols deodorizes bad breath after garlic consumption (Negishi et al., 2002). In the mouth, thiols can also be degraded by saliva enzymes (Buettner, 2002).

Finally, some research mentions interactions with melanoidins (Hofmann and Schieberle, 2002; Hofmann et al., 2001) or lipids (Bücking and Seinhart, 2002), the latter explaining why milk has a drastic effect on coffee sulfur notes (Bücking and Seinhart, 2002).

Sensorial Properties and Food Occurrence

As depicted in Tables 1–9, the thiols depicted in Figs. 2–5 are widespread in vegetables, fruits, beverages, meats, dairy products, and other foods. Most of them are characterized by a very low perception threshold (sometimes below the ppt level; Aznar et al., 2001; Demole et al., 1982; Gora and Brud, 1983; Maga, 1976; Mestres et al., 1999; Mottram et al., 1998; Reiners and Grosch, 1998) or BE-GC-LOADS (Best Estimated-Gas Chromatography-LOwest Amount Detected by Sniffing) (sometimes far below 1 ng; (Vermeulen and Collin, 2000b; Vermeulen et al., 2001). Therefore, it is often difficult to identify or quantify them in a complex matrix; the detection thresholds of most common detectors can only be reached with intense concentration steps (Tominaga et al., 1998b).

Colorimetric tests that use either 4,4'-bis-dimethylaminodiphenylcarbinol (Rohrbach et al., 1973) or 5-5'-dithiobis-(2-nitrobenzoic)-acid (Voldrich et al., 1995) are sometimes used to check for the presence of thiols in a medium (Fig. 6). These reactants are often sprayed on chromatographic thin layers to follow the progression of a chemical synthesis of thiols (Vermeulen et al., 2003a). By this way the spots corresponding to thiols are revealed by a change in color [from blue to colorless for the 4,4'-bis-dimethylaminodiphenylcarbinol and from colorless to yellow for the 5-5'-dithiobis-(2-nitrobenzoic)-acid].

Thiols are usually evil smelling, and therefore, are considered as detrimental to flavor (Bezman et al., 2001; Beloqui and Bertrand, 1995b; Block, 1992; Dan et.al., 1999; Hugues, 1998; Kadota and Ishida, 1972; Mestres et al., 1997; Mottram and Whitfield, 1995b; Walker and Gray, 1970). Nevertheless, minute concentrations of some polyfunctional thiols are required for the acceptability of some foods and beverages (Bel Rhlid et al., 1999a; Fitz et al., 2001; Helmlinger et al., 1976; Kumazawa et al., 2000a; Lüntzel, et al., 2000b; Masuda et al., 1988; Menneer et al.,



Table 1
Beverage/food occurrence, perception threshold, and odor of mercapto-alcohols illustrated in Fig. 2

No.	Matrix-concentration	Perception threshold	Odor
3	In vegetables: Onion (Maggs, 1976; Shankaranarayana et al., 1982)	—	—
4	In beverages: Wine—0–400 ppb (Beloqui and Bertrand, 1995a; Ferreira et al., 2003; Guedes de Pinho and Bertrand, 1995; Lavigne et al., 1998; Mestres et al., 2002; Rauhut, 1993; Tominaga et al., 1998a)	In water + 15% ethanol: 1–10 ppm (Beloqui and Bertrand, 1995b; Lavigne et al., 1998; Rauhut, 1993). In water + 20% ethanol: 100 ppb (Ferreira et al., 2003). In wine: 0.13–10 ppm (Mestres et al., 2000)	Alliaceous (Guedes de Pinho and Bertrand, 1995; Mestres et al., 2002; Tominaga et al., 1998a) (Beloqui and Bertrand, 1995a, b; Ferreira et al., 2003; Mestres et al., 2000). Rubber, burnt (Ferreira et al., 2003). Stale, off-flavor, unpleasant (Guedes de Pinho and Bertrand, 1995; Mestres et al., 2002; Tominaga et al., 1998a)
5	In beverages: Beer—7 ppb (Olsen, 1988)	In water: < 1 ppb (Olsen, 1988)	Onion (Olsen, 1988)
6	In vegetables: Onion (Lüntzel et al., 2000c; Widder et al., 2000)	BE-GC-LOADS: 0.004–0.007 ng (Vermeulen et al., in press) In air: 2(R)-3(S): 0.00007–0.0002 ppt (Lüntzel et al., 2000c) 2(S)-3(R): 0.003–0.007 ppt (Lüntzel et al., 2000c) In water: 0.15 ppb (Widder et al., 2000) 0.63 ppb (Widder et al., 1999) 2(R)-3(R): > 12 ppb (Lüntzel et al., 2000c) 2(S)-3(R): 0.04 ppb (Lüntzel et al., 2000c) 2(S)-3(S): > 30 ppb (Lüntzel et al., 2000c)	Burnt plastic, gas, citrus fruit, greenery, vinaigrette (Vermeulen et al., in press) Meat broth, sweat, leek (Lüntzel et al., 2000c; Widder et al., 1999, 2000). Onion (Widder et al., 2000). Sulfury, burnt gum, metallic, roasted (Widder et al., 1999)

(continued)

Table 1
Continued

No.	Matrix-concentration	Perception threshold	Odor
7	In beverages: Wine—0.25–10 ppb (Acuna et al., 2000; Blanchard et al., 1999; Bouchilloux et al., 1998a, b, 1999, 2000; Darriet et al., 2001a)	BE-GC-LOADS: 0.07 ng (Vermeulen et al., in press) In air: 0.004–0.4 ppt (Acuna et al., 2000) In water: 3 ppb (Bouchilloux et al., 1998b; Mestres et al., 2000) (R): 3–7 ppb (Bouchilloux et al., 2000) (S): 35–40 ppb (Bouchilloux et al., 2000) In water +12% ethanol: 20 ppb (Blanchard et al., 1999). (R): 20–27 ppb (Bouchilloux et al., 2000). (S): 0.12–0.13 ppm (Bouchilloux et al., 2000)	Broth, sweat (Acuna et al., 2000; Blanchard et al., 1999; Bouchilloux et al., 1998b; Mestres et al., 2000) Fruity, animal (Mestres et al., 2000) Herbaceous, exotic fruit, gassy, cooked vegetable (Acuna et al., 2000) Leek, onion (Acuna et al., 2000; Vermeulen et al., in press) Roasted meat (Acuna et al., 2000; Blanchard et al., 1999)
8	In beverages: Coffee—50–1500 ppb (Acuna et al., 2000; Blank et al., 1992; Boelens and van Gemert, 1993; Buettnner, 2002; Holscher et al., 1990, 1992; Tominaga and Dubourdieu, 2000; Tominaga et al., 1998a; van de Waal et al., 2002), wine—1.6–327 ppt (Acuna et al., 2000; Bouchilloux et al., 1998a, b; Mestres et al., 2000; Peyrot des Gachons et al., 1999; Tominaga and Dubourdieu, 2000; Tominaga et al., 1998a, b, 2000a; van de Waal et al., 2002)	BE-GC-LOADS: 0.2 ng (Vermeulen et al., in press) In water: 1.3 ppb (Tominaga et al., 1998a, 2000a) 2–6 ppb (Holscher et al., 1992) 2.1 ppb (Buettnner, 2002) In water +12% ethanol: 1.5 ppb (Mestres et al., 2000; Peyrot des Gachons et al., 1999; Tominaga et al., 1998a, b, 2000a)	Broth, meaty (Blank et al., 1992) Catty (Buettnner, 2002) Leek (Mestres et al., 2000; Peyrot des Gachons et al., 1999; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 2000a) Onion, tartare, chervil (Vermeulen et al., in press) Soup (Acuna et al., 2000; Holscher et al., 1990, 1992) Sweet, spicy, cooked food (Holscher et al., 1990, 1992)



- 9 In beverages: Wine—250 ppt—12.8 ppb BE-GC-LOADS: 0.004 ng (Vermeulen et al., in press) In water: 12–1 ppt (Bouchilloux et al., 1999; Bouchilloux et al., 1996, 1998a, b, 1999; Darriet et al., 2001a, b; Dubourdieu, 1995; Ferreira et al., 2001, 2002; Hatzimiditriou et al., 1996; Kotseridis and Baumes, 2000; Kotseridis et al., 2000; Lin et al., 2002; Masneuf et al., 1999, 2002; Mestres et al., 2000; Murat et al., 2001a, b, c, d; Peyrot des Gachons et al., 1999, 2000; 2002a, b, Spinnler and Bonnarme, 2002; Tominaga and Dubourdieu, 2000; Tominaga et al., 1995, 1996, 1998a, b, c, 2000a, b, 2003b; van de Waal et al., 2002) In fruits: Grapefruit (Lin et al., 2002), passion fruit—38 ppb (Acuna et al., 2000; Bouchilloux et al., 1998a, b; Dubourdieu, 1995; Engel and Tressl, 1991; Kotseridis et al., 2000; Lin et al., 2002; Tominaga and Dubourdieu, 2000; Tominaga et al., 1996, 1998a, b, 2000b; Weber et al., 1994, 1995; Werkhoff et al., 1998) In miscellaneous matrices: Yeast extract (Kotseridis and Baumes, 2000) BE-GC-LOADS: 0.004 ng (Vermeulen et al., in press) In water: 12–1 ppt (Bouchilloux et al., 1998b; Mestres et al., 2000) 17 ppt (Tominaga et al., 1998a, 2000a) In water + 12% ethanol: 0.8 ppt (Darriet et al., 2001a; Masneuf et al., 2002) 4 ppt (Lin et al., 2002; Peyrot des Gachons et al., 1999) 60 ppt (Blanchard et al., 1999; Ferreira et al., 2002; Mestres et al., 2000; Murat et al., 2001b; Peyrot des Gachons et al., 1999, 2002; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, b, 2000a; Werkhoff et al., 1998) Passion fruit (Acuna et al., 2000; Kotseridis and Baumes, 2000; Kotseridis et al., 2000; Marais and Swart, 1999; Masneuf et al., 2002; Mestres et al., 2000; Murat et al., 2001b; Peyrot des Gachons et al., 1999, 2002a, b; Tominaga et al., 1998a, b, 2000a, b, 2003b) Rhubarb, lime (Vermeulen et al., in press) Sweat (Dubourdieu, 1995; Tominaga et al., 1995) Tropical fruit, guava, mango, blackcurrant, buchu (Werkhoff et al., 1998) Vegetable, dry (Aznar et al., 2001; Ferreira et al., 2001)
- 10 In beverages: Wine (Lavigne et al., 1998) BE-GC-LOADS: 0.2 ng (Vermeulen et al., in press)

(continued)

Table 1
Continued

No.	Matrix-concentration	Perception threshold	Odor
11	In beverages: Wine—122 ppb (Bouchilloux et al., 1998a, b; Lin et al., 2002; Mestres et al., 2000; Murat et al., 2001c; Peyrot des Gachons et al., 1999, 2000, 2002a, b; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, b, c, 2000a; van de Waal et al., 2002)In fruits: Grapefruit (Lin et al., 2002)	BE-GC-LOADS: 0.009 ng (Vermeulen et al., 2001, in press) In water: 20 ppt (Tominaga et al., 1998a, 2000a) In water + 12% ethanol: 55 ppt (Lin et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002a; Tominaga et al., 1998a, b, 2000a)	Blackcurrant, solvent (Vermeulen et al., 2001, in press) Broom, box tree (Mestres et al., 2000; Vermeulen et al., 2001, in press) Citrus zest (Lin et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002a, b; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, b, 2000a) Grapefruit (Lin et al., 2002) Passion fruit (Marais and Swart, 1999; Mestres et al., 2000)

BE-GC-LOADS, Best Estimated-Gas Chromatography-LOwest Amount Detected by Sniffing.
ppm, mg/L; ppb, $\mu\text{g}/\text{L}$; ppt, ng/L.

Table 2
Beverage/food occurrence, perception threshold, and odor of mercapto-aldehydes illustrated in Fig. 3

No.	Matrix-concentration	Perception threshold	Odor
12	In fruits: Passion fruit (Engel and Tressl, 1991), tomato (Engel and Tressl, 1991) In meats: Beef liver (Werkhoff et al., 1996)	BE-GC-LOADS: 0.003 ng (Vermeulen and Collin, 2002b)	Citrus fruit peel (Vermeulen and Collin, 2002b) Sulfury, fruity, herbaceous, juicy, sweet, tropical fruit, passion fruit, guava, mango, buchu, blackcurrant, durian (Werkhoff et al., 1996)
13	In vegetables: Onion (Widder et al., 2000)	BE-GC-LOADS: 0.003–0.1 ng (Vermeulen and Collin, 2002b) In water: 0.95 ppb (Widder et al., 2000)	Meaty, onion, meat broth (Lüntzel et al., 2000; Vermeulen and Collin, 2002b; Widder et al., 2000) Pepper (Vermeulen and Collin, 2002b) Sulfury, pungent, sweat (Widder et al., 2000)

BE-GC-LOADS, Best Estimated-Gas Chromatography-LOwest Amount Detected by Sniffing.
ppb, $\mu\text{g/L}$.

Table 3
Beverage/food occurrence, perception threshold, and odor of mercapto-ketones illustrated in Fig. 3

No.	Matrix-concentration	Perception threshold	Odor
14	In meats: Pork (Liu et al., 2001)	—	Meaty, pickled (Güntert et al., 1990; Werkhoff et al., 1996) Sulfury (Güntert et al., 1990; Hofmann and Schieberle, 1995; Werkhoff et al., 1996)
15	In meats: Beef liver (Werkhoff et al., 1996), pork (Güntert et al., 1990) In miscellaneous matrices: Roasted sesame (Werkhoff et al., 1996)	In air: 1.7–6.8 ppt (Hofmann and Schieberle, 1995)	Meaty, pickled (Güntert et al., 1990; Werkhoff et al., 1996) Sulfury (Güntert et al., 1990; Hofmann and Schieberle, 1995; Werkhoff et al., 1996)
16	In meats: Beef liver (Werkhoff et al., 1996)	BE-GC-LOADS: 0.009 ng (Vermeulen et al., in press)	Cheese, solvent, skunkly, pungent (Vermeulen et al., in press) Sulfury, onion, durian, rubber (Güntert et al., 1992; Werkhoff et al., 1996)
17	In beverages: Wine (Pripis-Nicolau et al., 1999) In meats—0–70 ppt (Madruga and Mottram, 1995; Mottram and Madruga, 1994); Beef—20–44 ppb (Kerscher and Grosch, 1998), lamb—10 ppb (Kerscher and Grosch, 1998), pork—11–14 ppb (Kerscher and Grosch, 1998) In poultry: Chicken—13 ppb (Kerscher and Grosch, 1998) In miscellaneous matrices: Yeast extract (Kerscher and Grosch, 1998)	In air: 0.6 ppt (Kerscher and Grosch, 1998)	Broth, mashed potato (Mottram and Madruga, 1994) Garlic (Kerscher and Grosch, 1998) Onion (Pripis-Nicolau et al., 1999) Rotten meat, hydrogen sulfide (Mottram and Madruga, 1995) Sulfury (Kerscher and Grosch, 1998; Mottram and Madruga, 1995; Pripis-Nicolau et al., 1999)
18	In meats—0–70 ppt (Madruga and Mottram, 1995; Mottram and Madruga, 1994); Beef liver (Werkhoff et al., 1996) In miscellaneous matrices: Wheat flour (Bredie et al., 2002), yeast extract (Güntert et al., 1990; Münich and Schieberle, 1998; Werkhoff et al., 1996)	In air: 0.2–0.8 ppt (Ames and Mac Leod, 1985; Hofmann and Schieberle, 1995)	Burnt cereal/hamburger/vegetable/bread (Mottram and Madruga, 1995) Cooked meat (Mottram and Madruga, 1994; Wu and Cadwallader, 2002) Onion (Mottram and Madruga, 1994; Werkhoff et al., 1996) Roasted, meaty, fatty, durian, tropical fruit, blackcurrant (Werkhoff et al., 1996) Rotten (Ames and Mac Leod, 1985; Hofmann and Schieberle, 1995, 1997) Rubber, sour (Wu and Cadwallader, 2002) Sulfury (Ames and Mac Leod, 1985; Hofmann and Schieberle, 1995, 1997; Mottram and Madruga 1994, 1995; Schieberle and Hofmann, 1998; Werkhoff et al., 1996)

- 19 In beverages: Wine (Pripis-Nicolau et al., 1999) In cheeses (Werkhoff et al., 1996) In meats—(Madruga and Mottram, 1998); Beef—55–73 ppb (Gasser and Grosch, 1990; Kerscher and Grosch, 1998; Münch and Schieberle, 1995; Ames and Mac Leod, 1985) 0.15 ppt (Kerscher and Grosch, 1998) In water: 0.2 ppb (Wu and Cadwallader, 1998) In water: 0.2 ppb (Wu and Cadwallader, 2002) 0.7 ppb (Kerscher and Grosch, 1998; Münch and Schieberle, 1998) 66–117 ppb (Kerscher and Grosch, 1998) In poultry: Chicken—100 ppb (Gasser and Grosch, 1990b; Hofmann and Schieberle, 1995; Kerscher and Grosch, 1998; Madruga and Mottram, 1998; Münch and Schieberle, 1998; Werkhoff et al., 1996) In miscellaneous matrices: Yeast extract—0–170 ppb (Kerscher and Grosch, 1998; Münch and Schieberle, 1998; Münch et al., 1997)
- 20 In meats: Beef liver (Werkhoff et al., 1996) BE-GC-LOADS: 0.01 ng (Vermeulen et al., in press)
- In air: 0.045–0.18 ppt (Carrapiso et al., 2002; Gasser and Grosch, 1990a, 1990b) 0.05–0.2 ppt (Hofmann and Schieberle, 1995, 1997; Kerscher and Grosch, 1998; Pripis-Nicolau et al., 1999; Schieberle and Hofmann, 1998; Wu and Cadwallader, 2002) Garlic (Farmer et al., 1989) Ham, potato (Carrapiso et al., 2002) Hydrogen sulfide (Mottram and Madruga, 1995) Meaty (Carrapiso et al., 2002; Werkhoff et al., 1996) Onion, liver, herbaceous, fruity, tropical fruit, passion fruit, grapefruit, buchu (Werkhoff et al., 1996) Spicy (Baek et al., 2001) Sulfury (Bel Rhlid et al., 2002a; Gasser and Grosch, 1990a, b; Hofmann and Schieberle, 1995, 1997; Kerscher and Grosch, 1998; Mottram and Madruga, 1995; Münch and Schieberle, 1998; Münch et al., 1997; Pripis-Nicolau et al., 1999; Schieberle and Hofmann, 1998; Werkhoff et al., 1996) Urine (Farmer et al., 1989; Wu and Cadwallader, 2002) Meaty, roasted, lard, sulfury (Werkhoff et al., 1996; Güntert et al., 1992) Potato (Güntert et al., 1992; Werkhoff et al., 1996; Vermeulen et al., in press)

(continued)



Table 3
Continued

No.	Matrix-concentration	Perception threshold	Odor
21	In beverages; Beer (Polak et al., 1988; Schieberle, 1991a), tea (Kumazawa and Masuda, 1999, 2002), wine—4–400 ppt (Bouchilloux et al., 1996, 1998a, 1998b; Darriet et al., 1993, 1995, 2001a; Du Plessis and Augustyn, 1981; Dubourdin, 1995; Dubourdin and Darriet, 1993; Ferreira et al., 2001, 2002; Guth, 1997a, 1997b, 1998; Hatzimiditriou et al., 1996; Kotseridis and Baumes, 2000; Kotseridis et al., 2000; Kumazawa and Masuda, 1999; Lopez et al., 1999; Marais, 1994; Marais and Swart, 1999; Masneuf et al., 1999, 2002; Mestres et al., 2000; Murat et al., 2001c; Peyrot des Gachons et al., 1999, 2000; 2000a, 20002a, 20002b; Spinnler and Bonnarme, 2002; Tominaga and Dubourdin, 1997; Tominaga et al., 1995, 1996, 1998a, b, c, 2003a, van de Waal et al., 2002) In cheeses (Polak et al., 1988) In dairies (Maga, 1976) In fruits (Maga, 1976); Blackcurrant (Kumazawa and Masuda, 1999), grapefruit—0.8 ppb (Bredie et al., 2002; Buetner and Schieberle, 1999, 2001; Lin et al., 2002) In meats (Maga, 1976; Polak et al., 1988; Spencer, 1969; Wasserman, 1972) In miscellaneous matrices: Buchu (Boelens and van Gemert, 1993), olive oil (Kumazawa and Masuda, 1999), yeast extract (Kotseridis and Baumes, 2000) In vegetables (Maga, 1976; Polak et al., 1988)	BE-GC-LOADS: (Vermeulen et al., 2001, in press) In water: 0.066–0.165 ppt (Darriet et al., 1995) 0.1 ppt (Buetner and Schieberle, 2001; Kumazawa and Masuda, 2002; Polak et al., 1988; Vermeulen et al., 2001, in press) Box tree (Aznar et al., 2001; Bouchilloux et al., 1996, 1998b; Darriet et al., 1993, 1995; Ferreira et al., 2001; Hatzimiditriou et al., 1996; Kotseridis and Baumes, 2000; Kotseridis et al., 2000; Marais and Swart, 1999; Masneuf et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002a, 2002b; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 1998b, 2000a, 2000b) Broom (Masneuf et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002; Spinnler and Bonnarme, 2002; Tominaga et al., 1998, 2000; Vermeulen et al., in press) Catty (Buetner and Schieberle, 2001; Darriet et al., 1995; Farmer et al., 1989; Kotseridis et al., 2000; Marais and Swart, 1999; Marais, 1994; Mestres et al., 2000; Polak et al., 1988; Shankaranarayana et al., 1982; Spencer, 1969; Tominaga et al., 1996, 1998a, 1998b, 2000a, 2003a) 0.99–1.18 ppt (Darriet et al., 1995) In wine: 0.8–3 ppt (Mestres et al., 2000) 3 ppt (Bouchilloux et al., 1996; Darriet et al., 1995) 3.3 ppt (Darriet et al., 1995)	Blackcurrant (Boelens and van Gemert, 1993; Bredie et al., 2002; Buetner and Schieberle, 1999, 2001; Guth, 1997b; Hatzimiditriou et al., 1996; Kotseridis et al., 2000; Kumazawa and Masuda, 2002; Polak et al., 1988; Vermeulen et al., 2001, in press) Box tree (Aznar et al., 2001; Bouchilloux et al., 1996, 1998b; Darriet et al., 1993, 1995; Ferreira et al., 2001; Hatzimiditriou et al., 1996; Kotseridis et al., 2000; Marais and Swart, 1999; Masneuf et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002a, 2002b; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 1998b, 2000a, 2000b) Broom (Masneuf et al., 2002; Mestres et al., 2000; Peyrot des Gachons et al., 1999, 2002; Spinnler and Bonnarme, 2002; Tominaga et al., 1998, 2000; Vermeulen et al., in press) Catty (Buetner and Schieberle, 2001; Darriet et al., 1995; Farmer et al., 1989; Kotseridis et al., 2000; Marais and Swart, 1999; Marais, 1994; Mestres et al., 2000; Polak et al., 1988; Shankaranarayana et al., 1982; Spencer, 1969; Tominaga et al., 1996, 1998a, 1998b, 2000a, 2003a) 0.99–1.18 ppt (Darriet et al., 1995) In wine: 0.8–3 ppt (Mestres et al., 2000) 3 ppt (Bouchilloux et al., 1996; Darriet et al., 1995) 3.3 ppt (Darriet et al., 1995)
22	In fruits: Durian (Weenen et al., 1996)	BE-GC-LOADS: (Vermeulen et al., 2001, in press)	BE-GC-LOADS: 0.03 ng (Vermeulen et al., 2001, in press) Sulfury, cabbages (Weenen et al., 1996)

BE-GC-LOADS: Best Estimated-Gas Chromatography-Lowest Amount Detected by Sniffing.
ppb, $\mu\text{g}/\text{L}$; ppt, ng/L.



Table 4
Beverage/food occurrence, perception threshold, and odor of mercapto-esters illustrated in Fig. 3

No.	Matrix-concentration	Perception threshold	Odor
23	In beverages: Wine—23–134 ppb (Bouchilloux et al., 1998a; Lavigne et al., 1998; Mestres et al., 2000; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 2000b, 2003a)	In a wine-model solution: 40 ppb (Blanchard et al., 1999; Mestres et al., 2000; Lavigne et al., 1998)	Burnt wood, grilling (Lavigne et al., 1998) Roasted, roasted meat (Blanchard et al., 1999; Bouchilloux et al., 1998a, 1998b; Lavigne et al., 1998; Mestres et al., 2000; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 2000b)
24	In beverages: Wine—0–3278 ppt (Aznar et al., 2001; Blanchard et al., 1999; Bouchilloux et al., 1998a, 1998b; Ferreira et al., 2001; Kotseridis and Baumes, 2000; Kotseridis et al., 2000; Lin et al., 2002; Marais and Swart, 1999; Masneuf et al., 1999; Mestres et al., 2000; Murat et al., 2001b; Tominaga et al., 1996, 1998a, 2000a, 2003a) B-E-GC-LOADS: 0.02 ng (Vermeulen and Collin, in press) In water: 2–3 ppt (Bouchilloux et al., 1998b) 2.3 ppt (Mestres et al., 2000; Tominaga et al., 1996, 2000a) In a water-ethanol mixture: 4.2 ppt (Murat et al., 2001b; Tominaga et al., 1996, 1998a, 1998b, 2000a); Broom (Bouchilloux et al., 1998b; Mestres et al., 2000) Candy, blackcurrant (Vermeulen and Collin, in press) Fruity (Engel and Tressl, 1991; Kotseridis et al., 2000; Tominaga et al., 1996) Grapefruit (Kotseridis and Baumes, 2000; Lin et al., 2002; Tominaga et al., 1996, 2000b; Werkhoff et al., 1998) Mango, guava, blackcurrant, buchu (Werkhoff et al., 1998) Passion fruit (Bouchilloux et al., 1998b; Engel and Tressl, 1991; Marais and Swart, 1999; Mestres et al., 2000; Murat et al., 2001b; Peyrot des Gachons et al., 1999; Spinnler and Bonnarme, 2002; Tominaga et al., 1996, 1998b, 2000a; Vermeulen and Collin, in press; Werkhoff et al., 1998; Riesling wine (Engel and Tressl, 1991; Tominaga et al., 1996) (R): tropical fruit, passion fruit (Weber et al., 1992) (S): sulfury, cabbage (Weber et al., 1992)	Anise (Aznar et al., 2001) Banana (Kotseridis and Baumes, 2000) Box tree (Aznar et al., 2001; Blanchard et al., 1999; Bouchilloux et al., 1998b; Ferreira et al., 2001; Mestres et al., 2000; Murat et al., 2001b; Peyrot des Gachons et al., 1999; Spinnler and Bonnarme, 2002; Tominaga et al., 1996, 1998a, 1998b, 2000a); Broom (Bouchilloux et al., 1998b; Mestres et al., 2000) Candy, blackcurrant (Vermeulen and Collin, in press) Fruity (Engel and Tressl, 1991; Kotseridis et al., 2000; Tominaga et al., 1996) Grapefruit (Kotseridis and Baumes, 2000; Lin et al., 2002; Tominaga et al., 1996, 2000b; Werkhoff et al., 1998) Mango, guava, blackcurrant, buchu (Werkhoff et al., 1998) Passion fruit (Bouchilloux et al., 1998b; Engel and Tressl, 1991; Marais and Swart, 1999; Mestres et al., 2000; Murat et al., 2001b; Peyrot des Gachons et al., 1999; Spinnler and Bonnarme, 2002; Tominaga et al., 1996, 1998b, 2000a; Vermeulen and Collin, in press; Werkhoff et al., 1998; Riesling wine (Engel and Tressl, 1991; Tominaga et al., 1996) (R): tropical fruit, passion fruit (Weber et al., 1992) (S): sulfury, cabbage (Weber et al., 1992)	

(continued)



Table 4
Continued

No.	Matrix-concentration	Perception threshold	Odor
25	In fruits: Passion fruit—2 ppb (Engel and Tressl, 1991; Weber et al., 1992, 1994, 1995; Werkhoff et al., 1998)	—	Grapefruit, blackcurrant, buchu, tropical fruit, mango (Werkhoff et al., 1998) (R); tropical fruit, passion fruit (Weber et al., 1992) (S); sulfury, roasted, fruity (Weber et al., 1992)
26	In fruits: Passion fruit—1 ppb (Engel and Tressl, 1991; Weber et al., 1992, 1994, 1995; Werkhoff et al., 1998)	—	Grapefruit, guava, buchu, tropical fruit, passion fruit, blackcurrant (Werkhoff et al., 1998) (R); cabbage, sulfury (Weber et al., 1992) (S); sulfury (Weber et al., 1992)
27	In fruits: Passion fruit (Werkhoff et al., 1998)	In water: 10 ppb (Werkhoff et al., 1998)	Tropical fruit, passion fruit, buchu (Werkhoff et al., 1998)
28	In beverages: Wine—3–32 ppb (Bouchilloux et al., 1998a, 1998b; Lavigne et al., 1998; Mestres et al., 2000; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 2000b, 2003a) In meats (Lavigne et al., 1998)	BE-GC-LOADS: 0.9 ng (Vermeulen and Collin, in press) In a wine-model solution: 35 ppb (Lavigne et al., 1998; Mestres et al., 2000)	Burnt wood, grilling (Lavigne et al., 1998; Vermeulen and Collin, in press) Roasted, roasted meat (Bouchilloux et al., 1998a, 1998b; Lavigne et al., 1998; Mestres et al., 2000; Spinnler and Bonnarme, 2002; Tominaga et al., 1998a, 2000b; Vermeulen and Collin, in press)
29	In fruits: Passion fruit (Tominaga and Dubourdieu, 2000)	BE-GC-LOADS: 2 ng (Vermeulen and Collin, in press)	Grapefruit peel (Tominaga and Dubourdieu, 2000) Roasted meat, onion, vinegar, fruity (Vermeulen and Collin, in press)



- 30 In beverages: Beer (Boelens and van Gemert, 1993; Gresser, 1997; Grosch, 1993; Schieberle, 1991a), coffee—4.3–115 ppb (Blank et al., 1992; Boelens and van Gemert, 1993; Bückling et al., 2002; Czerny et al., 1999; Grosch, 1993; Holscher et al., 1990, 1992; Masanetz et al., 1995; Sanz et al., 2002; Schieberle, 1991a; Semmelroch and Grosch, 1995; van de Waal et al., 2002)
- 31 In beverages: Wine—40 ppt–12 ppb (Blanchard et al., 1999; Tominaga et al., 2003b) In fruits: Grape (Boelens and van Gemert, 1993; Kolor, 1983)
- 32 In beverages: Appel juice (Tominaga et al., 2003b), wine—50–800 ppt (Tominaga et al., 2003b) In fruits: Strawberry (Tominaga et al., 2003b)
- In air: 0.0002–0.0004 ppt (Blank et al., 1992; Boelens and van Gemert, 1993) 0.0003 ppt (Schieberle, 1991a) In water: 2–5 ppt (Boelens and van Gemert, 1993; Holscher et al., 1992; Masanetz et al., 1995; Schieberle, 1991a; Semmelroch and Grosch, 1995; Semmelroch et al., 1995) Roasted (Blank et al., 1992; Masanetz et al., 1995; Sanz et al., 2002; Semmelroch and Grosch, 1995) Sweat, fruity (Holscher et al., 1992)
- In water: 200 ppb (Boelens and van Gemert, 1993; Kolor, 1983) In a wine-model solution: 200 ppt (Tominaga et al., 2003b)
- In a wine-model solution: 500 ppt (Tominaga et al., 2003b)

BE-GC-LOADS: Best Estimated-Gas Chromatography-Lowest Amount Detected by Sniffing.
ppb, $\mu\text{g}/\text{L}$, ppt, ng/L.



Table 5
Beverage/food occurrence, perception threshold, and odor of mercapto-ethers illustrated in Fig. 4

No.	Matrix-quantity	Perception threshold	Odor
33	In miscellaneous matrices: Rue (van de Waal et al., 2002)	In air: 0.000082 ppt (van de Waal et al., 2002)	Onion, tropical fruit, sulfury (van de Waal et al., 2002)
34	In fruits: Tomato (van de Waal et al., 2002) In miscellaneous matrices: Mint (van de Waal et al., 2002), rue (van de Waal et al., 2002), sage (van de Waal et al., 2002)	In air: 0.000036 ppt (van de Waal et al., 2002) (R): 0.000109 ppt (van de Waal et al., 2002) (S): 0.00004 ppt (van de Waal et al., 2002)	Sulfury, herbaceous, green, pungent, repulsive, tropical fruit (van de Waal et al., 2002) (R): sulfury, onion, herbaceous (van de Waal et al., 2002) (S): herbaceous, sage, burnt sulfur, alliaceous, sweat (van de Waal et al., 2002)
35	In miscellaneous matrices: Rue (van de Waal et al., 2002)	In air: 0.043 ppt (van de Waal et al., 2002)	Tropical fruit, alliaceous, rubber (van de Waal et al., 2002)
36	In beverages: Tea (Kumazawa and Masuda, 1999; van de Waal et al., 2002), wine (Kumazawa and Masuda, 1999) In fruits: Blackcurrant (Boelens and van Gemert, 1993; Bouchilloux et al., 1996; Darriet et al., 1995; Kumazawa and Masuda, 1999; Le Quere and Latrasse, 1990; Polak et al., 1988; Reiners and Grosch, 1998, 1999; Rigaud et al., 1986; Tominaga and Dubourdieu, 1997; van de Waal et al., 2002) In miscellaneous matrices: Hop (Lermusieau et al., 2001), olive oil—0.1–4.3 ppb (Boelens and van Gemert, 1993; Grosch, 1993, 1994; Guth and Cirosch, 1993; Kumazawa and Masuda, 1999; Reiners and Grosch, 1998, 1999; van de Waal et al., 2002), rue (van de Waal et al., 2002)	In oil: 17–24 ppt (Reiners and Grosch, 1998) 30–60 ppt (Boelens and van Gemert, 1993) 45 ppt (Grosch, 1994; Guth and Grosch, 1993; Reiners and Grosch, 1998, 1999; Rigaud et al., 1986) Box tree (Darriet et al., 1993, 1995) Catty (Le Quere and Latrasse, 1990; Polak et al., 1988) Meaty 1 ppt (Rigaud et al., 1986) (Kumazawa and Masuda, 1999)	Blackcurrant (Boelens and van Gemert, 1993; Buettner and Schieberle, 1999; Grosch, 1994; Guth and Grosch, 1993; Reiners and Grosch, 1998, 1999; Rigaud et al., 1986) Box tree (Darriet et al., 1993, 1995) Catty (Le Quere and Latrasse, 1990; Polak et al., 1988) Meaty 1 ppt (Rigaud et al., 1986) (Kumazawa and Masuda, 1999)

ppt, ng/L



Table 6
Beverage/food occurrence, perception threshold, and odor of aliphatic and aromatic mercaptans illustrated in Fig. 4

No.	Matrix-concentration	Perception threshold	Odor
37	In meats: Pork (Liu et al., 2001) In vegetables: Onion (Kuo and Ho, 1992), scallion (Kuo and Ho, 1992)	—	—
38	In beverages: Beer (Meilgaard, 1975) In fish and crustaceans: Oyster (Maga, 1976) In meats: Beef (Maga, 1976)	In beer: 0.6 ppb (Meilgaard, 1975; Bodens and van Genert, 1993) In beer: 2-3 ppb (Haboucha et al., 1982)	Putrefaction, onion, garlic, cheese, fish, egg (Meilgaard, 1975)
39	In beverages: Beer—0.1-8 ppb (Haboucha et al., 1982; Hill and Smith, 2000) In meats: Beef (Maga, 1976; Wilson et al., 1973)	—	—
40	In beverages: Beer (Meilgaard, 1975) In fish and crustaceans: Fish protein (Maga, 1976; Qvist and von Sydow, 1974), oyster (Maga, 1976) In meats: Beef (Shankaranarayana et al., 1982; Wilson et al., 1973)	BE-GC-LOADS: 0.2 ng (Gijss et al., 2000b) In air: 1 ppb (Qvist and von Sydow, 1974) In beer: 2.5 ppb (Meilgaard, 1975; Bodens and van Genert, 1993)	Onion (Gijss et al., 2000b; Meilgaard, 1975) Putrefaction, garlic, egg (Meilgaard, 1975) Shallot (Gijss et al., 2000b)
41	In beverages: Beer (Meilgaard, 1975)	In beer: 0.07 ppt (Boelens and van Genert, 1993) 0.08 ppb (Meilgaard, 1975) In water: 0.7 ppt (Gora and Brud, 1983)	Putrefaction, onion, garlic, egg (Meilgaard, 1975)
42	In beverages: Beer—2 ppb (Peppard and Laws, 1979; Polak et al., 1988; Shankaranarayana et al., 1982; Solhoff, 1988) In fish and crustaceans: Oyster (Maga, 1976) In meats: Beef (Shankaranarayana et al., 1982)	In beer: 80 ppt (Boelens and van Genert, 1993) 90-500 ppt (Solhoff, 1988)	Unpleasant (Solhoff, 1988)
43	In fruits: Passion fruit (Werkhoff et al., 1998)	—	—
44	In miscellaneous matrices: Roasted sesame—5-50 ppb (Buettner, 2002; Schieberle, 1996)	In oil: 50 ppt (Buettner, 2002) 50 ppm (Schieberle, 1996)	Sulfury, rubber (Buettner, 2002; Schieberle, 1996)
45	In fish and crustaceans: Fish protein (Maga, 1976; Qvist and von Sydow, 1974), oyster (Maga, 1976; Shankaranarayana et al., 1982) In meats: Beef (Edwards et al., 1987) In miscellaneous matrices: Casein (Qvist and von Sydow, 1974) In vegetables: Potato (Maga, 1976; Shankaranarayana et al., 1982), soy (Qvist and von Sydow, 1974)	In air: 0.45 ppb (Qvist and von Sydow, 1974)	—
46	In fish and crustaceans: Oyster (Maga, 1976) In meats: Beef (Maga, 1976)	—	—
47	In meats: Beef (Maga, 1976; Wilson et al., 1973)	In beer: 0.2 ppb (Boelens and van Genert, 1993)	Repulsive (Maga, 1976)

(continued)



Table 6
Continued

No.	Matrix-concentration	Perception threshold	Odor
48	In beverages: Beer—<1 ppb (Blockmans et al., 1981); Boelens and van Gemert, 1993; Drost et al., 1990; Goldstein et al., 1993; Gunst and Verzel, 1978; Haboncha and Masschelein, 1979; Haboucha et al., 1982; Hill and Smith, 2000; Holscher et al., 1992; Hugues, 1998, 1999; Irwin et al., 1993; Kuroiwa et al., 1967; Maga, 1976; Mändli and Anderegg, 1991; Masuda et al., 2000; Polak et al., 1988; Sakuma et al., 1991; Seaton et al., 1981; Shankaranayana et al., 1982; Soltoft, 1988; Walker, 1991, 1992; Wilson et al., 2001). coffee—8.2–8.3 ppb (Bücking et al., 2002; Blank et al., 1992; Czerny et al., 1999; Holscher et al., 1990, 1992; Semmelroch and Grosch, 1995, 1996), sake (Kuroiwa et al., 1967), wine (Maga, 1976)	In beer: 0.46–3.38 ppt (Burns et al., 2001) 1 ppt (Walker, 1992) 1–30 ppt (Hugues, 1998) 1.25–320 ppt (Goldstein et al., 1993) 4.4–35 ppt (Irwin et al., 1993; Masuda et al., 2000) 7 ppt–1 ppb (Hill and Smith, 2000) <10 ppt (Wilson et al., 2001) <30 ppt (Boelens and van Genert, 1993) In water: 0.2–0.3 ppt (Boelens and van Gemert, 1993; Masuda et al., 2000) 0.2–0.4 ppt (Holscher et al., 1992) 0.3 ppt (Semmelroch and Grosch, 1996) <1 ppt (Burns et al., 2001) In air: 11–50 ppt (Maga, 1976)	Amine (Blank et al., 1992) Fox (Bücking and Steinhart, 2002; Holscher et al., 1990, 1992; Semmelroch and Grosch, 1995; Soltoft, 1988) Leek (Maga, 1976; Holscher et al., 1992; Hugues, 1998) Onion (Maga, 1976) Pungent, animal (Holscher et al., 1990, 1992) Skunk (Burns et al., 2001; Holscher et al., 1990, 1992; Hugues, 1998; Irwin et al., 1993; Masuda et al., 2000; Semmelroch and Grosch, 1995; Shankaranayana et al., 1982; Soltoft, 1988; Walker, 1992) Garlic (Maga, 1976; Soltoft, 1988)
49	In beverages: Beer (Soltoft, 1988) In vegetables: Allium vegetable (Negishi et al., 2002), garlic (Mateo and Zunmalacarregui, 1996), onion (Boelens et al., 1971; Maga, 1976; Shankaranayana et al., 1982) In meats: Chorizo (Mateo and Zunmalacarregui, 1996)	In air: 0.19–13 ppb (Maga, 1976) In milk: 1 ppb (Walker and Gray, 1970) In a wine-model solution: 0.3 ppt (Tominaga et al., 2003a, 2003b)	Cress (Walker and Gray, 1970) Repulsive, garlic (Maga, 1976) Smoky, empypneumatic, gun flint, cooked/smoked meat (Tominaga et al., 2003a, 2003b) Sulphy (Gasser and Grosch, 1988)
50	In beverages: Wine—10–400 ppt (Tominaga et al., 2003a, 2003b) In dairies: Butter (Shankaranayana et al., 1982), milk (Maga, 1976; Walker and Gray, 1970) In fish and crustaceans: Carp (Tominaga et al., 2003a) In meats: Beef (Gasser and Grosch, 1988; Shankaranayana et al., 1982)		



- 51 In beverages: Beer (Meilgaard, 1975) In cheeses: Cheddar (Maga, 1976) In fish and crustaceans: Oyster (Maga, 1976; Shankaranarayana et al., 1982) In meats: Beef (Shankaranarayana et al., 1982) In miscellaneous matrices: Corn (Macku and Shibamoto, 1991) In poultry: Chicken (Maga, 1976; Wilson and Katz, 1972) In vegetables: Potato (Maga, 1976)
- 52 In beverages: Beer—1.2–6.1 ppb (Haboucha et al., 1982; Hill and Smith, 2000; Meilgaard, 1975; Shankaranarayana et al., 1982; Soltoft, 1988; Walker, 1995), coffee (Maga, 1976; Shankaranarayana et al., 1982), tea (Maga, 1976), whiskey (Shankaranarayana et al., 1982), wine—0–11.1 ppm (Ferreira et al., 2003; Haye et al., 1977; Kataoka et al., 2000; Lavigne and Dubourdieu, 1996; Lavigne et al., 1993; Mestres et al., 1997, 1999, 2000; Nedjma and Maujean, 1995; Park et al., 2000; Rankine, 1968; Rauhut et al., 1996; Shankaranarayana et al., 1982) In cheeses: Cheddar (Cuer, 1982; Lieblich et al., 1970; Maga, 1976) In dairies: Butter (Shankaranarayana et al., 1982) In fish and crustaceans: Fish protein (Maga, 1976; Qvist and von Sydow, 1974), haddock (Maga, 1976), oyster (Maga, 1976; Shankaranarayana et al., 1982), parsnip (Maga, 1976; Shankaranarayana et al., 1982) In fruits: Coconut (Maga, 1976), durian (Shankaranarayana et al., 1982; Weenen et al., 1996) In meats (Shankaranarayana et al., 1982); Beef—170–280 ppb (Maga, 1976) In miscellaneous matrices: Casein (Maga, 1976; Qvist and von Sydow, 1974), corn (Maga, 1976) In poultry: Chicken (Maga, 1976; Nonaka et al., 1967; Shankaranarayana et al., 1982; Wilson and Katz, 1972) In vegetables: Bean (Maga, 1976), Brussels sprout (Maga, 1976; Shankaranarayana et al., 1982), carrot—50 ppb (Maga, 1976; Shankaranarayana et al., 1982), cauliflower (Maga, 1976; Shankaranarayana et al., 1982), cooked lettuce (Maga, 1976), leek (Maga, 1976), onion (Maga, 1976; Shankaranarayana et al., 1982), pea (Maga, 1976; Shankaranarayana et al., 1982), potato—100–220 ppb (Maga, 1976; Shankaranarayana et al., 1982), soy (Qvist and von Sydow, 1974)
- 53 In meats: Beef (Farmer et al., 1989; Shankaranarayana et al., 1982)
- 54 In meats: Beef (Shankaranarayana et al., 1982) In poultry: Chicken (Maga, 1976; Shankaranarayana et al., 1982; Wilson and Katz, 1972)
- In air: 1.0–18 ppb (Maga, 1976) In beer: 0.7 ppb (Boelens and van Gemert, 1993; Meilgaard, 1975) In water: 6 ppb (Maga, 1976)
- In air: 0.66 ppt–12 ppm (Maga, 1976) Fecal (Mestres et al., 2000) Onion (Lavigne et al., 1993; Mestres et al., 2000; Meilgaard, 1975; Rauhut, 1993; Soltoft, 1988) Putrefaction, garlic, leek, egg (Meilgaard, 1975; Mestres et al., 2000) Rubber (Mestres et al., 2000; Rauhut, 1993.)
- — —

(continued)



Table 6
Continued

No.	Matrix-concentration	Perception threshold	Odor
55	In beverages: Beer—0–16 ppb (Blockmans et al., 1981; Burmeister et al., 1992; Haboucha and Masschelein, 1979; Haboucha et al., 1982; Hill and Smith, 2000; Hugues, 1998; Meilgaard, 1975; Olsen, 1988; Peppard and Laws, 1979; Shankaranarayana et al., 1982; Soltoft, 1988; Walker, 1991, 1992; Walker and Simpson, 1993), coffee—210–600 ppb (Bücking et al., 2002; Czerny et al., 1999; Holtscher et al., 1990; Maga, 1976; Semmelroch and Grosch 1995, 1996; Shankaranarayana et al., 1982), orange juice (Shaw et al., 1980), tea (Maga, 1976) wine—0–3.3 ppm (Ferreira et al., 2003; Kataoka et al., 2000; Lavigne and Dubourdieu, 1996; Lavigne et al., 1993; Mestres et al., 1997, 1999; Park et al., 2000; Rauhut, 1993; Rauhut et al., 1996) In cheeses (Kadota and Ishida, 1972; Maga, 1976; Camembert (Jailais et al., 1999; Lecanu et al., 2002), cheddar—3–30 ppb (Chin et al., 1996; Cuer, 1982; Dias and Weimer, 1998; Lecanu et al., 2002; Maga, 1976; Manning and Price, 1977; Milo and Reineccius, 1997; Shankaranarayana et al., 1982), gouda—6 ppb (Maga, 1976), grana (Lecanu et al., 2002), grana (Lecanu et al., 1982), oryzae—1.38 ppb (Maga, 1976), trappist (Lecanu et al., 2002) In dairies: Butter (Shankaranarayana et al., 1982), milk (Maga, 1976; Shankaranarayana et al., 1982) In fish and crustaceans: Codfish (Shankaranarayana et al., 1982; Wu and Cadwallader, 2002), fish protein (Maga, 1976; Qvist and von Sydow, 1974), herring (Maga, 1976; Shankaranarayana et al., 1982), mackerel (Maga, 1976; Shankaranarayana et al., 1974), oyster (Maga, 1976; Shankaranarayana et al., 1982), parsnip (Maga, 1976), salmon (Girard and Durance, 2000), tuna (Maga, 1976; Shankaranarayana et al., 1982) In fruits: Coconut (Maga, 1976), durian (Shankaranarayana et al., 1982), fibert (Maga, 1976; Shankaranarayana et al., 1982; Kinlin et al., 1972), strawberry (Kolor, 1983), tomato (Buttery et al., 1990; Landy et al., 2002) In meats (Shankaranarayana et al., 1982); Beef—1.1–4.5 ppm (Edwards et al., 1987; Guth and Grosch, 1994; Maga, 1976; Shankaranarayana et al., 1982; Shibamoto and Russell, 1976; Wilson et al., 1973; Wu and Cadwallader, 2002), ham (Carrapiso et al., 2002; Maga, 1976), pork (Elmore et al., 2000; Maga, 1976; Shankaranarayana et al., 1982), pork liver (Shankaranarayana et al., 1982), In miscellaneous matrices: Barley (Shankaranarayana and Forcen, 1992), bread (Maga, 1976; Shankaranarayana et al., 1982), carob bean (MacLeod and Forcen, 1992), casein (Maga, 1976; Qvist and von Sydow, 1974), corn—35–70 ppb (Maga, 1976; Shankaranarayana et al., 1982), hop—0–75 ppb (Maga, 1976; Seaton et al., 1981), mushroom (Shankaranarayana et al., 1982), rape seed (Shankaranarayana et al., 1982), shiitake (Shankaranarayana et al., 1982), yeast extract (Ames and Mac Leod, 1985) In poultry: Chicken (Maga, 1976; Nonaka et al., 1967; Senter et al., 2000; Shankaranarayana et al., 1982; Wilson and Katz, 1972), turkey (Fan et al., 2002) In vegetables: Allium vegetable (Negishi et al., 2002), asparagus (Shankaranarayana et al., 1982), bean (Maga, 1976; Shankaranarayana et al., 1982), broccoli (Chin and Lindsay, 1994; Dan et al., 1997, 1999; Engel et al., 2002; Forney et al., 1991; Obenland and Aung, 1996; Tilio et al., 2002), Brussels sprout (Maga, 1976; Shankaranarayana et al., 1982), cabbage (Chin and Lindsay, 1994; Dan et al., 1999; Maga, 1976; Shankaranarayana et al., 1982), carrot (Maga, 1976; Shankaranarayana et al., 1982), cauliflower (Dan et al., 1999; Maga, 1976; Shankaranarayana et al., 1982), cooked lettuce (Maga, 1976), garlic (Maga, 1976; Shankaranarayana et al., 1982; Shibamoto and Russell, 1976), leek (Maga, 1976; Shankaranarayana et al., 1982; Shibamoto and Russell, 1976), onion (Boelens et al., 1971; Maga, 1976; Shankaranarayana et al., 1982; Shibamoto and Russell, 1976), pea (Maga, 1976; Shankaranarayana et al., 1982), potato—42–87 ppb (Maga, 1976; Shankaranarayana et al., 1982), rutabaga (Casey et al., 1965; Maga, 1976), sauerkraut (Maga, 1976), soy (Maga, 1976; Qvist and von Sydow, 1974; Shankaranarayana et al., 1982)	In air (Maga, 1976; Mestres et al., 2000) 2.1 ppb (Qvist and von Sydow, 1974) 41 ppb (Shankaranarayana et al., 1982) 2 ppb (Meilgaard, 1975) 2–4 ppb (Haboucha et al., 1982) 2–12 ppb (Rauhut, 1993; Soltoft, 1988) In beer: 2 ppb (Meilgaard, 1975) In water: 0.02 ppb (Engel et al., 2002; Fan et al., 2002; Forney et al., 1991; Landy et al., 2002) 0.02–0.02 ppb (Mestres et al., 2000; Rauhut, 1993; Shankaranarayana et al., 1982) 0.02– 20 ppb (Maga, 1976) 0.2 ppb (Guth and Grosch, 1994) 0.2– 25 ppb (Wu and Cadwallader, 2002) In wine-model solu- tion: 0.3 ppb (Lavigne et al., 1993; Mestres et al., 2000)	Cabbage (Edwards et al., 1987; Guth and Grosch, 1994; Landy et al., 2002; Lecanu et al., 2002; Mestres et al., 2000; Meilgaard, 1975; Rauhut, 1993; Semmelroch and Grosch, 1995; Soltoft, 1988) Cheese (Carrapiso et al., 2002; Lecanu et al., 2002) Drains, estery (Meilgaard, 1975) Garbage (Wu and Cadwallader, 2002) Fecal (Engel et al., 2002; Forney et al., 1991) Fish, meaty (Carrapiso et al., 2002) Garlic (Lecanu et al., 2002) Putrid (Bücking et al., 2002; Edwards et al., 1987; Engel et al., 2002; Forney et al., 1991; Holscher et al., 1990; Lavigne et al., 1993; Lecanu et al., 2002; Mestres et al., 2000; Semmelroch and Grosch, 1995) Rotten, egg (Carrapiso et al., 2002; Forney et al., 1991; Holscher et al., 1990; Lavigne et al., 1993; Lecanu et al., 2002; Mestres et al., 2000; Semmelroch and Grosch, 1995) Sulfur (Edwards et al., 1987; Guth and Grosch, 1994; Landy et al., 2002; Lecanu et al., 2002; Mestres et al., 2000; Semmelroch and Grosch, 1995; Wu and Cadwallader, 2002)



56	In meats: Beef (Maga, 1976; Shankaranarayana et al., 1982; Wilson et al., 1973)	—	Unpleasant (Maga, 1976)			
57	In meats: Beef (Farmer et al., 1989)	—	—			
58	In miscellaneous matrices: Corn (Macku and Shibamoto, 1991)	—	Painting, smoke, pharmacy (Gijs et al., 2000b)			
59	In beverages: Beer—0.11 ppb (Meilgaard, 1975; Walker, 1991, 1992; Walker and Simpson, 1993), coffee (Maga, 1976; Shankaranarayana et al., 1982), tea (Maga, 1976) In fish and crustaceans: Oyster (Maga, 1976; Shankaranarayana et al., 1982), parsnip (Maga, 1976) In fruits: Coconut (Maga, 1976), durian (Shankaranarayana et al., 1982; Weenen et al., 1996) In meats: Beef (Maga, 1976) In miscellaneous matrices: Casein (Maga, 1976), corn (Shankaranarayana et al., 1982; Macku and Shibamoto, 1991) In poultry: Chicken (Maga, 1976; Shankaranarayana et al., 1982; Wilson and Katz, 1972) In vegetables: Allium vegetable (Nagishi et al., 2002; Kubec et al., 1999), bean (Shankaranarayana et al., 1982), cauliflower (Maga, 1976), leek—6.02–10.99 ppm (Maga, 1976; Schulz et al., 1998; Shankaranarayana et al., 1982), onion—1.04–2.46 ppm (Boelens et al., 1971; Kuo and Ho, 1992; Maga, 1976; Schulz et al., 1998; Shankaranarayana et al., 1982), pea (Maga, 1976; Shankaranarayana et al., 1982), potato (Maga, 1976; Shankaranarayana et al., 1982), scallion (Kuo and Ho, 1992)	BE-GC-LOADS: 0.07 ng (Gijs et al., 2000b) In water: 0.8 ppb (Gijs et al., 2000b)	Cabbage (Maga, 1976) Onion (Meilgaard, 1975; Weenen et al., 1996) Putrefaction, garlic, egg (Meilgaard, 1975)			
60	In beverages: Beer (Meilgaard, 1975)	—	—			
61	In meats: Beef (Shankaranarayana et al., 1982)	In beer: 0.2 ppb (Meilgaard, 1975)	Putrefaction, onion, garlic, egg (Meilgaard, 1975)			
62	In beverages: Beer (Meilgaard, 1975) In meats: Beef (Shankaranarayana et al., 1982)	—	—			
		In beer: 0.00007 ppb (Meilgaard, 1975)	Putrefaction, guava, peach, fish, catty (Meilgaard, 1975)			

BE-GC-LOADS, Best Estimated-Gas Chromatography-Lowest Amount Detected by Sniffing.
ppm, mg/L; ppb, $\mu\text{g}/\text{L}$; ppt, ng/L.



Table 7
Beverage/food occurrence, perception threshold, and odor of terpenic mercaptans illustrated in Fig. 5

No.	Matrix-concentration	Perception threshold	Odor
63	In fruits: Grapefruit—10 ppt (Boelens and van Gemert, 1993; Bouchilloux et al., 1998a; Buettner and Schieberle, 1999, 2001; Darriet et al., 1995; Demole et al., 1982; Lin et al., 2002; Polak et al., 1988)	In air: 0.001 ppt (Huber and Bergamin, 1993) In water: 0.1 ppt (Bouchilloux et al., 1998a; Buettner and Schieberle, 1999, 2001; Darriet et al., 1995; Demole et al., 1982) (+)-(R): 0.02 ppt (Boelens and van Gemert, 1993; Demole et al., 1982) (−)-(S): 0.08 ppt (Boelens and van Gemert, 1993; Demole et al., 1982)	Fruity (Demole et al., 1982) Grapefruit (Buettner and Schieberle, 1999, 2001; Demole et al., 1982; Lin et al., 2002) Green citrus (Polak et al., 1988) Sulfury (Buettner and Schieberle, 2001) (+)-(R): grapefruit (Boelens and van Gemert, 1993), fruity (Polak et al., 1988) (−)-(S): sulfury (Boelens and van Gemert, 1993; Polak et al., 1988)
64	In fruits: Blackcurrant (Gora and Brud, 1983; Maga, 1976; Rigaud et al., 1986) In miscellaneous matrices: Buchu (Boelens and van Gemert, 1993; Darriet et al., 1995; Gora and Brud, 1983; Kaiser et al., 1975; Lamparsky and Schudel, 1971a; Polak et al., 1988; Rigaud et al., 1986; Sundt et al., 1971)	—	Blackcurrant (Maga, 1976; Polak et al., 1988; Sundt et al., 1971) Box tree (Darriet et al., 1993, 1995) Buchu, fruity, minty (Polak et al., 1988) 1(R)-4(R): tropical fruit, onion, dirty (Boelens and van Gemert, 1993) 1(R)-4(S): rubber, thiol, isopugelone, sulfury, buchu (Boelens and van Gemert, 1993) 1(S)-4(R): fruity, blackcurrant, passion fruit, tropical fruit (Boelens and van Gemert, 1993) 1(S)-4(S): tropical fruit, sulfury, buchu (Boelens and van Gemert, 1993)
65	In beverages: Beer (Peppard and Laws, 1979)	—	Solvent, sulfury, rubber (Peppard and Laws, 1979)



Table 8
Beverage/food occurrence, perception threshold, and odor of acyclic mercaptans containing another sulfur function illustrated in Fig. 5

No.	Matrix-concentration	Perception threshold	Odor
66	In meats: Beef (Drumm and Spanier, 1991), pork (Tai and Ho, 1997)	—	Sulfury, rubber, cheese, onion, meaty (Tai and Ho, 1997)
67	In meats: Beef (Shankaranarayana et al., 1982) In poultry: Chicken (Maga, 1976; Nonaka et al., 1967; Shankaranarayana et al., 1982; Wilson and Katz, 1972)	In air: 1.6–31 ppb (Maga, 1976) —	—
68	In meats: Beef (Shankaranarayana et al., 1982)	—	—
69	In meats: Beef (Shankaranarayana et al., 1982)	—	—
70	In meats: Beef (Shankaranarayana et al., 1982)	—	—
71	In meats: Beef (Shankaranarayana et al., 1982)	—	—
72	In meats: Beef (Boelens et al., 1974; Brinkman et al., 1972; Maga, 1976; Schutte and Koenders, 1972; Schutte, 1971; Shankaranarayana et al., 1982; Werkhoff et al., 1989)	In water: 1–5 ppb (Brinkman et al., 1972)	Meaty (Brinkman et al., 1972; Drumm and Spanier, 1991) Onion (Boelens et al., 1974; Brinkman et al., 1972; Drumm and Spanier, 1991; Werkhoff et al., 1989, 1990)

ppb, $\mu\text{g/L}$.

Table 9
Beverage/food occurrence, perception threshold, and odor of heterocyclic mercaptans illustrated in Fig. 5

No.	Matrix-concentration	Perception threshold	Odor
73	In meats: Beef (Gasser and Grosch, 1990) In poultry: Chicken (Gasser and Grosch, 1990; Huber and Bergamin, 1993)	In air: 0.0035–0.014 ppt (Gasser and Grosch, 1990)	Meaty (Gasser and Grosch, 1990)
74	In beverages: Coffee—19.1–2500 ppb (Ames et al., 2001; Blanchard et al., 2001; Blieking and Steinhart, 2002; Blank et al., 1992, 2002; Buettner, 2002; Boelens and van Gemert, 1993; Czerny et al., 1993; Farmer and Mottram, 1990; Gora and Brud, 1983; Grosch, 1993, 1994; Hofmann and Schieberle, 1995, 1998; Hofmann et al., 1990; Kerscher and Grosch, 1998; Maga, 1976; Meynier and Mottram, 1993; Mussinan and Katz, 1973; Sanz et al., 2002; Schieberle, 1996; Semmelroch and Grosch, 1995, 1996; Semmelroch et al., 1995; Shankaranarayana et al., 1982; Shibamoto and Russell, 1976; Tominaga et al., 2000a; Tressl and Silwar, 1981; Wu and Cadwallader, 2002), wine—2 ppt–5.5 ppb (Blanchard et al., 1999, 2001; Marchand et al., 2000; Spinnler and Bonnarme, 2002; Tominaga et al., 2000a, 2000b, 2003a, 2003b) In meats (Blanchard et al., 2001; Carrapiso et al., 2002; Gasser and Grosch, 1990a; Hofmann et al., 1996; Madruga and Mottram, 1995; Meynier and Mottram, 1995; Moitram and Madruga, 1994; Moitram et al., 1998; Tominaga et al., 2000b); Beef—1.5–42 ppb (Cerny and Grosch, 1992; Drumm and Ho, 1991; Farmer and Mottram, 1990; Gasser and Grosch, 1990b; Grosch, 1993, 1994; Guth and Grosch, 1994; Hofmann and Schieberle, 1995, 1998; Kerscher and Grosch, 1998; Madruga and Mottram, 1995; Meynier and Mottram, 1998; Tominaga et al., 1995; Moitram and Mottram, 1998; Wu and Cadwallader, 2002), ham (Carrapiso et al., 2002), lamb—9–14 ppb (Kerscher and Grosch, 1998), pork—8–10 ppb (Liu et al., 2001; Kerscher and Grosch, 1998; Madruga and Mottram, 1998; Mottram, 1985) In poultry: Chicken—2.4 ppb (Farkas et al., 1997; Farmer and Mottram, 1990; Gasser and Grosch, 1990b; Hofmann and Schieberle, 1995; Kerscher and Grosch, 1998; Madruga and Mottram, 1998; Wu and Cadwallader, 2002), hen (Farkas et al., 1997) In miscellaneous matrices: Bread (Blanchard et al., 2001; Hofmann et al., 1996; Kerscher and Grosch, 1998), popcorn (Ames et al., 2001; Blanchard et al., 2001; Buttery and Ling, 1998; Grosch, 1993, 1994; Hofmann and Schieberle, 1995, 1996; Kerscher and Grosch, 1998; Schieberle, 1991b, 1996), roasted sesame (Ames et al., 2001; Buettner, 2002; Grosch, 1994; Hofmann and Schieberle, 1995, 1998; Kerscher and Grosch, 1998; Schieberle, 1996; tortilla chip—>5 ppb (Buttery and Ling, 1998), wheat flour (Bredie et al., 2002), yeast extract—29–580 ppb (Ames and MacLeod, 1985; Hofmann and Schieberle, 1998; Kerscher and Grosch, 1998; Münch and Schieberle, 1998; Münch et al., 1997; Wu and Cadwallader, 2002))	Beef broth (Farmer et al., 1989) Burnt (Bredie et al., 2002; Marchand et al., 2000; Tominaga et al., 2003b) Caramel, sweet (Zhang and Ho, 1991) Coffee (Ames et al., 2001; Bel Rhlid et al., 2002b; Blanchard et al., 1999; Blank et al., 1992, 2002; Boelens and van Gemert, 1993; Bücking and Steinhart, 2002; Chen and Ho, 2002; Czerny et al., 1999; Farkas et al., 1997; Farmer et al., 1989; Gora and Brud, 1983; Hofmann and Schieberle, 1995, 1997; Holscher et al., 1990; Marchand et al., 2000; Moitram et al., 1998; Münch and Schieberle, 1998; Münch et al., 1997; Schieberle, 1991b, 1996; Schieberle and Hofmann, 1998; Shankaranarayana et al., 1982; Shibamoto, 1977; Spinnler and Bonnarme, 2002; Tominaga et al., 2000a, 2000b, 2003b; Tressl and Silwar, 1983) Cured ham, toasted, sewage, fatty, fruity (Carrapiso et al., 2002) Garlic (Drumm and Spanier, 1991; Farmer et al., 1989; Gora and Brud, 1983) Meaty (Buettner, 2002) Pungent (Drumm and Spanier, 1991; Farmer et al., 1989; Gora and Brud, 1983; Shankaranarayana et al., 1982) Roasted (Ames et al., 2001; Bel Rhlid et al., 2002b; Blank et al., 1992, 2002; Bücking and Steinhart, 2002; Chen and Ho, 2002; Czerny et al., 1999; Farkas et al., 1997; Gasser and Grosch, 1990a, 1990b; Hofmann and Schieberle, 1995, 1997; Holscher et al., 1990; Münch and Schieberle, 1998; Münch et al., 1997; Sanz et al., 2002; Schieberle, 1991b, 1996; Schieberle and Hofmann, 1998; Semmelroch and Grosch, 1995) Sulfury (Bel Rhlid et al., 2002b; Bredie et al., 2002; Czerny et al., 1999; Farmer et al., 1989; Tressl and Silwar, 1981; Wu and Cadwallader, 2002)	



- In beverages: Beer (Lermuseau et al., 2001), coffee (Blank et al., 1992; Bouchilloux et al., 1998a; Czerny et al., 1999; Hofmann and Schieberle, 1995; Hofmann and Schieberle, 1998; Hofmann et al., 1996; Holscher et al., 1990; Kerscher and Grosch, 1998; Münch and Schieberle, 1998; Semmelroch and Grosch, 1995; Wu and Cadwallader, 2002), grapefruit juice (Lin et al., 2002), orange juice (Bezman et al., 2001), wine (Aznar et al., 2001; Bezman et al., 2001; Blanchard et al., 1999; Bouchilloux et al., 1998a; Ferreira et al., 2001, 2002; Kotsiris and Baumes, 2000; Spinnler and Bonnarme, 2002; Tominga et al., 2003b). In fish and crustaceans: Tuna (Baek et al., 2001; Güntert et al., 1990; Hofmann and Schieberle, 1998; Huber and Bergamin, 1993; Kerscher and Grosch, 1992; Withycombe and Mussinan, 1988) In meats (Bouchilloux et al., 1998a; Gasser and Grosch, 1990a; Hofmann et al., 1996; Holscher et al., 1990; Madruga and Mottram, 1995, 1998; Meynier and Mottram, 1995; Mottram et al., 1998; Shankaranarayana et al., 1982); Beef—7–28 ppb (Baek et al., 2001; Boelens and van Gemert, 1993; Cerny and Grosch, 1992; Gasser and Grosch, 1988, 1990b; Grosch, 1993; Güntert et al., 1990; Hofmann and Schieberle, 1995, 1998; Huber and Bergamin, 1993; Kerscher and Grosch, 1998; Mottram and Whitfield, 1994; Wu and Cadwallader, 2002), ham (Carrapiso et al., 2002), lamb—5–11 ppb (Kerscher and Grosch, 1998), pork—6–9 ppb (Kerscher and Grosch, 1998) In poultry: Chicken—4.5 ppb (Boelens and van Gemert, 1993; Farkas et al., 1997; Gasser and Grosch, 1990b; Hofmann and Schieberle, 1995; Huber and Bergamin, 1993; Kerscher and Grosch, 1998; Wu and Cadwallader, 2002), hen (Farkas et al., 1997) In miscellaneous matrices: Bread (Hofmann et al., 1996), rice (Jezussek et al., 2002), yeast extract—22–530 ppb (Ames and MacLeod, 1985; Baek et al., 2001; Blanchard et al., 1999; Bouchilloux et al., 1998b; Ferreira et al., 2001; Gasser and Grosch, 1988; Güntert et al., 1990; Kerscher and Grosch, 1998; Kotsiris and Baumes, 2000; Münch and Schieberle, 1998; Werkhoff et al., 1989, 1990)

In air: 0.001–0.002 ppt (Blank et al., 1992) 0.0025 ppt (Carrapiso et al., 2002; Hofmann and Schieberle, 1998) 0.0025–0.01 ppt (Boelens and van Gemert, 1993; Chen and Ho, 2002; Gasser and Grosch, 1990a, 1990b; Hofmann and Schieberle, 1995; Huber and Bergamin, 1993) 0.005–0.01 ppt (Bel Rhlid et al., 2002b; Bezman et al., 2001; Bel Rhlid et al., 2002a, 2002b; Bezelman et al., 2001; Blank et al., 1992; Bocelens and van Gemert, 1993; Bouchilloux et al., 1998a; Chen and Ho, 2002; Farkas et al., 1997; Farmer and Mottram, 1990; Farmer et al., 1989; Gasser and Grosch, 1988, 1990a, 1990b; Hartman et al., 1994b; Hofmann and Schieberle, 1995; Holtscher et al., 1990; Jezussek et al., 2002; Jhoo et al., 2002; Kotsiris and Baumes, 2000; Lin et al., 2002; Maga, 1976; Meynier and Mottram, 1995; Mottram and Madruga, 1994; Mottram et al., 1998; Münch and Schieberle, 1998; Schieberle and Hofmann, 1998; Semmelroch and Grosch, 1995; Tominaga et al., 2003b; Werkhoff et al., 1989, 1990; Withycombe and Mussinan, 1988; Wu and Cadwallader, 2002; Zhang and Ho, 1991) Milk, sunflower seed (Kotsiris and Baumes, 2000) Onion, fatty (Aznar et al., 2001; Ferreira et al., 2001; Mottram and Madruga, 1994) Pungent, burnt, rubber (Farmer and Mottram, 1990; Meynier and Mottram, 1995) Roasted (Bel Rhlid et al., 2002a) Roasted nut (Bouchilloux et al., 1998a; Carrapiso et al., 2002; Kotsiris and Baumes, 2000;) Sulfury (Ames et al., 2001; Bel Rhlid et al., 2002b; Farmer and Mottram, 1990; Farmer et al., 1989; Gasser and Grosch, 1988; Hofmann and Schieberle, 1995; Jezussek et al., 2002) Vitamin (Baek et al., 2001; Bezman et al., 2001; Wu and Cadwallader, 2002)

(continued)

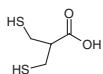
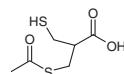
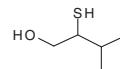
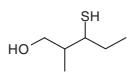
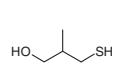
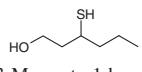
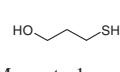


Table 9
Continued

No.	Matrix-concentration	Perception threshold	Odor
76	In meats: Pork(Madruga and Mottram, 1998) In miscellaneous matrices: Yeast extract (Güntert et al., 1990)	In air: 0.0032–0.0128 ppt (Hofmann and Schieberle, 1995)	Metallic (Farmer et al., 1989; Werkhoff et al., 1990) PVC, coal (Farmer et al., 1989) Roasted meat (Chen and Ho, 2002; Farmer and Mottram, 1990; Farmer et al., 1989; Hofmann and Schieberle, 1995; Maga, 1976; van den Ouveland and Peer, 1975; Werkhoff et al., 1989, 1990) Rubber (Werkhoff et al., 1990) Sulfury (Chen and Ho, 2002; Hofmann and Schieberle, 1995; Werkhoff et al., 1990)
77	In miscellaneous matrices: Syrup (Maga, 1975)	—	Burnt, onion (Maga, 1975)
78	In beverages: Wine (Marchand et al., 2000) In meats: Pork—hypothesis (Madruga and Mottram, 1998) In miscellaneous matrices: Syrup (Maga, 1975)	In air: 0.003–0.012 ppt (Hofmann and Schieberle, 1995) In water: 0.8 ppb (Marchand et al., 2000)	Burnt, rubber (Marchand et al., 2000) Coffee (Marchand et al., 2000; Maga, 1975) Egg, onion, fatty, leek (Chen and Ho, 2002) Garlic, sulfury, pungent (Farmer et al., 1989) Meaty, vitamin (Wu and Cadwallader, 2002) Roasted (Hofmann and Schieberle, 1995) Unpleasant, burned caramel (Farmer et al., 1989; Maga, 1976)
79	In vegetables: Onion (Block, 1992; Kuo and Ho, 1992), scallion (Block, 1992; Kuo and Ho, 1992)	—	—
80	In meats: Pork (Bouchilloux et al., 1998a; Madruga and Mottram, 1998)	In water: 5–10 ppb (Bouchilloux et al., 1998a)	Meaty (Bouchilloux et al., 1998a; Güntert et al., 1990)
81	In beverages: Wine—hypothesis (Guedes de Pinho et al., 1997)	—	Strawberry, sulfury (Guedes de Pinho et al., 1997)
82	In beverages: Coffee (Boelens and van Gemert, 1993; Tressl and Silwar, 1981) In miscellaneous matrices: Yeast extract (Münch and Schieberle, 1998)	In air: 0.019 ppt (Hofmann and Schieberle, 1997) In water: 0.006 ppb (Hofmann and Schieberle, 1997) 0.05 ppb (Boelens and van Gemert, 1993; Tressl and Silwar, 1981)	Coffee (Hofmann and Schieberle, 1997; Schieberle and Hofmann, 1998) Meaty (Tressl and Silwar, 1981) Roasted (Hofmann and Schieberle, 1997; Schieberle, 1996; Schieberle and Hofmann, 1998) Sulfury (Boelens and van Gemert, 1993; Schieberle, 1996; Tressl and Silwar, 1981)

Ppb, µg/L; ppt, ng/L.



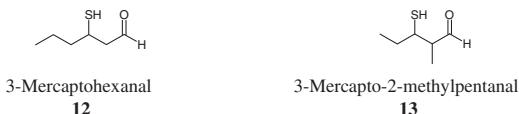
Mercapto-acids3,3'-Dimercaptoisobutyric acid
13-Thioacetoxy-3'-mercaptopisobutyric acid
2**Mercapto-alcohols**1-Mercapto-2-propanol
32-Mercapto-1-ethanol
42-Mercapto-3-methyl-1-butanol
53-Mercapto-2-methyl-1-pentanol
63-Mercapto-2-methyl-1-propanol
73-Mercapto-3-methyl-1-butanol
83-Mercapto-1-hexanol
93-Mercapto-1-propanol
104-Mercapto-4-methyl-2-pentanol
11**Figure 2.** The structure of two mercapto-acids (Yanagawa et al., 1972) and nine mercapto-alcohols occurring in foods or beverages.

2001; Murat et al., 2001d; 2000b; Price and Menneer, 2000; Reiners and Grosch, 1999; Rigaud et al., 1986; Stoffelsma and Pijpkér, 1973; Vermeulen and Collin, 2002a, b; Vermeulen et al., 2001; Tominaga et al., 2003a; Widder et al., 1999) (Table 10), and even in perfumes or cosmetics (Lamparsky and Schudel, 1971b; Lüntzel et al., 2000; Maga, 1976; Masuda et al., 1989, 1988; Stoffelsma and Pijpkér, 1973; Thorne, 1966; Widder et al., 1999). Minimal moieties have more recently been proposed (Vermeulen and Collin, 2002a) for predicting whether mercapto-aldehydes, -ketones, or -alcohols will exhibit rhubarb/carrot, onion/sweat/pungent/leek, or potato odors. Roasted/coffee/toasted/meaty descriptors often characterize the heterocyclic mercaptans.

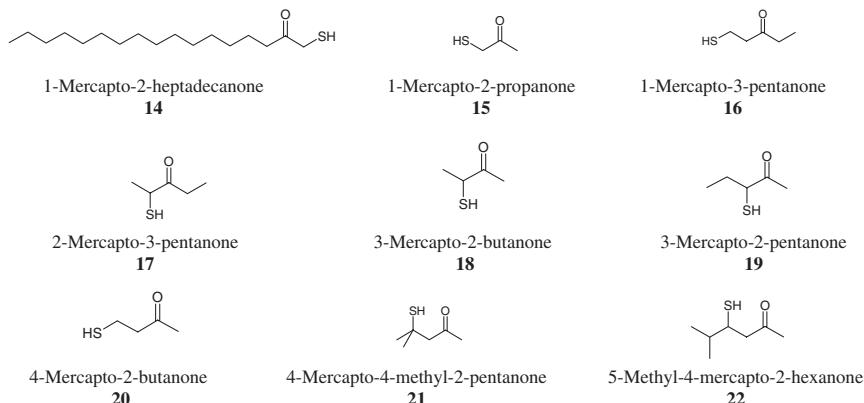
Although characterized by delicate pleasant odors at very low concentrations, most thiols become sharp, irritating, and repulsive when pure or highly concentrated (Boelens and van Gemert, 1993; Engel and Tressl, 1991; Gora and Brud, 1983; Marais, 1994; Mestres et al., 1999; Mottram and Whitfield, 1995c; Rigaud et al., 1986; Widder et al., 2000). Odor descriptors also depend on the accessibility of the sulfur-atom (Boelens and van Gemert, 1993; Madruga and Mottaram, 1998; Mottram and Madruga, 1994; Mottram and Whitfield, 1994), the chain length (Meilgaard, 1975; Node et al., 2001; Werkhoff et al., 1998), the chirality (Boelens and



Mercapto-aldehydes



Mercapto-ketones



Mercapto-esters

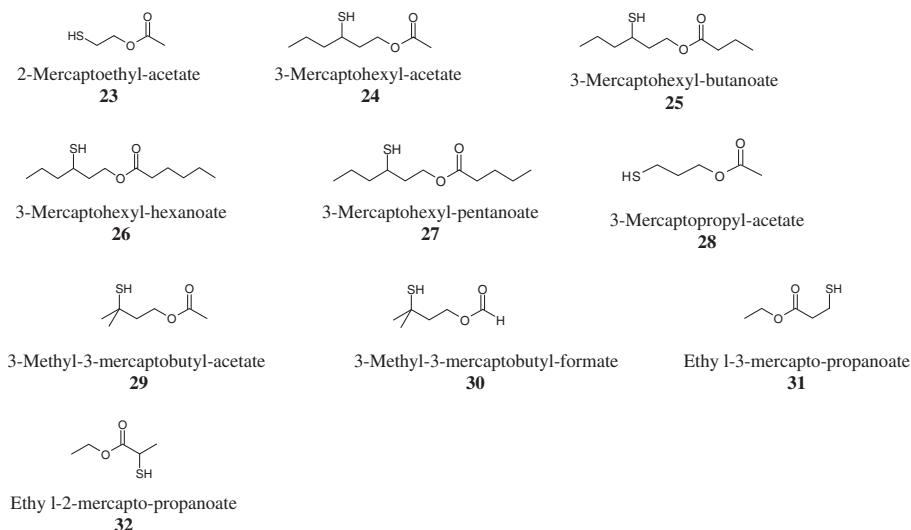
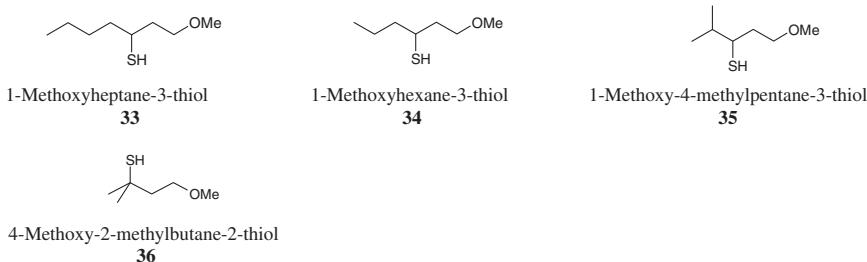


Figure 3. The structure of two mercapto-aldehydes, nine mercapto-ketones, and 10 mercapto-esters occurring in foods or beverages.



Mercapto-ethers



Aliphatic and aromatic mercaptans

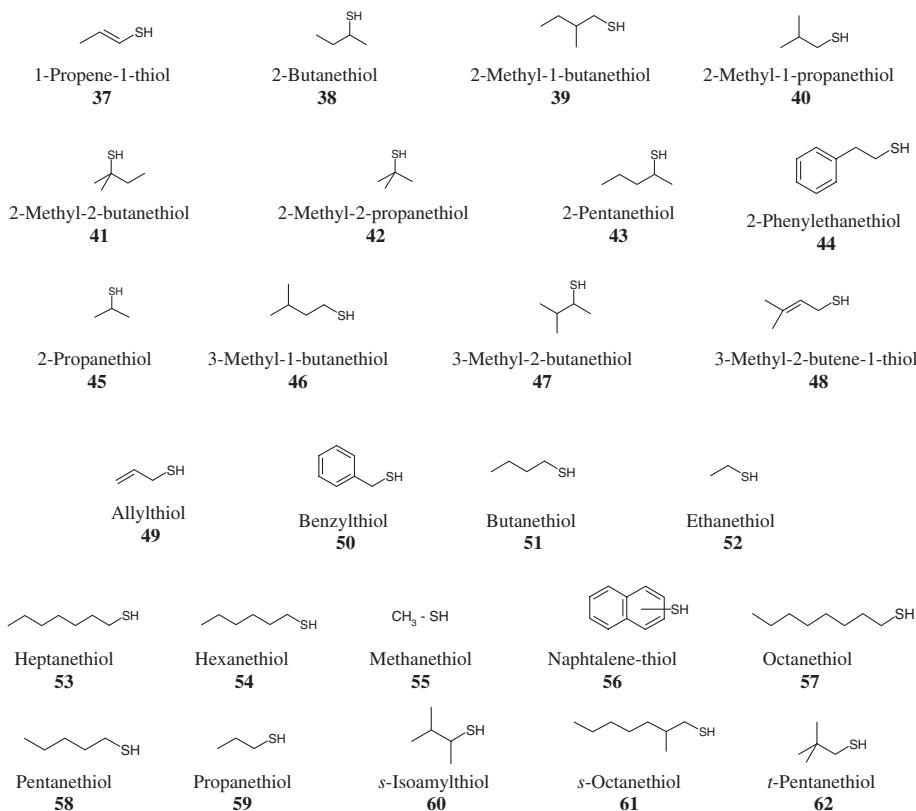
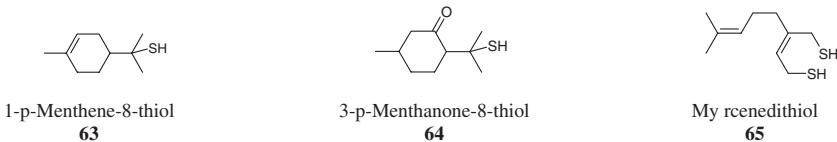


Figure 4. The structure of four mercapto-ethers and 26 aliphatic and aromatic mercaptans occurring in foods or beverages.

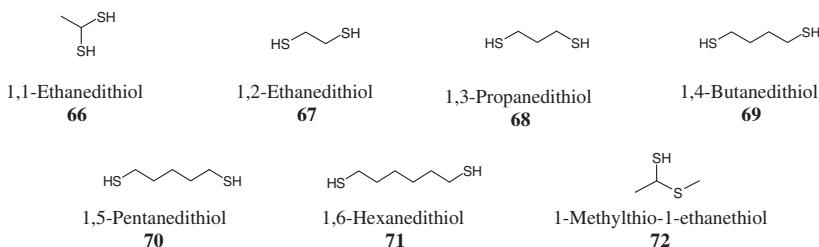
van Gemert, 1993; Bouchilloux et al., 2000; Lamparsky and Schudel, 1971a; Weber et al., 1995; Werkhoff et al., 1998), and the presence of other functional group(s) (Boelens and van Gemert, 1993; Polak et al., 1998). For example, tertiary thiols are often characterized by a catty smell (Polak et al., 1988), whereas the presence of a proton-attracting group such as C=O or C-O-C near the SH moiety seems to have



Terpenic mercaptans



Acyclic mercaptans containing another sulfur function



Heterocyclic mercaptans

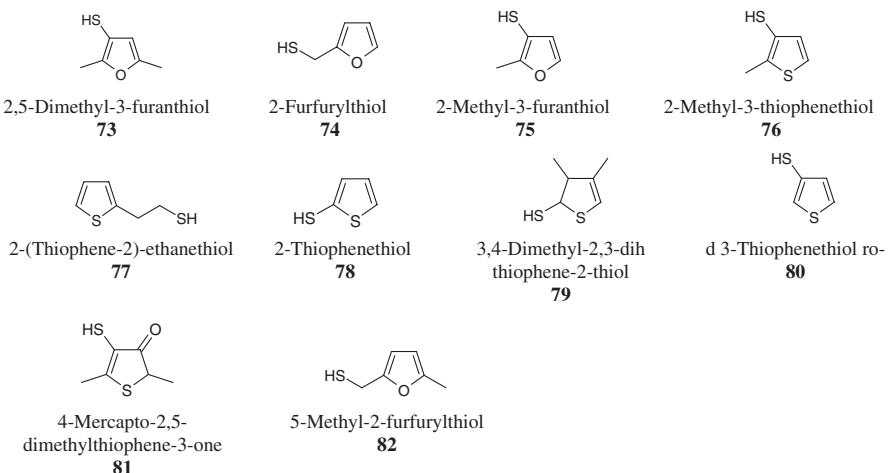


Figure 5. The structure of three terpenic mercaptans, seven acyclic mercaptans containing another sulfur function, and 10 heterocyclic mercaptans occurring in foods or beverages.

an influence on the sweetness of these organic compounds (Boelens and van Gemert, 1993). For their part, Vermeulen et al. emphasized that the descriptor “cheese” commonly associated with mercaptoaldehydes and thioesters is rarely used to qualify the odor of mercaptoalcohols or mercaptoketones. They also prove that most of the primary mercaptoalcohols containing at least six carbon atoms emerged as more delicate (rhubarb, carrot, greenery smell) than those with an intermediate size and branching, which are generally described as onion, plastic, or pungent (Vermeulen and Collin, 2002b).



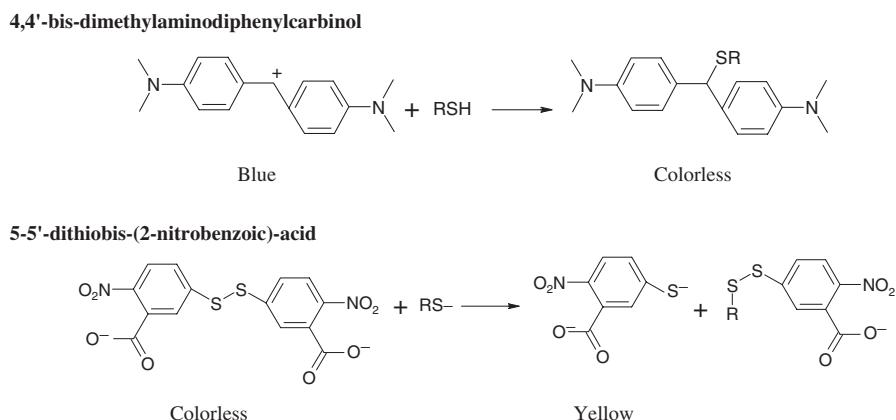


Figure 6. Reactivity between thiols and either 4,4'-bis(dimethylaminodiphenylcarbinol or 5,5'-dithiobis-(2-nitrobenzoic)-acid.

Chemical and Biological Synthetic Pathways

Thiols Issued from Secondary Metabolism of Microorganisms or Plants

The volatile thiols responsible for the box tree, grapefruit, and passion fruit nuances of Sauvignon wines are released by yeast from cysteinylated precursors: *S*-4-(4-methyl-2-pentanone)-L-cysteine, *S*-3-(1-hexanol)-L-cysteine, and *S*-4-(4-methyl-2-pentanol)-L-cysteine (Bouchilloux et al., 1998b, 1999; Darriet et al., 1993; Hatzimiditriou et al., 1996; Kotseridis and Baumes, 2000; Masneuf et al., 2002; Marchand et al., 2000; Marais and Swart, 1999; Murat et al., 20001b, 2001c, 2001d; Tominaga et al., 2000a). The mechanisms by which these odorless precursors found in grape skins are converted during fermentation into aromas have not yet been fully elucidated (Murat et al., 2001a). Nevertheless, β -lyase activities found in several microorganisms or plants (Fig. 7) may explain this phenomenon (Chin and Lindsay, 1994; Dubourdieu and Lees arômes, 1995; Guth, 1998; Murat et al., 20001c; Obenland and Aung, 1996; Peyrot des Gachons et al., 1999, 2002a; Tominaga et al., 1995). Similar pathways are suspected in passion fruits (Tominaga and Dubourdieu, 2000) and broccoli (Chin and Lindsay, 1994; Obenland and Aung, 1996). As for the corresponding D,L-homocysteine, glutathione, or sulfoxide conjugates, they hardly release free thiols (Gardner and Dauterman, 1992; Tominaga et al., 1995, 1998c). However, Peyrot des Gachons et al. suggested that *S*-3-(1-hexanol)-L-cysteine adducts might be issued from the catabolism of *S*-3-(1-hexanol)-glutathione (Peyrot des Gachons et al., 2002b). According to these scientists, quantification of such precursors in grapes or musts could allow assessment of the aromatic potential of Sauvignon blanc must (Peyrot des Gachons et al., 2000).

Moreover, Bel Rhlid et al. (2002a) showed that 2-methyl-3-furanthiol and 2-furfurylthiol can also be generated from their corresponding thioacetates during fermentation without any heat treatment. Such bioconversion could be exploited in the future to produce natural-labeled aromas (Bel Rhlid et al., 1998, 2001, 2002b; Bel Rhlid and Matthey-Doret, 1998; Kerkenaar et al., 1996a, 1996b; Huynh-Ba et al., 1997; Tominaga et al., 1995).



Table 10
 Relevance of thiols in foods

Matrix	Thiol	Reference
Beer	3-Methyl-3-mercaptopbutyformate 4-Mercapto-4-methyl-2-pentanone 4-Methoxy-2-methyl-2-butanethiol	(Schieberle, 1991a) (Schieberle, 1991a) (Rigaud et al., 1986; Reiners and Grosch, 1999)
Blackcurrant liquor	Methanethiol	(Shankaranarayana et al., 1982)
Butter	Methanethiol	(Dias and Weimer, 1998; Lecanu et al., 2002;
Cheddar		Manning and Price, 1977; Milo and Renneccius, 1997)
Coffee	2-Furfurylthiol	(Blank et al., 1992; Czerny et al., 1999; Holscher et al., 1990; Semmelroch and Grosch, 1996)
	2-Methyl-3-furanthiol	(Blank et al., 1992; Semmelroch and Grosch, 1995)
	3-Mercapto-3-methylbutyformate	(Blank et al., 1992; Semmelroch and Grosch, 1996)
	1- <i>p</i> -Menthene-8-thiol	(Buettnner and Schieberle, 2001; Demole et al., 1982; Lin et al., 2002)
Grapefruit juice	3-Mercaptobhexanol	(Lin et al., 2002)
	3-Mercaptobhexyl acetate	(Lin et al., 2002)
Olive oil	4-Mercapto-4-methyl-2-pentanol	(Lin et al., 2002)
Tea	4-Mercapto-4-methyl-2-pentanone	(Buettnner and Schieberle, 2001; Lin et al., 2002)
Wine	4-Mercapto-4-methyl-2-pentanone	(Reiners and Grosch, 1998)
	2-Methyl-3-furanthiol	(Kumazawa and Masuda, 1999)
	3-Mercapto-2-methylpropanol	(Bouchilloux et al., 1998a)
	3-Mercaptobhexanol	(Bouchilloux et al., 2000)
	3-Mercaptobhexyl-acetate	(Murat et al., 2001b; Tominaga et al., 1998b)
	4-Mercapto-4-methyl-2-pentanol	(Tominaga et al., 1998b)
	4-Mercapto-4-methyl-2-pentanone	(Tominaga et al., 1998b)
	Ethyl 3-mercaptopropionate	(Bouchilloux et al., 1996; Guth, 1997b, 1998; Marais and Swart, 1999; Marais, 1994; Tominaga et al., 1998a, 1998b)
		(Kolar, 1983)

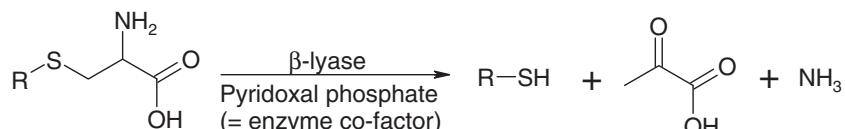


Figure 7. The ability of β -lyase to release thiols from cysteinylated precursors.

As reported in Table 11, some polyfunctional thiols might also be synthesized by H_2S nucleophilic reaction on carbonyl compounds (Blanchard et al., 2001; Boelens et al., 1974; Brinkman et al., 1972; Hofmann and Schieberle, 1998; Kleipool et al., 1976; Madruga and Mottram, 1995, 1998; Maujean, 2001; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994; Scanlan et al., 1973; Shankaranarayana et al., 1982; Spencer, 1969; Thiel et al., 1958; Tominaga et al., 2003a, 2003b; Wasserman, 1972; Werkhoff et al., 1989, 1996; Whitfield and Mottram, 1999; Whitfield et al., 1988; Zheng et al., 1997). Hydrogen sulfide is produced by yeast (Fig. 8), and its occurrence is highly regulated (Table 12) (Beloqui and Bertrand, 1995b; Breton and Surdin-Kerjan, 1977; Cherest and Surdin-Kerjan, 1992; Dott and Trüper, 1978; Elskens et al., 1991; Gijs et al., 2003; Giudici and Kunkee, 1994; Hansen and Kielland-Brandt, 1996; Heinzel and Trüper, 1978; Henschke and Jiranek, 1991; Jangaard et al., 1974; Jiranek et al., 1995; Mestres et al., 2000; Nagami et al., 1980; Ono et al., 1994, 1996; Peppard and Laws, 1979; Rankine, 1963; Smith et al., 1995; Stratford and Rose, 1985; Spiropoulos and Bisson, 2000; Thomas et al., 1990, 1992; Vermeulen and Collin, 2002b; Wainwright, 1970, 1971; Walker, 1995). Various α,β -unsaturated ketones or aldehydes are often found in worts, most of them coming from oxidation of unsaturated fatty acids. They may react with H_2S to form addition products such as mercapto-ketones or -aldehydes, which could be further reduced to the corresponding alcohols by yeast reductases or dehydrogenases. Esterification or methylation would then occur, leading to mercapto-esters (Murat et al., 2001b; Peyrot des Gachons et al., 1999; Tominaga et al., 1996; Vermeulen and Collin, 2003b) or methoxy-alkylthiols. Such pathways have been chemically mimicked to synthesize thiol libraries by combinatorial chemistry (Vermeulen and Collin, 2002b, in press; Vermeulen et al., 2001, 2003a, 2003b).

Thiols Issued from Radical Reactions Induced by Light

Many thiols result from photodegradation reactions. Methional is thus known to impart off-flavors to ice creams, beer, and other foods after releasing methanethiol (Gijs et al., 2000a; Haboucha and Masschelein, 1979; Hugues, 1998; Kattein et al., 1988; Sakuma et al., 1991), which is further transformed to dimethyltrisulfide (onion-like defect).

In the presence of light (350–500 nm) and riboflavin (photosensitiser), hop bitter iso- α -acids and cysteine yield in beer the well-known beer skunky flavor: 3-methyl-2-butene-1-thiol (Fig. 9) (Chen and Ho, 2002; Drost et al., 1990; Duyvis et al., 2002; Gunst and Verzele, 1978; Haboucha and Masschelein, 1979; Hashimoto and Eshima, 1979; Hugues, 1998, 1999; Irwin et al., 1993; Kattein et al., 1988; Masuda et al., 2000; Olsen, 1988; Sakuma et al., 1991; Shankaranarayana et al., 1982; Wilson et al., 2001). To prevent the occurrence of 3-methyl-2-butene-1-thiol, brewers use



Table 11
Thiols related to H₂S and carbonyl compounds reaction

Identified thiol	Odor	Identified thiol	Odor
1,1-Propanedithiol	Onion (Boelens et al., 1974)	3-Mercaptobutanal (Badings et al., 1976; Kleipool et al., 1976; Vermullen and Collin, 2002b)	Omelet, broth, cheese, pungent (Badings et al., 1976; Vermeulen and Collin, 2002b)
1-Ethylthio-1-ethanethiol (Boelens et al., 1974)	Onion, leek, blackcurrant (Boelens et al., 1974)	3-Mercaptoheptanal (Vermullen and Collin, 2002b)	Flower, citrus fruit peel (Vermeulen and Collin, 2002b)
1-Mercapto-3-butaneone (Vermullen et al., in press)	Potato (Vermullen et al., in press)	3-Mercaptohexanal (Kleipool et al., 1976; Vermeulen and Collin, 2002b)	12 (Table 2)
1-Mercapto-3-pentanone (Vermullen et al., in press)	Cheese, solvent, pungent, skunky (Vermullen et al., in press)	3-Mercaptononanal (Kleipool et al., 1976; Vermeulen and Collin, 2002b)	Stale odor, greenery (Vermeulen and Collin, 2002b)
1-Methylthio-1-ethanethiol (Boelens et al., 1974; Brinkman et al., 1972; Schutte and Koenders, 1972; Shankaranayana et al., 1982)	72 (Table 8)	3-Mercaptooctanal (Vermullen and Collin, 2002b)	Citrus fruit peel, grapefruit, greenery, fresh (Vermeulen and Collin, 2002b)
1-Methylthio-1-hexanethiol (Boelens et al., 1974)	Onion, blackcurrant, rhubarb, green bell-pepper (Boelens et al., 1974)	3-Mercaptopentanal (Vermullen and Collin, 2002b)	Broth, raw onion, flowery (Vermeulen and Collin, 2002b)
1-Methylthio-1-propanethiol (Boelens et al., 1974)	Onion, meaty (Boelens et al., 1974)	3-Mercaptopropanal (Vermullen and Collin, 2002b)	Rotten potato, broth (Vermeulen and Collin, 2002b)
1-Propylthio-1-propanethiol (Boelens et al., 1974)	Onion, blackcurrant (Boelens et al., 1974)	4-Mercapto-2-nonenone (Vermullen et al., in press)	Rhubarb, lemon, cannabis, spicy (Vermeulen et al., in press)



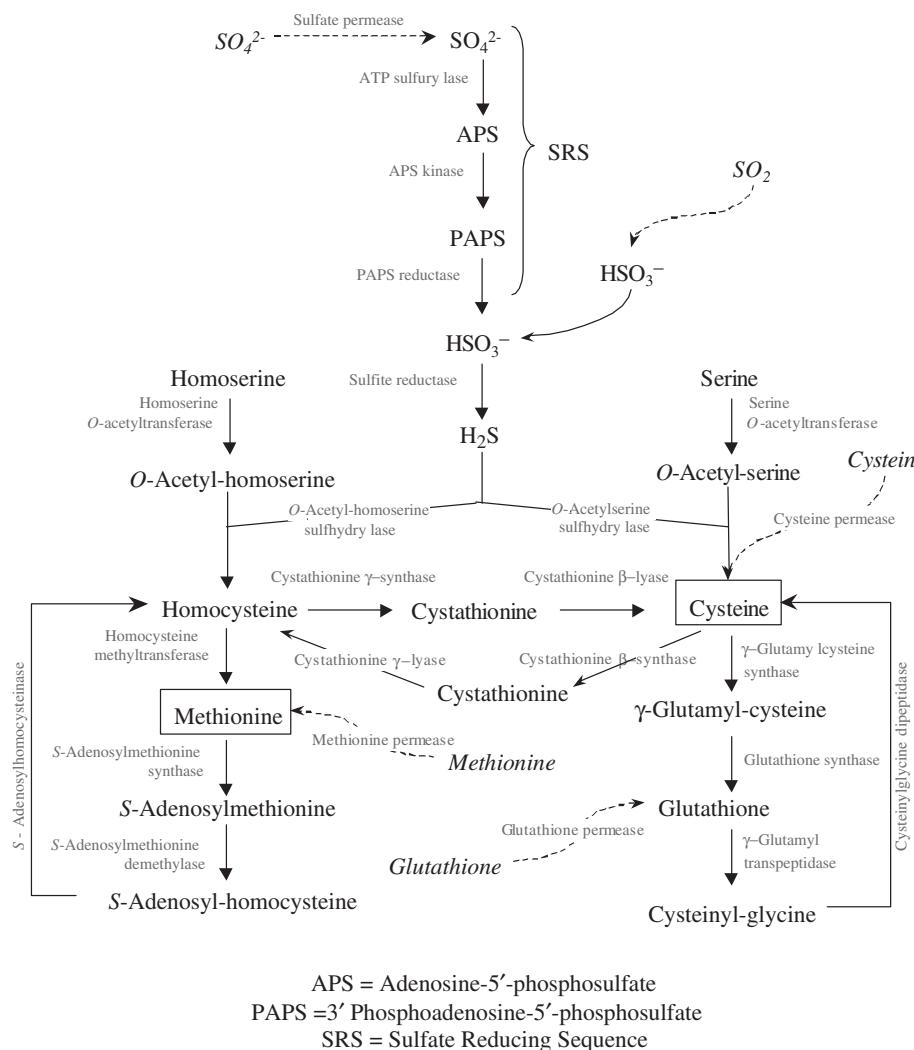
2-Furfurylthiol (Ames et al., 2001; Blanchard et al., 2001; Chen and Ho, 2002; Farmer et al., 1989; Holscher et al., 1990; Madruga and Mottram, 1995; Meynier and Mottram, 1995; Münch et al., 1997)	74 (Table 9)	4-Mercapto-2-pentanone (Vermeulen et al., 2001, in press)	Greenery, potato, blackcurrant (Vermeulen et al., 2001, in press)
2-Mercapto-3-pentanone (Mottram and Madruga 1994, 1995; Pripis-Nicolau et al., 1999)	17 (Table 3)	4-Mercapto-3-methyl-2-pentanone (Vermeulen et al., 2001, in press)	Sweat, cooked milk (Vermeulen et al., 2001, in press)
3-Mercapto-2-butanone (Ames et al., 2001; Mottram and Madruga 1994, 1995)	18 (Table 3)	4-Methyl-4-mercaptop-2-pentanone (Vermeulen et al., 2001, in press; Shankaranarayana et al., 1982; Spencer, 1969)	21 (Table 3)
3-Mercapto-2-butylpropanal (Vermeulen and Collin, 2002b)	Plastic, rhubarb, pun- gent (Vermeulen and Collin, 2002b)	5-Mercapto-3-hexanone (Vermeulen et al., 2001, in press)	Box tree, fresh, empyreumatic (Vermeulen et al., 2001, in press)
3-Mercapto-2-ethylpropanal (Vermeulen and Collin, 2002b)	Broth, rotten potato, plastic, groundnut (Vermeulen and Collin, 2002b)	5-Methyl-4-mercaptop-2-hexanone (Vermeulen et al., 2001, in press)	Exotic fruit, sweet, sulfury (Vermeulen et al., 2001, in press)
3-Mercapto-2-methylbutanal (Vermeulen and Collin, 2002b)	Broth, onion, meaty, cheese (Vermeulen and Collin, 2002b)	Bis-(1-mercaptoethyl)-sulfide (Boelens et al., 1974)	Onion, chive, meaty (Boelens et al., 1974)
3-Mercapto-2-methylpentanal (Vermeulen and Collin, 2002b)	13 (Table 2)	Bis-(1-mercaptohexyl)-sulfide (Boelens et al., 1974)	Onion, green, fatty (Boelens et al., 1974)
3-Mercapto-2-methylpropanal (Vermeulen and Collin, 2002b)	Meat, broth, raw bread paste (Vermeulen and Collin, 2002b)	Bis-(1-mercaptoisobutyl)-sulfide (Boelens et al., 1974)	Onion, mushroom, soup (Boelens et al., 1974)



Table 11
Continued

Identified Thiol	Odor	Identified Thiol	Odor
3-Mercapto-2-pentanone (Ames et al., 2001; Mottram and Madruga 1994, 1995; Pripis-Nicolau et al., 1999)	19 (Table 3)	Bis-(1-mercaptopropyl)-sulfide (Boelens et al., 1974)	Green, fruity, onion, garlic (Boelens et al., 1974)
3-Mercapto-3-methylbutanal (Vermeulen and Collin, 2002b)	Broth, cheese, pungent (Vermeulen and Collin, 2002b)	Ethanethiol (Rauhut, 1993; Rankine, 1968)	52 (Table 6)



**Figure 8.** *S. cerevisiae* sulfur metabolism.

lightproof containers (dark glass or cans) or reduced iso- α -acids (Burns et al., 2001; Drost et al., 1990; Wilson et al., 2001, 2002).

Thiols Issued from Thermal Reactions

Maillard reactions most probably produce thiols efficiently in cooked meat and roasted or baked foods (Ames et al., 2001; Bouchilloux et al., 1998a; Elmore et al., 2002; Farmer and Mottram, 1990; Farmer et al., 1989; Hofmann and Schieberle, 1998; Holscher et al., 1990; Huber and Bergamin, 1993; Marchand et al., 2000; Mottram and Edwards, 1983; Mottram and Madruga, 1994; Mottram and Nobrega, 2002; Mulders, 1973; Münch and Schieberle, 1998; Münch et al., 1997; Schieberle, 1991b; Schieberle and Hofmann, 1998; Tai and Ho, 1997; Tominaga et al., 2000b; van Seeventer et al., 2001; Whitfield and Mottram, 1999; Whitfield et al., 1988;



Table 12
Many molecules can regulate the H₂S production by yeast

H ₂ S Production is promoted by	Explanation
ATP, NADPH	They act as enzymatic cofactors in the sulfate-reducing sequence. It can give H ₂ S by decomposition.
Cysteine	It decreases the homoserine occurrence, which is precursor of methionine (see below).
Threonine	It is a sulfur reserve for yeast.
[Glutathione] _{cell}	They are all potential sources of sulfur.
[Sulfate, sulfite, thiosulfate, sulfur, sulfur-containing pesticides] _{medium}	It is a co-factor in the synthesis of O-acetylserine and O-acetylhomoserine sulfhydrylase, which are the enzymes involved in the H ₂ S incorporation in organic molecules. It is also a sulfate reductase inhibitor.
H ₂ S production is inhibited by Pantothenate (vitamin B ₅)	They are considered as good sources of nitrogen. The serine and aspartate are even indirect precursors of cysteine and methionine, respectively (see below). They are considered as partial nitrogen sources (see below).
Sérine, glutamine, aspartate, arginine, asparagine	Probably to spare energy, they are responsible of retroinhibitions. They act in the sulfate assimilation pathway just before enzymes requiring ATP.
Glycine, tryptophane, valine, lysine, histidine	They stop the activity of sulfate permease, ATP sulfurylase, and sulfite reductase. They also deactivate a lot of enzymes implicated in sulfur amino acid synthesis.
[Sulfate, APS, PAPS, sulfite, sulfide] _{cell}	They favor the production of amino acids, methionine and cysteine included—inhibitors in the H ₂ S biosynthesis. Moreover, in the presence of nitrogen, H ₂ S is “overconsumed” for the biosynthesis of sulfur amino acids. It is, however, not the case at the end of fermentation when the yeast is no more able to assimilate ammonium.



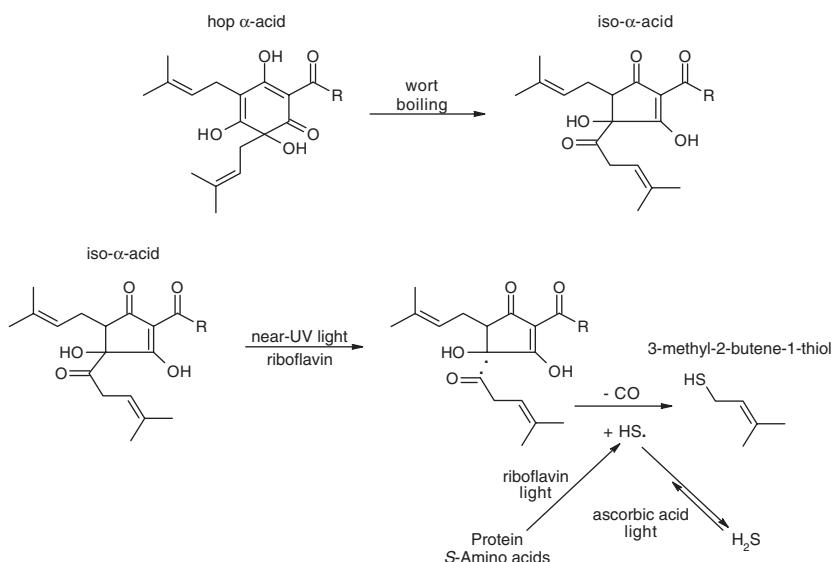


Figure 9. The formation of 3-methyl-2-butene-1-thiol from hop α -acids, sulfur products, riboflavin, and light.

Zhang and Ho, 1991), especially under acidic conditions (Ames et al., 2001; Madruga and Mottram, 1995, 1998; Meynier and Mottram, 1995; Mottram and Madruga, 1994; Whitfield and Mottram, 2001). Table 13 summarizes most structures known to be produced in this way.

Some thiols can also be produced by thermal degradation of thiamine (Table 14). The extent of this degradation and the nature of the products formed appear to be determined by the pH (122): alkaline conditions lead to the formation of H₂S and 3-mercaptopropanoic acid, which are excellent precursors of thiols (Fig. 10).

Other Formation Pathways Potentially Leading to Thiols

Some examples of other potential formation pathways mentioned in the literature include

- Cysteine (Beloqui and Bertrand, 1995a; Chen and Ho, 2002; Ferreira et al., 2003; Güntert et al., 1990; Madruga and Mottram, 1998; Mestres et al., 2000; Shu et al., 1985a; Yeo and Shibamoto, 1991), methionine (Cuer, 1982; Dias and Weimer, 1998; Rauhut, 1993; Segal and Starkey, 1969; Shankaranarayana et al., 1982), or glutathione degradation (Zheng and Ho, 1994), leading to small thiols like H₂S and methanethiol.
- Alcohol nucleophilic substitution to thiol (Holscher et al., 1992; Madruga and Mottram, 1995; Macku and Shibamoto, 1991; Maujean, 2001; Nedjma and Maujean, 1995; Spinnler and Bonnarme, 2002; Werkhoff et al., 1996).
- Retro Michael-type reaction, breaking, for instance, methional into methanethiol (Maujean, 2001; Tressl et al., 1994).



Table 13
Thiols produced in Maillard conditions

Identified thiol	Odor	Identified thiol	Odor
?-Ethyl-3-furanthiol (Farmer et al., 1989)	—	2-Methyl-4-thiophenethiol (van Ouweland and Peer, 1975)	Rubber (van Ouweland and Peer, 1975)
1,2-Ethanedithiol (Engel and Schieberle, 2002a)	Cabbage (Engel and Schieberle, 2002a)	2-Methyl-tetrahydro-3-furanthiol (Mottram and Whitfield, 1994; Whitfield and Mottram, 1999)	—
1,2-Ethenyldithiol (Umano et al., 1995)	—	2-Methyl-tetrahydro-3-thiophenethiol (Mottram and Whitfield, 1994; Whitfield and Mottram, 1999)	—
1-Heptanethiol (Farmer and Mottram, 1990; Farmer et al., 1989)	—	2-Propanethiol (Mulders et al., 1973)	—
1-Mercapto-2-butanone (Whitfield and Mottram, 1999)	—	2-Thiophenemethanethiol (Madruga and Mottram, 1998; Mottram and Nobrega, 2002)	—
1-Mercapto-2-propanone (Hofmann and Schieberle, 1995; Madruga and Mottram, 1998; Shu et al., 1985b; Zhang and Ho, 1991)	15 (Table 3)	2-Thiophenethiol (Ames et al., 2001; Farmer and Mottram, 1990; Farmer et al., 1989; Hofmann and Schieberle, 1995, 1997; Madruga and Mottram, 1998; Meynier and Mottram, 1995; Mottram and Whitfield, 1994, 1995a; Scanlan et al., 1973; Shu et al., 1986; Whitfield et al., 1988; Wu and Cadwallader, 2002; Yeo and Shibamoto, 1991)	78 (Table 9)



1-Mercapto-3-pentanone (Farmer et al., 1989; Madruga and Mottram, 1998)	16 (Table 3)	3-Mercapto-2-butanone (Ames et al., 2001; Farmer and Mottram, 1990; Güntert et al., 1990; Hofmann and Schieberle, 1995, 1997; Madruga and Mottram, 1998; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994; Münch and Schieberle, 1998; Schieberle and Hofmann, 1998; van Seeverter et al., 2001; Whitfield and Mottram, 1999, 2001; Zhang and Ho, 1991)	18 (Table 3)
1-Octanethiol (Farmer and Mottram, 1990; Farmer et al., 1989)	—	3-Mercapto-2-pentanone (Ames et al., 2001; Farmer and Mottram, 1990; Farmer et al., 1989; Güntert et al., 1990; Hofmann and Schieberle, 1995, 1997; Madruga and Mottram, 1998; Meynier and Mottram, 1995; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994; Münch and Schieberle, 1998; Schieberle and Hofmann, 1998; Shu et al., 1985b; van Seeverter et al., 2001; Whitfield and Mottram, 1999, 2001; Wu and Cadwallader, 2002)	19 (Table 3)
1-Pantanethiol (Ames et al., 2001; Mulders, 1973)	58 (Table 6)	3-Mercaptopropanoic acid (Hofmann and Schieberle, 1995, 1997)	Sulfury, seasoning-like (Hofmann and Schieberle, 1997)
1-Propanethiol (Zhang and Ho, 1991; Mulders, 1973)	59 (Table 6)	3-Methyl-2-butanethiol (Zheng et al., 1997)	47 (Table 6)

(continued)



Table 13
 Continued

Identified thiol	Odor	Identified thiol	Odor
2-(1-Mercaptoethyl)-furan (Güntert et al., 1990; Hofmann and Schieberle, 1997; Schieberle and Hofmann, 1998)	Burnt, (Hofmann and Schieberle, 1997)	3-Oxo-tetrahydro-4-furanthiol (van Ouweland and Peer, 1975)	Green, meaty, vegetable, meat extract (van den Ouweland and Peer, 1975)
2-(1-Mercaptoethyl)-thiophene (Hofmann and Schieberle, 1997)	—	3-Thiophenethiol (Ames et al., 2001; Elmore et al., 2002; Farmer and Mottram, 1990; Güntert et al., 1990; Hofmann and Schieberle, 1997; Madruga and Mottram, 1998; Mottram and Nobrega, 2002; Mottram and Whitfield, 1995a; Whitfield and Mottram, 1999; Whitfield et al., 1988)	80 (Table 9)
2-(Mercaptomethyl)-4-methyl-1,3-dioxolan (Güntert et al., 1990)	—	4-Mercapto-2,5-dimethyl-3-thiophenone (Guedes de Pinho et al., 1997)	81 (Table 9)
2-Mercapto-3-butanone (Zheng et al., 1997)	—	4-Methyl-4-mercaptop-2-pentanone (Farmer et al., 1989)	21 (Table 3)
2-Mercapto-3-pentanone (Ames et al., 2001; Engel and Schieberle, 2002a; Farmer and Mottram, 1990; Madruga and Mottram, 1998; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994; Whitfield and Mottram, 1999; Zheng et al., 1997)	17 (Table 3)	5-Hydroxy-3-mercaptop-2-pentanone (Mottram and Whitfield, 1994)	—
2-Mercaptopropanoic acid (Hofmann and Schieberle, 1995, 1997)	Sulfury, seasoning-like (Hofmann and Schieberle, 1997)	5-Mercapto-2-hexanone (Whitfield and Mottram, 1999)	Whitfield and —



2-Methyl-2,3-dihydro-3-thiophenethiol (van den Ouweland and Peer, 1975)	Sweet, roasted meat (van den Ouweland and Peer, 1975)	5-Methyl-2-furfurylthiol (Chen and Ho, 2002; Hofmann and Schieberle, 1997; Münch and Schieberle, 1998; Schieberle and Hofmann, 1998; Umano et al., 1995)	82 (Table 9)
2-Methyl-2,3-dihydro-4-hydroxy-3-thiophenethiol (van den Ouweland and Peer, 1975)	Meaty, savory (van den Ouweland and Peer, 1975)	5-Methyl-2-thienylthiol (Hofmann and Schieberle, 1997)	—
2-Methyl-2,3-dihydro-4-thiophenethiol (van den Ouweland and Peer, 1975)	Rubber, meaty (van den Ouweland and Peer, 1975)	5-Methyl-3-oxo-tetrahydro-4-furanthiol (van den Ouweland and Peer, 1975)	Meaty, vegetable, meat extract (van den Ouweland and Peer, 1975)
2-Methyl-2-pentanethiol (Zheng et al., 1997)	—	Cyclopentanethiol (Mussinan and Katz, 1973)	—
2-Methyl-3-furanthiol (Ames et al., 2001; Bouchilloux et al., 1998a; Chen and Ho, 2002; Elmore et al., 2002; Engel and Schieberle, 2002a; Farmer and Mottram, 1990; Farmer et al., 1989; Gasser and Grosch, 1988; Hofmann and Schieberle, 1995, 1997, 1998; Huber and Bergamin, 1993; Madruga and Mottram, 1995, 1998; Meynier and Mottram, 1995; Mottram and Madruga, 1994; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994, 1995a; Mottram et al., 1998; Münch and Schieberle, 1998; Schieberle and Hofmann, 1998; Tominaga et al., 2003b; van Seestenter et al., 2001; Whitfield and Mottram, 1999; Whitfield et al., 1988; Wu and Cadwallader, 2002; Zhang and Ho, 1991)	75 (Table 9) 52 (Table 6)		

(continued)



Table 13
Continued

Identified Thiol	Odor	Identified Thiol	Odor
2-Methyl-3-thiophenethiol (Ames et al., 2001; Chen and Ho, 2002; Elmore et al., 2002; Farmer and Mottram, 1990; Farmer et al., 1989; Güntert et al., 1990; Hofmann and Schieberle, 1995; Madruga and Mottram, 1998; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994, 1995a; van den Ouwehand and Peer, 1975; Werkhoff et al., 1989; Whitfield and Mottram, 1999)	76 (Table 9) —	Ethyl-2-mercaptopropionate (Hofmann and Schieberle, 1997)	(Hofmann —
2-Methyl-4,5-dihydro-3-furanthiol (Güntert et al., 1990; Madruga and Mottram, 1998; van den Ouwehand and Peer, 1975; Whitfield and Mottram, 1999)	—	2-Furfurylthiol (Ames and MacLeod, 1985; Ames et al., 2001; Chen and Ho, 2002; Elmore et al., 2002; Engel and Schieberle, 2002a; Farmer and Mottram, 1990; Farmer et al., 1989; Günfert et al., 1990; Hofmann and Schieberle, 1995, 1997, 1998; Madruga and Mottram, 1998; Marchand et al., 2000; Meynier and Mottram, 1995; Mottram and Nobrega, 2002; Mottram and Whitfield, 1994; Mottram et al., 1998; Mussinan and Katz, 1973; Schieberle and Hofmann, 1998; Schieberle, 1991b; Tominaga et al., 2000b, 2003b; Tressl et al., 1994; van Seeveren et al., 2001; Whitfield et al., 1988; Wu and Cadwallader, 2002; Zhang and Ho, 1991)	74 (Table 9)



2-Methyl-4,5-dihydro-3-thiophenethiol (Mottram and Whitfield, 1994; van den Ouweland and Peer, 1975; Whitfield and Mottram, 1999)	Meaty (van den Ouweland and Peer, 1975)	den Peer, 1995; Mulders, 1973; Pripis-Nicolau et al., 2000; Umano et al., 1995)	Methanethiol (Meynier and Mottram, 1995; Mulders, 1973; Pripis-Nicolau et al., 2000; Umano et al., 1995)	55 (Table 6)
2-Methyl-4,5-dihydro-4-thiophenethiol (van den Ouweland and Peer, 1975)	Roasted meat (van den Ouweland and Peer, 1975)	Roasted meat (van den Ouweland and Peer, 1975)	<i>N</i> -(2-Mercaptoethyl)-1,3-thiazoline (Engel and Schieberle, 2002a, 2002b)	Roasty, popcorn (Engel and Schieberle, 2002a, 2002b)
2-Methyl-4-furanthiol (van den Ouweland and Peer, 1975)	Green, meaty (van den Ouweland and Peer, 1975)	Green, meaty (van den Ouweland and Peer, 1975)	<i>N</i> -(2-Mercaptoethyl)pyrrole (Engel and Schieberle, 2002a)	Roasty, burnt (Engel and Schieberle, 2002a)



Table 14
Thiols related to thiamine degradation

Identified thiol	Odor	Identified thiol	Odor
1-(2-Methyl-3-furylthio)-ethanethiol (Werkhoff et al., 1989, 1990)	Roasted, brothy, spicy, onion, garlic, vegetable, meaty, gravy (Werkhoff et al., 1989, 1990)	2-Methyl-4,5-dihydro-3-furanthiol (Güntert et al., 1990, 1992; Hartman et al., 1984a; Mottram and Whitfield, 1994; Werkhoff et al., 1990)	Roasted meat (Güntert et al., 1990)
1-(2-Methyl-3-thienylthio)-ethanethiol (Werkhoff et al., 1989, 1990)	Sulfury, carrot, leek, meaty, yeast, onion (Werkhoff et al., 1989, 1990)	2-Methyl-4,5-dihydro-3-thiophenethiol (Werkhoff et al., 1990)	Meaty (van Ouwendal and Peer, 1975)
1,1-Ethanedithiol (Güntert et al., 1992)	66 (Table 8)	2-Tetrahydrothiophenethiol (Güntert et al., 1990)	Onion, roasty, tropical fruit, meaty, sulfury (Güntert et al., 1990)
1,4-Dimercapto-3-pentanone (Güntert et al., 1990)	—	2-Thiophenethiol (Hofmann and Schieberle, 1995)	78 (Table 9)
1-Hydroxy-4-mercaptop-3-pentanone (Güntert et al., 1990)	—	3,5-Dimercapto-2-pentanone (Güntert et al., 1990; Werkhoff et al., 1990)	—
1-Mercapto-3-pentanone (Güntert et al., 1992)	16 (Table 3)	3-Hydroxy-5-mercaptop-2-pentanone (Güntert et al., 1990)	—
1-Mercapto-4-hydroxy-3-pentanone (Güntert et al., 1990)	—	3-Mercapto-2-butanone (Güntert et al., 1990, 1992)	18 (Table 3)
1-Methylthio-ethanethiol (Güntert et al., 1992; Werkhoff et al., 1989, 1990)	72 (Table 8)	3-Mercapto-2-pentanone (Güntert et al., 1990, 1992; Hartman et al., 1984a; Hofmann and Schieberle, 1995)	19 (Table 3)
1-Methylthio-methanethiol (Güntert et al., 1992; Werkhoff et al., 1989, 1990)	—	3-Mercapto-5-hydroxy-2-pentanone (Güntert et al., 1990; Hartman et al., 1984a; Jhoo et al., 2002; Mottram and Whitfield, 1994; Werkhoff et al., 1990)	—

2-(1-Mercaptoethyl)-furan (Güntert et al., 1990)	Mocha, roasty, elderberry (Güntert et al., 1990)	3-Mercaptopropanol (Güntert et al., 1990; Jhoo et al., 2002)	10 (Table 2)
2,5-Dimethyl-3-furanthiol (Hartman et al., 1984a)	73 (Table 9)	3-Mercaptopropyl-acetate (Güntert et al., 1990, 1992)	28 (Table 4)
2-Mercapto-3-pentanone (Güntert et al., 1992)	17 (Table 3)	3-Thiophenethiol (Güntert et al., 1990)	80 (Table 9)
2-Methyl-2-tetrahydrothiophenethiol (Güntert et al., 1990, 1992)	Tropical fruit, sultry, buchu, meaty, blackcurrant (Güntert et al., 1990)	4-Mercapto-2-butanone (Güntert et al., 1992)	20 (Table 3)
2-Methyl-3-furanthiol (Ames and MacLeod, 1985; Baek et al., 2001; Bezman et al., 2001; Bouchilloux et al., 1998b; Carrapiso et al., 2002; Gasser and Grosch, 1988; Güntert et al., 1990, 1992; Hartman et al., 1984a, 1984b; Huber and Bergamin, 1992; Jhoo et al., 2002; Mottram and Madruga, 1994; Mottram and Whitfield, 1994; Mottram et al., 1998; Werkhoff et al., 1990) and Whitfield, 1994)	75 (Table 9)	5-(2-Mercaptoethyl)-4-methylthiazole (Güntert et al., 1992)	Tuna, metallic, sulfury, tropical fruit (Güntert et al., 1992)
2-Methyl-3-tetrahydrofuranthiol (Mottram and Whitfield, 1994)	—	5-Mercapto-2-pentanone (Güntert et al., 1992)	—
2-Methyl-3-tetrahydrothiophenethiol (Güntert et al., 1992)	—	Furfurylthiol (Mottram et al., 1998; Güntert et al., 1990)	74 (Table 9)
2-Methyl-3-thiophenethiol (Güntert et al., 1990, 1992; Werkhoff et al., 1990)	76 (Table 9)	Mercaptopropane (Güntert et al., 1990, 1992)	15 (Table 3)



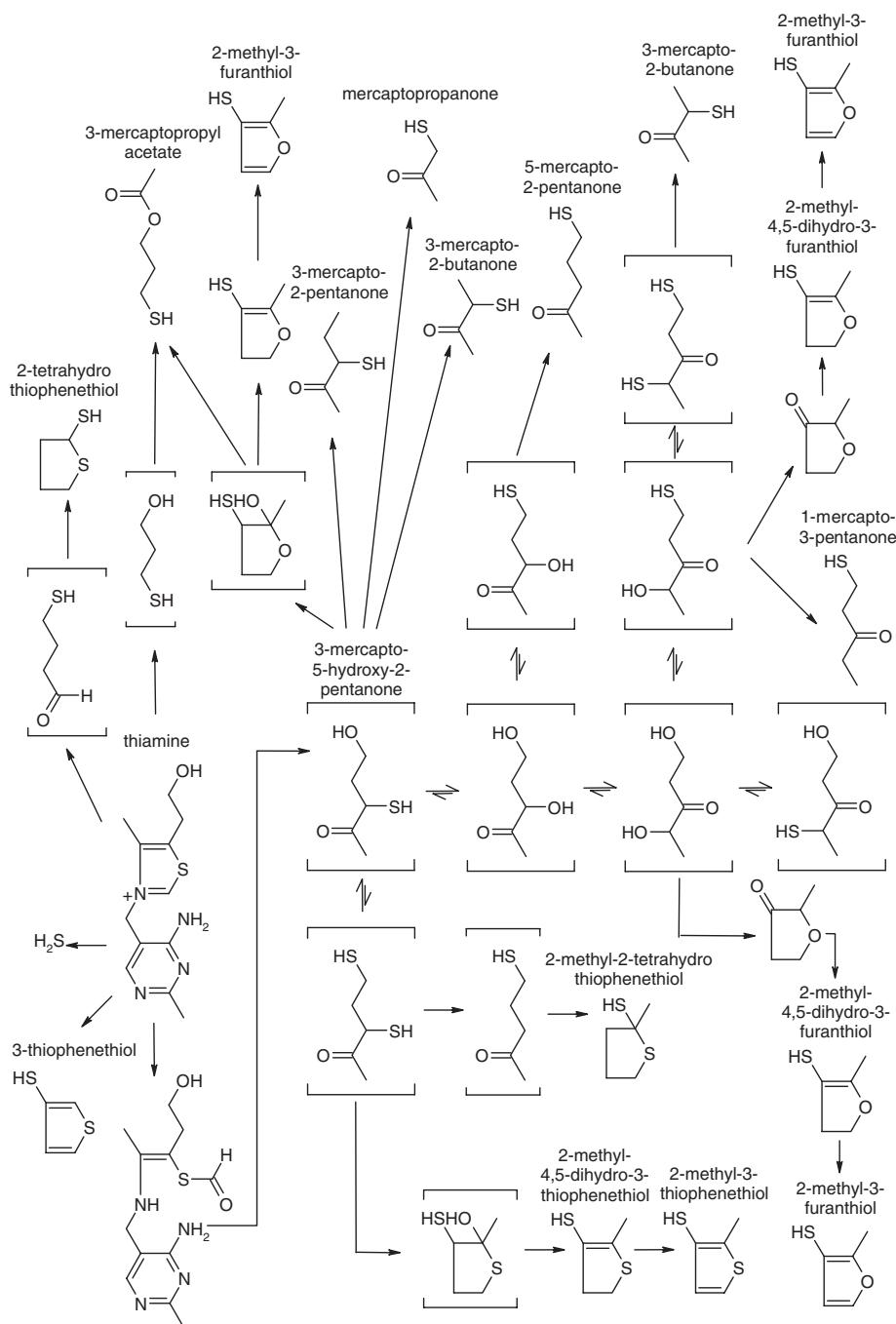


Figure 10. Some thiol formation pathways associated with the thermal degradation of thiamine.



- Ionizing γ radiation, a method for pathogen inactivation in various foods increasing H₂S and methanethiol concentrations (Fan et al., 2002),
 - Cow metabolism, leading to a benzylthiol precursor in milk (Walker and Gray, 1970).

Conclusion

Because of their extremely low odor threshold, thiols are surely the most powerful odorants in many vegetables and fruits, fermented foods, and beverages. Although pungent at high concentrations, they prove highly desirable to consumers in many cases. Many chemical and biochemical pathways can explain their occurrence, but for most matrixes, accurate mechanisms are not yet well understood. More sensitive analytical methods are now required to more easily identify the thiol odorants detected by GC olfactometry or with sulfur-specific detectors.

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