Elucidation of Beef Flavor Character from Flavor Precursor Compounds

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Introduction

Beef palatability is considered to be the combination of tenderness, juiciness, and flavor (Neely et al., 1998). Flavor is often considered the most important palatability trait when tenderness is found to be acceptable (Goodson et al., 2002; Killinger et al., 2004; Behrends et al., 2005a, b).

Taste attributes are often rated by consumers as being among the most important “purchasing motivators” (Moeller and Courington, 1998; Reicks et al., 2011). Additionally, flavor has been identified as the single most important determinant of consumer acceptability when meat was prepared at home (Huffman et al., 1996).

Flavor can be simply defined as the combination of taste and aroma. Taste refers to the five basic receptors: sweet, salty, sour, bitter, and umami. Flavor is the perception of chemical compounds reacting with receptors in the oral and nasal cavities (aroma) in combination with taste. Flavor is developed during cooking through a combination of numerous chemical reactions (Figure 1), including the Maillard reaction and oxidation of lipids (Mottram, 1998; Calkins and Hodgen, 2007).

The development of favorable beef flavor is a result of cooking. Raw meat, having a bloody, salty, and metallic taste, does not possess the desirable flavor characteristics of cooked beef (Wasserman, 1972; Mottram, 1998). The chemical composition of beef

![Figure 1. Chemical contributors to beef flavor development and pathways to volatile flavor compounds (Dashdorj et al., 2015).]
has been shown to greatly influence the flavor and aroma developed during cooking. Termed “precursor compounds,” low molecular weight, water-soluble compounds, lipids and vitamins have been shown to be responsible for the flavor developed during cooking (Mottram, 1998; Koutsidis et al., 2008a, c). The development of flavor during cooking is the result of thermal breakdown and interactions between precursor compounds resulting in a great number of reaction products (Mottram, 1998). Beef flavor is influenced by compounds that contribute to the taste fraction of flavor; however, volatile compounds formed during cooking contribute the most to characteristic beef flavor (Mottram, 1998). During cooking, the Maillard reaction and thermal degradation of lipids are the primary means by which volatile flavor compounds are produced (Mottram, 1998; Calkins and Hodgen, 2007).

The Maillard reaction, also termed non-enzymatic browning, is the term used to define the series of reactions that occur following the condensation of free-amino compounds (amino acids and peptides) with the carbonyl group of a reducing sugar (Fay and Brevard, 2005; Calkins and Hodgen, 2007). The resulting glycosylamine of this initial condensation reaction is further rearranged and dehydrated forming furfural, derivatives of furanone, hydroxyketones, and dicarbonyl compounds (Calkins and Hodgen, 2007). These low molecular weight compounds may further lead to the formation of compounds which contribute to cooked flavor, such as furans, pyrazines, pyroles, oxazoles, thiazoles, and several other heterocyclic compounds (Fay and Brevard, 2005). While many of the previously named compounds contribute to flavor, the reaction may further progress via the Amadori rearrangement, Strecker degradation, and Schiff base pathways (Calkins and Hodgen, 2007). Results of the Schiff base pathways and Strecker degradation include melanoidins, which have been shown to result from the condensation reactions between cyclic compounds (Fay and Brevard, 2005).

However, it has also been shown that when in an oxidized state, cysteine and glucose may produce pyrazines and furans (Tai and Ho, 1997). Cysteine and ribose can also produce 2-methyl-3-furanthiol which may further produce a number of thiols and disulfides (Calkins and Hodgen, 2007).

As previously described, amino compounds (such as amino acids) are important to the formation of beef flavor via the Maillard reaction. The concentration of free amino acids available for reaction with reducing sugars may be an important factor affecting beef flavor development. In addition to providing a means of flavor development through the Maillard reaction, free amino acids also supply free ammonia, while some sulfur-containing free amino acids may produce hydrogen sulfide and volatile compounds containing sulfur upon heating (Gasser and Grosh, 1988; Block, 1992). Cysteine and cystine have been observed to be generators of meaty aromas as a result of heating (Shahidi et al., 1986; Zhang and Ho, 1991; Whitfield and Mottram, 1992).
Methionine is another amino acid that has been shown to be important to the development of beef flavor. Methionine can interact with reducing sugars in the Maillard reaction as well as contribute to flavor through degradation by heating (Casey et al., 1965). Degradation of methionine produces volatile flavor compounds dimethyl sulfide, dimethyl disulfide, and methional, each of which can impact beef flavor development (Shigematsu et al., 1977).

The importance of reducing sugars to flavor development by the Maillard reaction has previously been stated. However, the propensity of specific sugar molecules to influence flavor development should be further discussed. Presently, several sugars have been verified in beef including ribose, ribose phosphates, glucose, fructose, mannose, glucose-6-phosphate, and fructose-6-phosphate (Koutsidis et al., 2008a). These sugars and sugar-related metabolites are the result of post-mortem changes, such as degradation of ribonucleotides to yield ribose and the depletion of glycogen to form glucose (Koutsidis et al., 2008b). Differences in the mechanisms of ribose and ribose phosphate have been observed, with ribose phosphate being more reactive in model systems (Mottram and Nobrega, 2002). The additions of both ribose and ribose phosphate have been shown to increase key volatile flavor compounds in cooked beef (Farmer et al., 1999). In contrast, glucose and glucose-6-phosphate were observed to have much smaller effects compared to ribose and ribose phosphate when added to beef (Farmer et al., 1999).

Lipids are known to produce strong odors as a result of oxidation. However, during cooking, thermal oxidation of lipids can produce flavor compounds which contribute to beef flavor. Volatile flavor compounds derived from thermal oxidation of lipids include aldehydes, ketones, and lactones (Farmer, 1999). Lipid oxidation products were also observed to interact with amino- and sulfur-containing thiol groups through the Maillard reaction at both initial reactions and in the final, volatile, flavor-compound-forming reactions (Mottram, 1998).

Within beef there are two lipid fractions (LF), neutral lipids (NL) or triglycerides and polar lipids (PL) or phospholipids. Triglycerides are found within the intramuscular fat depots or marbling within muscles and the intermuscular fat depots or seam fat found between muscles. Phospholipids make up the lipid bi-layer of cell walls. Interestingly, it has been concluded that more saturated triglycerides contribute little to the characteristic odor of cooked beef (Mottram and Edwards, 1983). However, triglycerides play an important role in the release and perception of flavor (Chevance and Farmer, 1999). Phospholipids, specifically highly unsaturated phospholipids, have been shown to influence the development of flavor (Mottram, 1998). The primary polyunsaturated fatty acids (PUFA) associated with phospholipids include linoleic acid (C18:2) and arachidonic acid (C20:4) (Mottram, 1998; Lin and Blank, 2003). Additional highly unsaturated fatty acids include docosapentaenoic acid (C22:5) and tetracosahexaenoic acid (C22:6) (Lin and Blank, 2003). It is believed that phospholipids containing greater amounts of unsaturated fatty acids are more susceptible to thermal lipid oxidation during cooking (Mottram, 1998).

The importance of phospholipids to the development of beef flavor was investigated by Mottram and Edwards (1983). It was observed that when triglycerides from intramuscular and intermuscular fat were removed before cooking, differences in the aroma between control and treatment steaks could not be determined (Mottram and Edwards, 1983). However, when all lipids (triglycerides and phospholipids) were removed, differences in aroma were observed, with the aroma of treatment steaks described as biscuit-like (Mottram and Edwards, 1983). The importance of phospholipids to the development of cooked beef flavor was further identified through observations of the volatile compounds associated with control and treatment steaks. When control steaks and steaks with the triglycerides removed were compared, similar volatile profiles were observed, having a variety of aliphatic aldehydes and alcohols (Mottram and Edwards, 1983). However, when volatile profiles of control steaks were compared with volatile profiles of steaks having the phospholipids removed, greatly different profiles were observed, with increased amounts of alkyl pyrazines in the phospholipid-removed steaks (Mottram and Edwards, 1983).
implied that pyrazines are inhibited by phospholipids or their degradation compounds in normal steaks (Mottram and Edwards, 1983). These observations speak to the complex interactions lipids and lipid products have on the Maillard reaction.

In summation: Flavor is a multi-dimensional experience influenced by taste and aroma. In most foods, including beef, aroma-active compounds heavily affect perceived flavor. Beef aroma or flavor compounds are developed primarily through thermal oxidation of lipids and the Maillard reaction between amino acids and reducing sugars (Mottram, 1991, 1998; Gandemer, 1999).

Flavor development is primarily dependent on two factors: reactant mixture and reaction conditions. Reactant mixture refers to the precursors of flavor, i.e. fatty acids, amino acids, reducing-sugars, nucleotides, etc. Reaction conditions refer to thermal kinetics as a result of varied time and temperature exposure (cooking). Knowing the reactant mixture make-up allows for determination of characteristic flavor as a result of specific reaction conditions. In other words, beef flavor character may be determined based on precursor compound concentrations prior to cooking.

Factors that affect beef flavor

It is well documented that beef flavor experience is affected by final composition and production background. A fundamental influence on beef flavor is quality grade. An increase in intramuscular fat, with increases in quality grade of beef steaks, has been associated with increased flavor liking by consumers and flavor intensity rated by trained panelists (Smith et al., 1983; Smith et al., 1985; Savell et al., 1987; Lorenzen et al., 1999; Lorenzen et al., 2003; O’Quinn et al., 2012; Emerson et al., 2013; Hunt et al., 2014).

Furthermore, beef production and processing factors, such as cattle breed, finishing diet, and post-mortem aging method influence beef flavor (Melton et al., 1982a; Melton et al., 1982b; Warren and Kastner, 1992; Jeremiah et al., 1998; Brewer, 2006; Emerson et al., 2013). Perhaps the most noticeable flavor variances have been detected between beef from forage-finished cattle in comparison with those on grain-finishing diets (Melton, 1990; Killinger et al., 2004; Sitz et al., 2005). Grain-based diets are considered to produce a more acceptable flavor compared with grass-finished beef (Melton, 1990). Grain-finished U.S. beef was determined to have greater flavor and overall liking compared to Argentine grass-finished beef in a beef consumer study conducted in Chicago and San Francisco (Killinger et al., 2004). Often, sensory panelists use terms like “grassy,” “milky,” “gamey,” or “fishy” to define the less desirable grass-finished beef in contrast to “beef-fat” for grain-finished beef (Melton et al., 1982a; Larick and Turner, 1990). The “grass” flavor of beef Loin Steaks was positively correlated to 14 different volatile compounds from the melted subcutaneous fat of forage-fed cattle (Larick et al., 1987). Grass-fed flavors like “gamey,” “grassy,” or “fishy” were determined to develop with high levels of linolenic acid (Wood et al., 2004).

The length of the grain-finishing period before harvest has been found to be directly proportional to the desirable flavor of cooked beef fat (Harrison et al., 1978). Previously, it was determined that there was a decrease in “grassy” flavor with an increase in the time of grain feeding (Larick et al., 1987). Flavors described as “milky-oily,” “sour,” and “fishy” decreased and “beef fat” flavor increased with increased days on a grain-finishing diet (Melton et al., 1982b). Grain type was shown to subtly influence beef flavor when barley-fed cattle were compared with corn-fed cattle (Busboom et al., 2000). In other work, consumers in Chicago and Denver preferred the flavor of U.S. corn-fed beef in comparison with Canadian barley-fed beef (Sitz et al., 2005).

Currently, little information exists regarding the composition of flavor precursor compounds from multiple production systems. The objective of this white paper was to explore results from checkoff-funded works in regard to flavor precursor compounds and production system. Chemical data was collected in conjunction with sensory evaluation in an initial project at Texas Tech University (Brooks et al., 2012; Legako et al., 2015; Legako et al., 2016). This initial project included Strip Loin Steaks from USDA Prime, Low Choice, and Standard quality grades.
Table 1. Beef product types sampled for determination of flavor-related compounds (Brooks, 2014).

<table>
<thead>
<tr>
<th>Whole-muscle Strip Loin Steaks</th>
<th>Ground Strip Loin Patties</th>
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<tbody>
<tr>
<td>USDA High Choice (HC)*</td>
<td>USDA Choice- no Beta Adrenergic Agonist (ChBA)1</td>
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<tr>
<td>USDA Select (Sel)</td>
<td>USDA Commercial Choice (CChoice)2</td>
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<tr>
<td>USDA Top Choice: Holstein (TChol)**</td>
<td>USDA Select- no Beta Adrenergic Agonist (SelBA)3</td>
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<tr>
<td>USDA Select: Holstein (SelHol)</td>
<td>USDA Choice- Holstein (Chol)4</td>
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<tr>
<td>Grass-finished (GF)</td>
<td>USDA Top Choice- w/ Beta Adrenergic Agonist (TCh14)5</td>
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<tr>
<td>Australian Wagyu (AUW)</td>
<td>USDA Choice- Barley-Fed (ChBarl)6</td>
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<tr>
<td>American Wagyu (AMW)</td>
<td>USDA Top Choice- Long-Aged (TCLong)7</td>
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<tr>
<td>USDA Top Choice: Dry-Aged (TChDry)8</td>
<td>USDA Prime- Dry-Aged (PrDry)9</td>
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<tr>
<td></td>
<td>Wagyu- Dry-Aged (WagDry)10</td>
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<tr>
<td></td>
<td>USDA Choice- Natural (CNatl)11</td>
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<tr>
<td></td>
<td>Grass-fed- American (Grassf)12</td>
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* Upper 1/3 USDA Choice. ** Upper 2/3 USDA Choice.
1Premium Choice, Angus, implanted, fed corn-based diet ≥ 100 days, wet-aged 14 days; 2Low Choice, Angus, implanted, fed corn-based diet ≥ 100 days, wet-aged 14 days; 3Select, Angus, implanted, fed corn-based diet ≥ 100 days, wet-aged 14 days; 4Low Choice, calf-fed Holstein, implanted, fed corn-based diet ≥ 200 days, wet-aged 14 days; 5Low Choice, Angus, implanted and supplemented with β agonists, fed corn-based diet ≥ 100 days, wet-aged 14 days; 6Low Choice, Angus, implanted and supplemented with β agonists, fed barley-based diet ≥ 100 days, wet-aged 14 days; 7Premium Choice, Angus, implanted, fed corn-based diet ≥ 100 days, wet-aged 46 days; 8Premium Choice, Angus, implanted, fed corn-based diet ≥ 100 days, wet-aged 17 days, dry-aged 30 days; 9Prime, Angus, implanted, fed corn-based diet ≥ 100 days, wet aged 17 days, dry-aged 30 days; 10Prime, American Wagyu, no growth enhancement, fed corn-based diet ≥ 100 days, wet-aged 17 days, dry-aged 30 days; 11Low Choice, Angus, no growth enhancement, fed corn-based diet ≥ 100 days, wet-aged 14 days; 12Select, Angus, no growth enhancement, grass-fed (no grain), wet-aged 14 days.

Figure 2. Concentrations of neutral (NL) and polar (PL) lipid fractions (LF) plotted against total fatty acid (FA) concentrations (mg/g dry matter) of raw and cooked USDA Prime, Low Choice, and Standard Longissimus lumborum steaks; Adopted from Legako et al. (2015).
constant concentrations of PL. In contrast, NL FA increased as quality grade increased from USDA Standard to Prime. This response to changes in intramuscular fat content along with quality grade is in agreement with past work (Wood et al., 2008), and reveals a great difference in lipid components between quality grades. Figures 3 and 4 further indicate the overall composition of lipid components in response to quality grade and cooking. It was well recognized from these data and throughout this study that NL contributes substantially to the accumulation of total fat content. Increased intramuscular fat content is associated with the continuous deposition of NL stored in the adipose tissues, whereas the PL, serving as a structural component, remains at a fairly constant concentration. The PL concentration was decreased, whereas the NL concentration was increased after cooking (Figure 3).

Proportionally, raw Prime steaks had the most NL and the least PL (85.43 and 14.57%, respectively; Figure 4), whereas raw Low Choice and Standard steaks had similar LF percentages (77.38 and 72.45% NL and 22.62 and 27.55% PL, respectively). In cooked steaks, Prime and Low Choice steaks had similar LF percentages, which were greater in NL and lower in PL compared with Standard steaks. Cooking increased the proportion of NL and decreased the proportion of PL in Prime, Low Choice, and Standard steaks by 5, 11, and 7%, respectively (Figure 4). Regardless of quality grade and in both raw and cooked steaks, the percentage of the NL was greater than that of the PL. However, as reported previously, the magnitude of the differences was not the same among quality grades and after cooking.

The greatest component of beef lipids are monounsaturated fatty acids (MUFA). Concentrations of MUFA were determined to be affected by quality grade in both NL and PL (Figure 5). When MUFA were explored as percentages of total fatty acids (Figure 6), it was revealed that Prime steaks had increased proportions of MUFA in their NL fractions compared with other quality grades. Monounsaturated fatty acid proportion in the PL fraction also increased as quality grade increased from Standard to Prime. This finding was significant since PL are considered to be primary contributors to flavor development. Compositional
shifts in lipid content with quality grade, therefore, may ultimately affect beef flavor.

Frequently, polyunsaturated fatty acids (PUFA) are described as having negative correlations with beef flavor. When the effect of quality grade was explored for each LF (Figure 7) it was determined that PUFA concentrations were affected by quality grade in NL. Polar lipid PUFA were considered similar between quality grades. However, when the proportions of PUFA were explored (Figure 8), it was determined that NL composition was not altered with quality grade. Polyunsaturated fatty acid percentage was reduced as quality grade increased from Standard to Prime. Again, this compositional change may have great importance to flavor development during cooking. In addition to having negative correlations to beef flavor, PUFA are also correlated with off-flavors and off-odors in beef. Reduction of PUFA proportions in the less stable PL among higher quality grade beef may in turn reduce the development of off-flavors and off-odors.

The effects of cooking were also explored to further understand the potential contributions of FA within each LF. Cooking was found to have little effect on NL MUFA and PUFA proportions (Figure 9 and 10), meaning NL FA composition was not altered by cooking. In contrast, the PL FA composition was greatly affected by cooking. Figure 9 revealed

**Figure 6.** Percentages of monounsaturated fatty acids (MUFA) from neutral and polar lipid fractions of combined raw and cooked USDA Prime, Low Choice, and Standard *Longissimus lumborum* steaks; Adopted from Legako et al. (2015).

**Figure 7.** Concentration (mg/g dry matter) of polyunsaturated fatty acids (PUFA) from neutral and polar lipid fractions of combined raw and cooked USDA Prime, Low Choice, and Standard *Longissimus lumborum* steaks; Adopted from Legako et al. (2015).

**Figure 8.** Percentages of polyunsaturated fatty acids (PUFA) from neutral and polar lipid fractions of combined raw and cooked USDA Prime, Low Choice, and Standard *Longissimus lumborum* steaks; Adopted from Legako et al. (2015).

**Figure 9.** Percentages combined across USDA Prime, Low Choice, and Standard monounsaturated fatty acids (MUFA) from neutral and polar lipid fractions of raw and cooked *Longissimus lumborum* steaks; Adopted from Legako et al. (2015).

**Figure 10.** Percentages combined across USDA Prime, Low Choice, and Standard polyunsaturated fatty acids (PUFA) from neutral and polar lipid fractions of raw and cooked *Longissimus lumborum* steaks; Adopted from Legako et al. (2015).
a proportional decrease in PL MUFA with cooking. This finding is unique since previous works primarily pointed to PUFA as being susceptible to alteration (Igene and Pearson, 1979). MUFA losses affected the PUFA content of PL where proportional increases in PL PUFA percentage occurred with cooking. This increase was due to the great losses of prominent MUFA within the PL leading to greater proportions of PL PUFA. These results are in line with many past works which pointed to PL as being more susceptible to thermal degradation (Terrell et al., 1968; Igene et al., 1980; Mottram, 1998).

**Beef production type and lipid components**

Multiple beef types were evaluated to explore effects of breed, finishing diet, and post-mortem aging on lipid components. **Figure 11** represents the impact of beef type on the concentration of NL FA. As previously discussed, the accumulation of intramuscular lipids is primarily realized through concentration increases in NL. Beef type was found to affect NL concentrations, where Wagyu dry-aged (WagDry) had the greatest NL concentration, followed by USDA Prime dry-aged (PrDry), USDA Top Choice long-aged (TCLong) and USDA Top Choice dry-aged (TChDry). The impact of aging, specifically dry-aging, has been noted to alter the flavor of beef through the concentration of macromolecules with moisture loss. When total PL FA concentrations were explored (Figure 12), it was revealed that PL FA in dry-aged product were lower in concentration than their wet-aged counterpart (TCLong). This data implies that the dry-aging environment may have promoted oxidation within PL FA.

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**Figure 10.** Percentages combined across USDA Prime, Low Choice, and Standard polyunsaturated fatty acids (PUFA) from neutral and polar lipid fractions of raw and cooked Longissimus lumborum steaks; Adopted from Legako et al. (2015).

**Figure 11.** Concentrations combined across USDA Prime, Low Choice, and Standard polyunsaturated fatty acids (PUFA) from neutral and polar lipid fractions of raw and cooked Longissimus lumborum steaks; Adopted from Legako et al. (2015).

**Figure 12.** Total concentrations (mg/g dry matter) of polar lipid from raw Longissimus lumborum patties of multiple beef types (see Table 1); Adopted from Brooks (2014).
Meanwhile, wet-aged PL were maintained in their original state. Previous research points to the importance of PL FA and development of flavor (Mottram and Edwards, 1983). Therefore, the composition of polar lipids were explored to determine beef type effects.

The proportions of SFA, MUFA, and PUFA within PL were also found to be affected by beef type. Grass-fed-American (Grassf), USDA commercial Choice (CChoice), USDA Choice-no Beta Ardenergic agonist (ChBA), USDA Choice barley-fed (ChBarl), TChDry, and TCLong were determined to have the greatest percentage of PL saturated fatty acids (SFA) (Figure 13). The lowest percentage of SFA was within WagDry. Compositional changes of SFA within PL was not observed when quality grade was compared (Legako et al., 2015). Likewise, the proportional changes of PL SFA in this study also did not seem to be affected by quality grade, but more so by diet and finishing regime. The percentage of PL MUFA was greatest in ChBA, ChBarl, USDA Choice Holstein (CHol), Grassf, PrDry, TChDry, and TCLong beef types (Figure 14). Meanwhile, the PL MUFA percentage was lowest in CChoice, USDA Choice Natural (CNatl), and WagDry beef. CChoice, CNatl, and USDA Top Choice with Beta Adrenergic agonist (TCh14) had the greatest percentages of PL PUFA (Figure 15). This compositional shift occurred regardless of total fatty acid content. Recent results indicate that cooking greatly affects percentages of both the MUFA and PUFA of PL (Legako et al., 2015). Therefore, the observed compositional shifts due to diet and aging may affect flavor character.

When FA data was explored for another data set (Corbin et al., 2015), it was revealed that total
NL FA concentration was affected by beef type. Concentrations of NL FA in American Wagyu (AMW) and Australian Wagyu (AUW) were greatest, followed by USDA High Choice (HC) and USDA Top Choice Holstein (TChol) being somewhat lower at an intermediate level though greater than Select (Sel), USDA Select Holstein (SelHol), and grass-finished (GF) (Figure 16). These results indicated a stair step in NL content existed across beef types.

Total PL FA concentrations (mg/g dry matter) differed due to an interaction between beef type and cooking (Figure 17). Among raw PL, all beef types were considered similar, although the concentrations of PL in the AUW treatment were greater than the other types, and the Sel treatment concentrations were lower. PL concentrations were comparable between cooked and raw beef of the same type, except for treatment AUW which showed reduced concentrations of PL after cooking.

Similar to previous data (Figure 3), cooking had little impact on NL quantities when considered on a dry matter basis. Meanwhile, similar to previous data (Figure 3), when comparing beef types, PL quantities were affected by cooking; however, the magnitude of the difference was not equal for each beef type.

Within the PL fraction, previous data (Figure 9 and 10) revealed significant changes to percentages of MUFA and PUFA after cooking. Within this data a similar trend was determined, where beef type and cooking were found to affect PL MUFA percent. Each beef type was found to have percentage reductions of PL MUFA, except Sel where raw and cooked MUFA percentages were similar (Figure 18).
This data is well in line with previous data (Figure 9).

Also similar to previously described data (Figure 10), PUFA percentage results were due to an interaction between beef type and cooking (Figure 19). Again, this increase seems counterintuitive but is squarely the result of the great percentage decrease in predominant MUFA during cooking (Figure 18). PL PUFA concentrations for all beef types were affected by cooking, with the exception being the Sel treatment (Figure 19).

**Water-soluble compounds, USDA quality grade and reducing sugars**

The primary source of reducing sugars post-mortem is glucose and glucose-6-phosphate, resulting from the reduction of glycogen. Ribose, while less numerically prominent, has been determined to contribute to beef flavor. Cooking reduces sugar quantity as sugars participate in the Maillard reaction or are hydrolyzed from heat. When reducing sugars were determined from raw and cooked beef steaks of three quality grades, several interactions were determined. Figures 20, 21 and 22 represent these interactions. Glucose, glucose-6-phosphate, and ribose were each determined to be greater in raw USDA Standard and Low Choice steaks when compared with raw Prime steaks.

Post-cooking, sugar concentrations did not differ between quality grades. Sugars may provide sweetness, but are also major contributors to the Maillard reaction.
Beef production type and reducing sugars

Results for the total sum of reducing sugars from multiple beef types is represented in Figure 23. Similar to the quality grade comparison, when reducing sugars were determined for all beef types, raw and cooked, an interaction existed between beef type and cooking. Sugar content was reduced post-cooking in all treatments, with the exception of ChBarl and PrDry. Initial sugar quantity in raw beef was greater in leaner beef, Grassf and SelBA, compared with many USDA Choice counterparts, ChBarl, TCh14, TCLong, CChoice, and ChBA. A tendency towards greater sugar content was seen in dry-aged product, WagDry, and TChDry. However, PrDry did not follow this trend. The same was true for ribose (Figure 24), where TChDry and WagDry were considered to have greater sugar content.

When sugar concentrations were explored for beef Strip Loin Steaks (Brooks, 2014), no interaction was determined between beef type and cooking for any sugar. Each sugar was reduced by cooking, as would be expected. Beef type was found to affect quantity of many sugars (ribose, myo-inosital, mannose-6-phosphate, and glucose-6-phosphate). For each
sugar, mean comparisons were similar to ribose (Figure 25). Interestingly, ribose was considered to be greatest in Sel and GF beef. Meanwhile, AMW and AUW had the lowest ribose concentration values. This trend is in line with previously described results for quality grade, where beef with greater intramuscular fat had lower ribose content. It is unclear what mechanism is at work here. Sugars are considered water-soluble components coming from intracellular fluid and lean tissue. Meanwhile, the accumulation of intramuscular fat primarily displaces moisture.

**USDA quality grade and free amino acids**

Free amino acids contribute to flavor through participation in the Maillard reaction. Additionally, certain amino acids contribute to taste sensations, such as sweetness and bitterness (Dashdorj et al., 2015). When free amino acids were explored among three quality grades of raw and cooked beef, two trends emerged. First, the majority of free amino acids were increased with cooking. Heat denaturation of skeletal muscle proteins provides great quantities of amino acids post-cooking. The few exceptions to this were cystine, proline, and hydroxyproline, each of which were decreased or unchanged with cooking. Cystine is a dimer of cysteine by a relatively weak sulfur bond. It may be speculated that this sulfur bond is broken with heat, and cystine is reduced to cysteine during cooking. Proline and hydroxyproline are each prominent components of collagen. The cooking procedures of this study were dry-heat and relatively quick. Therefore, the cooking procedures of this study may not have allowed the time and temperature required for solubilization of collagen and the release of these
amino acids. Several interactions were determined for free amino acids. In the case of isoleucine, arginine, and leucine, concentration in raw steaks were considered similar between quality grades. However, post-cooking divergence occurred. Figures 26, 27 and 28 represent the cooked concentrations of these amino acids. These basic aliphatic amino acids have been cited to elicit a bitter taste. In each case, quantities were considered to be greatest in Standard steaks and least in Prime steaks.

**Beef production type and free amino acids**

Concentrations of free amino acids were increased post-cooking, similar to the effects seen in the quality grade work; however, within this group increases were not dependent on beef type. Furthermore, several differences were determined between beef types. Methionine is a sulfur-containing compound frequently described to contribute to the development of important beef flavor compounds. Methionine was determined to have the greatest concentration in TChDry, followed by TCLong, WagDry and PrDry beef (Figure 29). This accumulation of methionine in both wet- and dry-aged product may indicate further proteolysis of skeletal muscle proteins during the aging period.
Similar results were determined for isoleucine (Figure 30). Isoleucine is of interest due to its direct influence on the Strecker degradation pathway of the Maillard reaction which yields Strecker aldehydes that are important to beef flavor. Like methionine, isoleucine was elevated in aged product.

Beef type was determined to impact the sum of free amino acids (Figure 31). Results indicated the sum of free amino acids to be greatest in GF. Meanwhile, SelHol was considered similar to Sel and AUW. Both HC and TCHol were considered similar to each other and similar with Sel and AUW. The lowest quantity was in AMW beef steaks. These results would imply a simple reduction through the addition of intramuscular fat. However, AMW was determined to have 18.37% fat content while AUW had 26.64% (Corbin et al., 2015). In this case, AUW had approximately 8% more fat content, yet AUW was determined to have greater free amino acid content. It is not clear what the mechanism is behind this difference but fat content does not appear to be related to free amino acid content. A potential for a dietary influence exists since the AMW were finished primarily on a corn-based diet in comparison to AUW finished on a barley-based diet. The elevation of total free amino acids in GF beef may be confounded by aging. Strip Loins of the GF treatment received an additional 20 days aging due to the time required for importation from New Zealand.

**USDA quality grade and nucleotides, nucleosides and other nitrogen-containing compounds**

Nucleotides and other nitrogen compounds have previously been described as contributing to the taste of beef (Dashdorj et al., 2015). Several nucleotides (guanosine 5’-monophosphate, adenosine 5’-monophosphate, hypoxanthine, uridine, inosine 5’-monophosphate, carnosine, and creatine) were determined to have interactions between three quality grades and cooking effects (Brooks et al., 2012). In the case of inosine, raw quantities were considered to be greatest in Standard steaks, followed by Low Choice and Prime being lowest (Figure 32). Meanwhile, quantities of inosine in cooked steaks were similar between all quality grades. A similar interaction, between three quality grades, was also apparent for guanosine 5’-monophosphate.
grades and cooking effects, was determined for hypoxanthine (Figure 33). Nucleotides and other nitrogen compounds have been described as providing a bitter sensation (Dashdorj et al., 2015). Specifically, creatine and creatinine have been recognized for their effect on taste of cooked meat (Snider and Baldwin, 1981), although carnosine, a dipeptide, plays an important role as a buffering compound and an antioxidant in the meat system (Cambero et al., 1992; Lee et al., 1998). The ability of carnosine to chelate transition metals and to scavenge free radicals suggests that carnosine is important to the oxidation of lipids and amino acids during cooking (Lee et al., 1998), which ultimately affects volatile formation. It is unclear what impact the initial differences in raw beef may have on flavor. However, it may be concluded that lower-fat-content beef tends to have greater quantities of several of these nitrogen-containing compounds.

**Beef production type and nucleotides, nucleosides and other nitrogen-containing compounds**

The sum of all nucleotide and nitrogen compounds differed as a result of a treatment interaction between beef type and cooking (Figure 34). Depending on beef type, nucleotides were reduced with cooking (CChoice, ChBA, ChBarl, Grassf, TCLong) or did not differ due to cooking (CHol, CNatl, PrDry, SelBA, TCh14, TChDry, WagDry). Initial raw quantity was greatest in Grassf. Choice and Select beef were similar. Lowest quantities of total nucleotides, nucleosides and nitrogen-containing compounds were found in PrDry and WagDry beef. It is of further interest that, for dry-aged TChDry and WagDry, the nucleotides concentration was nearly unchanged statistically and numerically in raw and cooked. Nucleotide concentration in PrDry was statistically unchanged after cooking and numerically increased after cooking. Conversely, nucleotide concentrations in extended wet-aged TCLong and all other wet-aged product had statistical and/or numerical decreases with cooking.
Creatine was determined to be greatest in Grassf, CHol, CNatl, SelBA, and TChDry (Figure 35).

Meanwhile, creatine was lowest in WagDry, PrDry, and TCLong. These results imply a heavy influence of aging upon creatine. Further evidence of this implication is supported by the observation of hypoxanthine (Figure 36), where TChdry and TCLong had the greatest amount; meanwhile, product which did not undergo extended aging (CChoice, ChBA, ChBarl, CHol, CNatl, Grassf, SelBA, and TC14) were each determined to have similar, lower concentrations of hypoxanthine. The observed influence of aging is in line with the long well-accepted notion that post-harvest processing conditions are a great influencer of beef flavor.

Exploration of total nucleotides from beef Strip Steaks revealed greater quantities in GF, SelHol, and Sel steaks (Figure 37). AMW and AUW were considered to have the lowest quantities. This effect carried over to several individual nucleotides (carnosine, creatine, creatinine, and hypoxanthine). However, with inosine concentrations, AMW was considered among the greatest
concentration of inosine, while AUW had the least quantity compared to all other types. (Figure 38) As previously described, AMW beef resulted from a corn-based diet, while AUW resulted from a barley-based diet. A divergence based on quality grade was true in this data set for the comparison of HC with Sel beef steaks. However, quantity of inosine appeared to be more related with diet differences in AMW and AUW, and GF compared with Sel and SelHol beef.

Figure 38. Mean concentrations (nmol/g dry matter) of inosine from combined raw and cooked Longissimus lumborum steaks of multiple beef types (see Table 1); Adopted from Brooks (2014).
References


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