Innovations in beef production systems that enhance the nutritional and health value of beef lipids and their relationship with meat quality

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Abstract

Consumers are becoming more aware of the relationships between diet and health and this has increased consumer interest in the nutritional value of foods. This is impacting on the demand for foods which contain functional components that play important roles in health maintenance and disease prevention. For beef, much attention has been given to lipids. This paper reviews strategies for increasing the content of beneficial omega-3 polyunsaturated fatty acids (PUFA) and conjugated linoleic acid (CLA) and reducing saturated fatty acids (SFA) in beef. Particular attention is given to intramuscular fat (IMF) and the relationships between fatty acid composition and key meat quality parameters including colour shelf life and sensory attributes. Despite the high levels of ruminal biohydrogenation of dietary PUFA, nutrition is the major route for increasing the content of beneficial fatty acids in beef. Feeding grass or concentrates containing linseed (rich in \( \alpha \)-linolenic acid, 18:3 \( \omega \)/C03) in the diet increases the content of 18:3 \( \omega \)/C03 and its longer chain derivative eicosapentaenoic acid (EPA, 20:5 \( \omega \)/C03) in beef muscle and adipose tissue, resulting in a lower \( n-6 : n-3 \) ratio. Grass feeding also increases docosahexaenoic acid (DHA, 22:6 \( \omega \)/C03). Feeding PUFA rich lipids which are protected from ruminal biohydrogenation result in further enhancement of the PUFA in meat with concomitant beneficial improvements in the ratio of polyunsaturated:saturated fatty acids (P:S ratio) and \( n-6 : n-3 \) ratio. The main CLA isomer in beef is CLA \( cis-9, trans-11 \) and it is mainly associated with the triacylglycerol lipid fraction and therefore is positively correlated with level of fatness. The level of CLA \( cis-9, trans-11 \) in beef is related to (1) the amount of this isomer produced in the rumen and (2) synthesis in the tissue, by delta-9 desaturase, from ruminally produced trans-vaccenic acid (18:1 \( trans \)-11; TVA). Feeding PUFA-rich diets increases the content of CLA \( cis-9, trans-11 \) in beef. \( trans \)-fatty acids in foods are of rising importance and knowledge of the differential effects of the individual \( trans \)-isomers is increasing. TVA is the major \( trans \)-18:1 isomer in beef and as the precursor for tissue CLA in both animals and man should be considered as a neutral or beneficial \( trans \)-isomer. Increasing the content of \( n-3 \) PUFA in beef can influence colour shelf life and sensory attributes of the meat. As the content of \( n-3 \) PUFA increases then sensory attributes such as “greasy” and “fishy” score higher and colour shelf life may be reduced. Under these situations, high levels of vitamin E are necessary to help stabilise the effects of incorporating high levels of long chain PUFA into meat. However, grass feeding not only increases \( n-3 \) PUFA and CLA but, due to its high content of vitamin E, colour shelf life is improved. It is evident that opportunities exist to enhance the content of health promoting fatty acids in beef and beef products offering opportunities to add value and contribute to market differentiation. However, it is imperative that these approaches to deliver “functional” attributes do not compromise on the health value (lipoperoxidation) or the taste of beef products.

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I. Introduction

Consumer requirements for food which is safe, healthier, of consistent eating quality, diverse and convenient is increasing. In response, the food industry, supported by the research community, continues to drive new opportunities to address the needs of the consumer. In addition to consumer related issues, increased globalisation, reduced commodity prices, World Trade negotiations, increased animal welfare concerns, the need for traceability and environmental legislation have increased pressure at various points across the food chain. The primary producer in particular, has been most affected with considerable reductions in profit margins. Competitiveness in developed food markets is linked to the ability to develop new differentiated products which increasingly seek to move away from the cost and price-based competition associated with commodity-driven markets (Grunnert, Bredahl, & Brunsø, 2004). This is commonly accepted for food products which require a higher degree of processing but it is increasingly apparent in fresh foods, including meat (Grunnert et al., 2004).

These trends are also occurring in the fresh beef market as reflected in the demand for higher quality and the drive to differentiate beef on the basis of product brandings, geographical origin, sensory or processing characteristics. Definition of quality is becoming increasingly complex as it encompasses the physical intrinsic qualities of the meat (colour, shape, appearance, tenderness, juiciness, flavour) and extrinsic qualities (brand, quality mark, origin, healthiness, production environment etc.) (Steenkamp, 1997). Consumers are increasingly aware of the relationships between diet and health, particularly in relation to cancer, atherosclerosis and obesity/type 2 diabetes. Knowledge of these relationships has augmented consumer interest in the nutritional quality of food such that this is becoming a more important dimension of product quality.

Beef is considered to be a highly nutritious and valued food. The importance of meat as a source of high biological value protein and micronutrients (including for example vitamins A, B_6, B_12, D, E, iron, zinc, selenium) is well recognised (Biesalski, 2005; Williamson, Foster, Stanner, & Buttriss, 2005). However, over the last 10–15 years, these positive attributes have often been overshadowed due to the prominence given to several negative attributes. The latter include the perception that beef contains high amounts of fat which is rich in saturated fat, associations between red meat and cancer and non-nutritional issues such as animal health scares, i.e. BSE. The relationships between dietary fat and incidence of lifestyle diseases, particularly coronary heart disease are well established and this has contributed towards the development of specific guidelines from the World Health Organisation in relation to fat in the diet (WHO, 2003). It is recommended that total fat, saturated fatty acids (SFA), n−6 polynsaturated fatty acids (PUFA), n−3 PUFA and trans fatty acids should contribute <15–30%, <10%, <5−8%, <1−2% and <1% of total energy intake, respectively. Reducing the intake of SFA (which are known to raise total and low-density lipoprotein (LDL) cholesterol) and increasing the intake of n−3 PUFA is particularly encouraged. Among the n−3 PUFA, eicosapentaenoic acid (EPA, 20:5n−3) and docosahexaenoic acid (DHA; 22:6n−3) have been demonstrated to have important roles in reducing the risk of cardiovascular disease, are critical for proper brain and visual development in the foetus, the maintenance of neural and visual tissues throughout life (Calder, 2004; Leaf, Xiao, Kang, & Billamn, 2003) and may have...
roles in reducing cancer and obesity/type-2 diabetes (WHO, 2003). Meat, fish, fish oils and eggs are important sources of these $n-3$ PUFA for man. However, the opportunity for increased intake of long chain $n-3$ PUFA from fish and fish oils appears limited due to low consumption of fish and concerns over the future sustainability of this source (Williams & Burdge, 2006). This has resulted in increased attention being devoted to increasing these fatty acids in other important food sources. Attention has also focused on the extent to which consumption of the precursor of the $n-3$ series, $\alpha$-linolenic acid can provide sufficient amounts of tissue EPA and DHA through the $n-3$ PUFA elongation–desaturation pathway (Williams & Burdge, 2006).

Beef and other ruminant products such as milk are dietary sources of conjugated linoleic acid (CLA; Ritzenthaler et al., 2001). The dominant CLA in cow's milk is the cis-9, trans-11 isomer, which has been identified as possessing a range of health promoting biological properties including antitumoral and anticarcinogenic activities (De la Torre, Debbon et al., 2006).

Due to the above, considerable attention has been placed on improving the nutritional value of beef and the development of products which are beneficial to human health and disease prevention. While protein content and amino acid profiles are little influenced by animal production factors such as nutrition and genetics, it is recognised that micronutrient content, fat content and fatty acid composition may be altered. Most attention has been devoted to lipid composition. Hence, this paper is primarily concerned with progress on altering the fatty acid composition of beef, including its relationship to some components of meat quality such as colour shelf life and sensory attributes. Emphasis is placed on intramuscular fat (IMF), including a review of genetic and nutritional factors influencing the amount and fatty acid composition of IMF.

2. Fat content and fatty acid composition of beef

Fat in beef is present as membrane fat (as phospholipid), intramuscular fat (between the muscles), IMF and subcutaneous fat. Fat content varies widely depending on the cut and degree of trimming. Lean beef has a low IMF content, typically 2–5% and in many countries this is accepted as being “low in fat”. Marbling fat is an important meat quality trait in relation to juiciness, aroma and tenderness and is the fat depot of most interest in relation to fatty acid composition and human health. It refers to the white flecks or streaks of adipose tissue between the bundles of muscle fibres. It is thus closely linked to IMF content. In continental Europe, IMF content in beef is low, but still higher than that in poultry and pork, but this very much depends upon muscle and genotype. Modern European broilers may have 5% fat in the thigh meat but <1% in the skin-off breast meat. Flavour score markedly increases with increasing IMF content above 4–5% (Goutefongea & Valin, 1978).

If tenderness is controlled, flavour and juiciness scores show curvilinear positive relationships with IMF content up to 14–20% (Thompson, 2004). These relationships along with the interest in the fatty acid composition of IMF have increased the awareness of producers in altering the amount and composition of this fat depot in beef.

2.1. Fatty acid profile of IMF and relationships to human health

Intramuscular fat consists on average, of 0.45–0.48, 0.35–0.45 and up to 0.05 of total fatty acids as SFA, mono-unsaturated fatty acids (MUFA) and PUFA, respectively. The PUFA:SFA (P:S, taken as (18:2 + 18:3)/(14:0 + 16:0 + 18:0)) ratio for beef is typically low at around 0.1 (Choi, Enser, Wood, & Scollan, 2000; Scollan et al., 2001), except for double muscled animals which are very lean (<1% IMF) where P:S ratios are typically 0.5–0.7 (Raes, De Smet, & Demeyer, 2001). The $n-6/n-3$ ratio for beef is beneficially low, typically less than 3, reflecting the considerable amounts of beneficial $n-3$ PUFA in beef, particularly 18:3n-3 and the long chain PUFA, EPA and DHA.

The predominant SFA are 14:0 (myristic acid), 16:0 (palmitic acid) and 18:0 (stearic acid), the latter representing 0.3 of total SFA. SFA influence plasma cholesterol, though 18:0 is regarded as neutral in this regard (Yu, Derr, Etherton, & Kris-Etherton, 1995) and 16:0 is less potent than 14:0 (Williamson et al., 2005). Linoleic and $\alpha$-linolenic acids are the main PUFA while oleic acid (18:1n-9) is the most prominent MUFA, with the remainder of the MUFA occurring mainly as cis and trans isomers of 18:1. The PUFA and MUFA are generally regarded as beneficial for human health and there is evidence of beneficial effects of trans-vaccenic acid (TV). Rats given supplements of CLA cis-9, trans-11 would indicate that TVA (the precursor of CLA in tissue and which is the major trans fatty acid in beef) could also add to the beneficial effects of CLA cis-9, trans-11 on cancer (Corl, Barbano, Bauman, & Ip, 2003) and atherogenesis (Lock, Horne, Baumann, & Salter, 2005; Valeille et al., 2005). Beef also contains small amounts of the long chain C20/22 PUFA, EPA and DHA and recent research has demonstrated that red meat is an important source of these fatty acids for man (Howe, Meyer, Record, & Baghurst, 2006). Dannenberger et al. (2004) reported 10 isomers of CLA in beef with CLA cis-9, trans-11 representing approximately 70% of total CLA isomers. Biological effects have been widely investigated for two of these isomers. The anticarcinogenic and antiatherogenic effects of cis-9, trans-11 and the anti-obesity effects of trans-10, cis-12 have been well documented (Belury, 2003). It is evident from this discussion that different fatty acids have different effects on health and disease prevention and this has placed more attention on beneficially altering the fatty acid profile of a particular food and not simply its fat content.
Intramuscular fat mainly consists of triacylglycerols and phospholipids. The triacylglycerols serve as a concentrated source of energy for the body and are deposited in adipocytes. The total IMF content generally depends on the amount of triacylglycerols, whereas the amount of phospholipid, as the building blocks of cell membranes, is relatively constant. Hence there is a strong relationship between IMF and the content of triacylglycerols which is mainly dependent on the degree of overall body fatness, breed and muscle type. The SFA 16:0 and 18:0 and the MUFA 18:1 are mainly dependent on the degree of overall body fatness, breed and muscle type. The SFA 16:0 and 18:0 and the MUFA 18:1 account for approximately 0.8 of total triacylglycerol fatty acids. The dominant PUFA are 18:2n – 6 and 18:3n – 3 representing approximately 0.02 of total triacylglycerol fatty acids. In ruminants, the fatty acids in triacylglycerols are influenced by diet but to a much lesser extent than in monogastrics due to biohydrogenation of dietary fatty acids in the rumen. In phospholipid the proportion of PUFA is much higher than in triacylglycerols, containing not only the essential fatty acids 18:2n – 6 and 18:3n – 3 but also their longer chain derivatives such arachidonic acid (20:4n – 6), EPA, DPA and DHA. Dannenberger et al. (2004) reported that the proportion of PUFA in muscle phospholipids of German Holstein bulls at 630 kg live weight was 0.37–0.41 relative to 0.02 in the triacylglycerols. The phospholipids play central roles in cell membrane function and the PUFA composition is strictly controlled by a complex enzymatic system responsible for the conversion of 18:2n – 6 and 18:3n – 3 to their longer chain derivatives (Raes, De Smet, & Demeyer, 2004). The phospholipid fatty acids are less influenced by diet, but differences in the content of n – 6 and n – 3 long chain PUFA do occur. For example, pasture feeding caused an accumulation of the n – 3 fatty acids in phospholipids and triacylglycerols compared to concentrate feeding (Dannenberger et al., 2004; see subsequent sections). Before considering further the relationships between nutrition and fatty acid composition of IMF, it is appropriate to provide an overview of the physiological regulation of IMF deposition.

2.2. Regulation of IMF deposition

Intramuscular fat is stored to a major extent within the intramuscular adipocytes. Marbling fat is indeed a true adipose tissue embedded within a connective tissue matrix in close proximity to a blood capillary network. Therefore, the number and the diameter of intramuscular adipocytes may be good predictors of marbling (Cianzo, Topel, Whitehurst, Beitz, & Self, 1985).

The number of preadipocytes in the muscle, which ultimately differentiate into intramuscular adipocytes, depends on stem or progenitor cells (Harper & Pethick, 2004). The different lineages to derive adipose, muscle and fibroblastic cells remain however largely unknown. Alteration in cell cycling, preferential clonal selection of some specific progenitor populations, differential proliferation of different stem cells and/or interactions between (pre)adipocytes and myoblasts may control the relative proportions of the different cell types present in the muscle tissue. For instance, myostatin promotes the differentiation of multipotent mesenchymal cells into the adipogenic lineage and inhibits myogenesis (Artaza et al., 2005).

IMF also results from the balance between uptake, synthesis and degradation of triacylglycerols. Therefore, many metabolic pathways (fat uptake from blood, de novo fatty acid synthesis, mitochondrial activity, etc.) in both adipocytes and myofibres could contribute to the variability of IMF content (Hocquette, Ortigues-Marty, Pethick, Herpin, & Fernandez, 1998). In fact, IMF content results from a balance between synthesis and degradation of fats within muscles, rather than from one specific energy metabolic pathway (Gondret, Hocquette, & Herpin, 2004). This is probably the reason why muscles which have a great ability to deposit fat are in fact oxidative muscles (rich in mitochondria and with a high fat turnover) (Hocquette et al., 2003).

In practice, it is clear that the development of IMF content or marbling score is late maturing. More precisely, it is due to maintained or increased fat synthesis in combination with declining muscle growth as animals get older (Pethick, Harper, & Oddy, 2004). The IMF content at birth or at the beginning of the finishing period is likely to be mainly explained by the number of preadipocytes which depends itself on genetic and nutritional factors. For instance, late-maturing beef breeds (Belgian blue, Limousin and Blonde d’Aquitaine) deposit more muscle and less fat compared to dairy breeds or early-maturing beef breeds (Angus and Japanese Black cattle). The major nutritional and/or management tool for increasing the development of marbling is to maximise the availability of net energy (and glucose) for fat synthesis during finishing (Harper & Pethick, 2004). This is the reason why the IMF content is lower for pasture than for grain finishing. At the cellular level, this may be due to increased levels of anabolic hormones (insulin) which stimulates lipogenesis and/or to a preference of marbling adipocytes for carbohydrate carbon to synthesise fatty acids unlike adipocytes of the carcass (Pethick et al., 2004).

2.3. Genetic control of IMF accumulation

Marbling and IMF content have much higher genetic variability ($h^2 = 0.35–0.50$) than tenderness, flavour or juiciness scores (see reviews of Burrow, Moore, Johnston, Barense, & Bindon, 2001; Hocquette, Renand, Levézil, Picard, & Cassar-Malek, 2005), and whilst IMF content is often positively correlated to tenderness, especially when large numbers of animals are studied (Thompson, 2004), the relationships are usually weak. Selection on marbling score (highly correlated with IMF content) may improve tenderness, but as marbling is positively correlated to carcass fatness, selection on IMF or marbling will have undesirable effects on carcass composition. Genetic selection in favour of leaner carcasses decreased IMF content and also
induced a lower activity level of some mitochondrial enzymes especially in oxidative muscles. A positive correlation between IMF content and a marker of adipocyte differentiation (the expression of the A-FABP gene) has been shown among animals (Hocquette et al., 2004).

As reviewed by Kühn et al. (2005), several QTL and genetic markers for marbling were reported from experiments performed in North America or in Australia under feedlot production conditions. The markers include polymorphisms of the thyroglobulin gene (precursor of thyroid hormones), of microsatellite loci CSSM34 and ETH10, of the DGAT1 gene encoding diacylglycerol-O-acyltransferase (involved in the last stages of fat synthesis) and of the retinoid related orphan receptor C (gamma) (RORC). Mutation in GDF8 (myostatin) not only decreases IMF content but also increases muscle mass underlying the relationships between muscle and IMF development (Harper & Pethick, 2004). Research programmes (such as the EU-funded project GeMQual, www.gemqual.org) are currently in progress for the identification of single nucleotide polymorphisms (SNP) in a large set of candidate genes with the objective of being able to evaluate their association with meat quality variables (including IMF content). Finally, the advent of genomics has great potential to discover new molecular markers. It has for instance confirmed the importance of A-FABP for IMF deposition (Wang et al., 2005) and the orientation towards fast glycolytic type muscles in double muscled cattle (which produce lean beef) (Bouley et al., 2005), but has also provided evidence for new genes associated with high muscle growth potential and/or less IMF (Bouley et al., 2005; Sudre et al., 2005). Thus, genomics is likely to provide future opportunities, as well as new challenges, in the quest for achieving marbling performance and later will provide knowledge on the control of muscle fatty acid composition.

3. Strategies influencing the fatty acid composition of beef

Genetic and nutritional approaches have been widely studied in relation to fatty acid composition of beef, although it is acknowledged that genetic factors generally provide smaller differences than dietary factors (see De Smet, Raes, & Demeyer, 2004 for review). Nevertheless, as concluded by De Smet et al. (2004), even though breed differences are generally small they do reflect differences in underlying gene expression or enzymes involved in fatty acid synthesis (as discussed above), and therefore warrant consideration. Taniguchi, Mannen et al. (2004) reported that stearoyl CoA desaturase (delta-9-desaturase) mRNA expression level was related to MUFA percentage in Holstein Japanese Black cattle and describe a SNP in Japanese Black cattle which contributed to higher MUFA percent (0.5–0.6) in the double-muscled Belgian Blue bulls (Raes et al., 2001). In contrast the n – 6/n – 3 ratio in meat of double-muscled Belgian Blue bulls is high (5–6), but may be improved by using the nutritional approaches outlined below (Raes, De Smet, Balcaen, Claey, & Demeyer, 2003, 2004).

3.1. Forages and the fatty acid composition of beef

Plants are the primary source of n – 3 PUFA, both in the terrestrial and marine ecosystems. Plants have the unique ability to synthesise de novo 18:3n – 3 which is the building block of the n – 3 series of essential fatty acids and elongation and desaturation of this fatty acid results in the synthesis of EPA and DHA. The formation of these long chain n – 3 PUFA by marine algae and their transfer through the food chain to fish, accounts for the high amounts of these important fatty acids in fish oils (see subsequent section).

Forages such as grass and clover contain a high proportion (50–75%) of total fatty acids as α-linolenic acid (Dewhurst, Shingfield, Lee, & Scollan, in press). Exploiting the potential of herbage as an alternative to marine sources of PUFA is an important nutritional strategy for enhancing the content of n – 3 PUFA in beef. The transfer of 18:3n – 3 from forage through meat is dependent on two important processes, (1) increasing the level of 18:3n – 3 in the forage (and hence into the animal) and (2) reducing the extent of ruminal biohydrogenation. These factors have recently been reviewed by Palmquist et al. (2005) and Dewhurst et al. (in press) and will not be considered further here.

Feeding fresh grass or grass silage compared to concentrates, rich in 18:3n – 3 and 18:2n – 6, respectively, results in higher concentrations of n – 3 PUFA in muscle lipids, both in the triacylglycerol and phospholipid fractions (Tables 1(i) and 2; Nuernberg, Dannenberger et al., 2005;
Significantly, grass compared to concentrate feeding not only increased $18:3\,n-3$ in muscle phospholipid but also EPA, DPA and DHA (see Table 2; Dannenberger et al., 2004; Warren et al., 2002). In comparison, concentrates rich in $18:2\,n-6$ lead to higher concentrations of $18:2\,n-6$ and associated longer chain derivatives (20:4n-6). Studies in Ireland showed that both the proportion of grass in the diet (Table 1(iii); French et al., 2000) and length of time on grass (Table 1(ii) Noci, Monahan, French, & Moloney, 2005) were important in determining the response in beef fatty acids. French et al. (2000) also found significant reductions in the proportion of SFA, both 16:0 and 18:0 with grass feeding. Collectively these responses in both SFA and $n-3$ PUFA contribute towards beneficial changes in P:S (increasing) and $n-6:n-3$ ratios (decreasing). The recent report by Razminowicz, Kreuzer, and Scheeder (2006) confirmed these grass forage/pasture effects in retail beef. They noted that pasture beef relative to “conventional” beef or intensively produced young bulls had higher amounts of $n-3$ PUFA and resulted in an $n-6:n-3$ ratio consistently below 2. Feeding steers indoors on maize silage and concentrate resulted in higher concentrations of $18:2\,n-6$ (and less $18:3\,n-3$) and a less favourable $n-6:n-3$ ratio than pasture-finished steers (Varela et al., 2004).

Feeding mixtures of grass and red clover relative to grass alone increased the deposition of both $n-6$ and $n-3$ PUFA in muscle of finishing beef steers, resulting in increases in the P:S ratio (Table 1(iv); Scollan et al., Table 1

**Influence of forage on the fatty acid composition (mg/100 g tissue) of beef longissimus muscle**

(i) Grass v. concentrate (Adapted from Warren et al. (2003))

<table>
<thead>
<tr>
<th>Fatty acids</th>
<th>Grass</th>
<th>Concentrate</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>2581</td>
<td>1724</td>
<td>139.3</td>
<td>***</td>
</tr>
<tr>
<td>$18:2,n-6$</td>
<td>62.0</td>
<td>146.9</td>
<td>6.68</td>
<td>***</td>
</tr>
<tr>
<td>$18:3,n-3$</td>
<td>32.0</td>
<td>7.2</td>
<td>1.60</td>
<td>***</td>
</tr>
<tr>
<td>$20:5,n-3$</td>
<td>17.7</td>
<td>4.5</td>
<td>1.05</td>
<td>***</td>
</tr>
<tr>
<td>$22:5,n-3$</td>
<td>10.3</td>
<td>10.8</td>
<td>1.28</td>
<td>***</td>
</tr>
<tr>
<td>$22:6,n-3$</td>
<td>5.0</td>
<td>1.3</td>
<td>0.30</td>
<td>***</td>
</tr>
<tr>
<td>$n-6,n-3$</td>
<td>1.2</td>
<td>8.9</td>
<td>0.24</td>
<td>***</td>
</tr>
<tr>
<td>P:S</td>
<td>0.09</td>
<td>0.24</td>
<td>0.010</td>
<td>***</td>
</tr>
</tbody>
</table>

(ii) Proportion of grass (g/kg DM) in the diet (Adapted from French et al. (2000))

<table>
<thead>
<tr>
<th>Fatty acids</th>
<th>0</th>
<th>510</th>
<th>770</th>
<th>1000</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>3410</td>
<td>4490</td>
<td>4020</td>
<td>4360</td>
<td>650.5</td>
<td>NS</td>
</tr>
<tr>
<td>$18:2,n-6$</td>
<td>120.5</td>
<td>105.8</td>
<td>94.4</td>
<td>85.9</td>
<td>6.05</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>$18:3,n-3$</td>
<td>29.3</td>
<td>35.4</td>
<td>41.1</td>
<td>46.0</td>
<td>1.78</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>$20:5,n-3$</td>
<td>4.9</td>
<td>11.0</td>
<td>9.8</td>
<td>9.4</td>
<td>1.32</td>
<td>* (quadratic)</td>
</tr>
<tr>
<td>$22:6,n-3$</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.606</td>
<td>NS</td>
</tr>
<tr>
<td>$n-6,n-3$</td>
<td>4.15</td>
<td>2.86</td>
<td>2.47</td>
<td>2.33</td>
<td>0.019</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>P:S</td>
<td>0.09</td>
<td>0.10</td>
<td>0.11</td>
<td>0.13</td>
<td>0.010</td>
<td>*** (linear)</td>
</tr>
</tbody>
</table>

(iii) Length of grass feeding (days) (Adapted from Noci, Monahan, et al. (2005))

<table>
<thead>
<tr>
<th>Fatty acids</th>
<th>0</th>
<th>40</th>
<th>99</th>
<th>158</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>2461</td>
<td>2329</td>
<td>2754</td>
<td>2515</td>
<td>177.5</td>
<td>NS</td>
</tr>
<tr>
<td>$18:2,n-6$</td>
<td>62.1</td>
<td>63.7</td>
<td>59.4</td>
<td>59.0</td>
<td>3.32</td>
<td>NS</td>
</tr>
<tr>
<td>$18:3,n-3$</td>
<td>19.6</td>
<td>25.4</td>
<td>30.9</td>
<td>34.4</td>
<td>1.86</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>$20:5,n-3$</td>
<td>5.6</td>
<td>5.5</td>
<td>6.4</td>
<td>7.7</td>
<td>0.50</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>$22:5,n-3$</td>
<td>3.22</td>
<td>2.86</td>
<td>2.78</td>
<td>2.72</td>
<td>0.606</td>
<td>NS</td>
</tr>
<tr>
<td>$n-6,n-3$</td>
<td>2.21</td>
<td>1.99</td>
<td>1.63</td>
<td>1.46</td>
<td>0.108</td>
<td>*** (linear)</td>
</tr>
<tr>
<td>P:S</td>
<td>0.12</td>
<td>0.14</td>
<td>0.12</td>
<td>0.15</td>
<td>0.009</td>
<td>*** (linear)</td>
</tr>
</tbody>
</table>

(iv) Grass v. red clover (Adapted from Scollan et al. (2006))

<table>
<thead>
<tr>
<th>Fatty acids</th>
<th>Grass silage</th>
<th>50:50 mix grass/red clover</th>
<th>Red clover</th>
<th>Red clover + vitamin E</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>3081</td>
<td>3639</td>
<td>4001</td>
<td>3074</td>
<td>604.7</td>
<td>NS</td>
</tr>
<tr>
<td>$18:2,n-6$</td>
<td>73.2a</td>
<td>92.8b</td>
<td>113.2c</td>
<td>99.3b</td>
<td>6.68</td>
<td>***</td>
</tr>
<tr>
<td>$18:3,n-3$</td>
<td>22.5a</td>
<td>34.1b</td>
<td>50.7</td>
<td>37.5b</td>
<td>3.83</td>
<td>***</td>
</tr>
<tr>
<td>$20:5,n-3$</td>
<td>12.9</td>
<td>13.4</td>
<td>14.9</td>
<td>14.5</td>
<td>1.33</td>
<td>NS</td>
</tr>
<tr>
<td>$22:5,n-3$</td>
<td>21.65</td>
<td>23.89</td>
<td>25.11</td>
<td>24.25</td>
<td>2.93</td>
<td>NS</td>
</tr>
<tr>
<td>$22:6,n-3$</td>
<td>2.51</td>
<td>2.34</td>
<td>2.78</td>
<td>2.65</td>
<td>0.275</td>
<td>NS</td>
</tr>
<tr>
<td>$n-6,n-3$</td>
<td>3.28</td>
<td>2.73b</td>
<td>2.30a</td>
<td>2.66b</td>
<td>0.15</td>
<td>***</td>
</tr>
<tr>
<td>P:S</td>
<td>0.09a</td>
<td>0.09b</td>
<td>0.10b,c</td>
<td>0.12a</td>
<td>0.02</td>
<td>**</td>
</tr>
</tbody>
</table>

* In this and other tables NS = not significant; *P < 0.05; **P < 0.01; ***P < 0.001.

A. Not identified on chromatogram.
Companion studies have revealed that the red clover response is related to reductions in ruminal biohydrogenation of PUFA, which is possibly related to the protective effects of the enzyme polyphenol oxidase (PPO; Lee et al., 2004). Studies in milk have revealed that Alpine pasture results in a higher content of 18:3n–3 than lowland pasture, as a result of reduced ruminal biohydrogenation of dietary 18:3n–3 (Leiber, Kreuzer, Nigg, Wettstein, & Scheeder, 2005). Norwegian sheep finished on mountain pastures had 25% more PUFA than similar sheep raised on improved lowland pastures (Adnoy et al., 2005). Similar results are not available for beef, but identification of the “Alpine factor” responsible for the reduction in biohydrogenation should be pursued.

3.2. Supplementary lipids and the fatty acid composition of beef

3.2.1. Unprotected lipids

The main sources of supplementary fatty acids in ruminant rations are plant oils and oilseeds, fish oil, marine algae and fat supplements (Givens et al., 2000). Since dietary inclusion of fatty acids must be restricted (to 60 g/kg dry matter consumed, approx.) to avoid impairment of rumen function, the capacity to manipulate the fatty acid composition by use of ruminally-available fatty acids is limited. Despite ruminal biohydrogenation, a proportion of dietary PUFA bypasses the rumen intact and is absorbed and deposited in body fat (Wood & Enser, 1997). Thus, linseed or linseed oil (rich in 18:3n–3) can increase the concentration of 18:3n–3 in tissue with an associated desirable decrease in the n−6: n−3 PUFA ratio (Scollan et al., 2001, Table 3(i)). Similarly, sunflower seed or sunflower oil (rich in 18:2n–6) can increase the concentration of 18:2n–6 in tissue but with an associated undesirable increase in the n−6: n−3 PUFA ratio (Garcia, Amstalden, Morrison, Keisler, & Williams, 2003; Noci, O’Kiely, Monahan, Stanton, & Moloney, 2005). Dietary inclusion of 18:3n–3 generally also increases the concentration of EPA but not DHA in tissue (Scollan et al., 2001). The potential of fish oil (rich in both the long-chain n−3 PUFA) to increase their concentration in beef is illustrated in Table 3 (Scollan et al., 2001) and the increase is dependent on the level of dietary inclusion (Noci, Monahan, Scollan, & Moloney, 2006). While the supplementation strategies described above can cause sizeable changes in the n−6:n−3 PUFA ratio they generally do not increase the P:S ratio in the meat above the 0.1–0.15 normally observed.

3.2.2. Protected lipids

Durand, Scisloowski, Gruffat, Chillard, and Bauchart (2005) demonstrated the potential to markedly increase the concentration of n−3 PUFA in beef muscle by infusing 18:3n–3 (as linseed oil) directly into the small intestine. Thus, infusing an amount of linseed oil similar to that consumed, increased the concentration of 18:3n–3 in total lipid from 26.3 to 176.5 mg/100 g muscle. Infusion also resulted in a high P:S ratio (0.495 relative to the recommended target of >0.4) and low n−6:n−3 ratio (1.04 relative to the recommended target of <2–3). For practical exploitation of the capacity of muscle to deposit n−3 PUFA, methods to protect dietary lipids from ruminal degradation are under on-going investigation. A variety of procedures have been explored including the use of intact oilseeds, heat/chemical treatment of intact/processed oilseeds, chemical treatment of oils to form calcium soaps or amides, emulsification/encapsulation of oils with protein and subsequent chemical protection (see Ashes, Gulati, Kitessa, Fleck, & Scott, 2000; Gulati, Garg, & Scott, 2005). Using the latter technology, Scollan, Enser, Gulati, Richardson, and Wood (2003) showed that a protected plant oil supplement (with n−6:n−3 PUFA ratio of 2.4:1) markedly improved the P:S ratio (from 0.08 to 0.27) but increased the n−6:n−3 PUFA (from 2.75 to 3.59) in muscle. It is interesting that in this study the increase in P:S was associated with an increase in PUFA content but also a reduction in IMF (as discussed above; Fig. 1). In a subsequent study, a protected plant oil supplement with n−6:n−3 PUFA ratio of 1:1 decreased the n−6:n−3 PUFA ratio in muscle (from 3.59 to 1.88) while maintaining the high P:S ratio (Scollan, Enser, Richardson, Gulati, Hallett, Nute et al., 2004, Table 3(ii)). No effect was observed on the concentration of DHA in either study. Ruminal protection of fish oil however, increased the concentration of EPA and DHA in tissue but had little effect on the P:S ratio and improved the n−6:n−3 PUFA ratio only at the highest level fed (Richardson, Hallett et al., 2004, Table 3(iii)). This may reflect the inclusion of 100 g unprotected fish oil in all treatments. As discussed previously, the long-chain n−3 PUFA are incorporated mainly into membrane phospholipids and are not incorporated into triacylglycerols to any important extent in ruminants. This provides the opportunity to manipulate intramuscular fatty acid composition of ruminant meat without large increases in fatness per se. Since the concentrations of EPA and DHA in fish oil are dependent on the species of fish and represent, at most, 25% of fish oil fatty acids, often the rest being rich in SFA (Givens et al., 2000), a prudent future strategy would be to concentrate these fatty acids prior to ruminal protection. Moreover, since the most

<table>
<thead>
<tr>
<th>Concentrate</th>
<th>Grass silage</th>
<th>SED</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>18:2n–6</td>
<td>23.3</td>
<td>8.7</td>
<td>0.36</td>
</tr>
<tr>
<td>18:3n–3</td>
<td>0.8</td>
<td>3.7</td>
<td>0.05</td>
</tr>
<tr>
<td>20:4n–6</td>
<td>2.7</td>
<td>1.2</td>
<td>0.06</td>
</tr>
<tr>
<td>20:5n–6</td>
<td>10.5</td>
<td>6.3</td>
<td>0.17</td>
</tr>
<tr>
<td>20:5n–3 EPA</td>
<td>0.8</td>
<td>3.4</td>
<td>0.06</td>
</tr>
<tr>
<td>22:5n–3 DPA</td>
<td>2.1</td>
<td>4.6</td>
<td>0.09</td>
</tr>
<tr>
<td>22:6n–3 DHA</td>
<td>0.2</td>
<td>0.9</td>
<td>0.04</td>
</tr>
</tbody>
</table>

Table 2
Influence of concentrate or grass silage on fatty acid composition (proportion x 100) of the phospholipid fraction of beef longissimus muscle (Warren et al., 2002)
Effective protection strategies to date have been on a non-commercial scale and involved formaldehyde, the use of which may not be permitted by some regulatory authorities, development of alternative protection technologies is needed. The recent report on the efficacy of a whey protein gel complex to ruminally protect PUFA is encouraging in this regard (Carroll, DePeters, & Rosenberg, 2006).

3.3. Dietary effects on trans fatty acids in beef

Human metabolic studies have shown that trans fatty acids and SFA like lauric acid, myristic acid and palmitic acid elevate LDL cholesterol (Li, Siramornpun, Wahlquist, Mann, & Sinclair, 2005). In response to concerns about the consumption of trans fatty acids and potential impact on health, the US Dietary Guidelines Committee concluded that the intake of trans fatty acids should be below 1% of energy (Willet, 2005). In Canada and the US it is mandatory to declare the trans fatty acid content of food from January 2006. Evidence is accumulating that different trans-18:1 isomers have differential effects on plasma LDL cholesterol and this is an area of active investigation (Willet, 2005). For example, there is support that trans-9 and trans-10 18:1 are more powerful in increasing plasma LDL cholesterol than trans-11 18:1 (Willet, 2005). It is also recognised that trans-vaccenic acid (trans-11 18:1, TVA) is the precursor for tissue synthesis of beneficial CLA (CLA cis-9, trans-11) in both man and in animals. Important differences exist in the profile of trans fatty acids of different foods and attention has been given to that of partially hydrogenated vegetable oils compared to that of ruminant fats. Industrial hydrogenation results in a wide range of equally distributed isomers relative to IMF in beef (Fig. 2). The daily consumption of trans fatty acids from industrially hydrogenated fat is up to ten times higher than that from ruminant fat (Stender & Dyerberg, 2003).

TVA is the most abundant trans-18:1 isomer in beef and lamb (Dannenberger et al., 2004; Nuernberg, Nuernberg et al., 2005, Fig. 2). The intramuscular lipids of bulls contain approximately 2.8–3.2% of total trans 18:1 isomers (Nuernberg et al., 2005). As reflected in Fig. 2, pasture feeding increased the relative proportion of TVA in muscle.

<table>
<thead>
<tr>
<th>Table 3</th>
<th>Influence of fat sources on the fatty acid composition (mg/100 g tissue) of beef longissimus muscle</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i) Different sources of oil (Adapted from Scollan et al. (2001))</td>
<td></td>
</tr>
<tr>
<td>Fatty acids</td>
<td>Control</td>
</tr>
<tr>
<td>-----------------</td>
<td>---------</td>
</tr>
<tr>
<td>Total</td>
<td>3529</td>
</tr>
<tr>
<td>18:2n-6</td>
<td>81</td>
</tr>
<tr>
<td>18:3n-3</td>
<td>22a</td>
</tr>
<tr>
<td>20:5n-3</td>
<td>11a</td>
</tr>
<tr>
<td>22:5n-3</td>
<td>15</td>
</tr>
<tr>
<td>22:6n-3</td>
<td>2.2a</td>
</tr>
<tr>
<td>n-6n-3</td>
<td>2.00a</td>
</tr>
<tr>
<td>P:S</td>
<td>0.07</td>
</tr>
</tbody>
</table>

(ii) Plant oils protected from ruminal biohydrogenation (Adapted from Scollan, Enser, Richardson, Gulati, Hallett, Wood et al. (2004))

Control | PLS (g/d) | ED | Significance |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>4685</td>
<td>4976</td>
<td>4880</td>
</tr>
<tr>
<td>18:2n-6</td>
<td>120</td>
<td>255</td>
<td>279</td>
</tr>
<tr>
<td>18:3n-3</td>
<td>29a</td>
<td>102b</td>
<td>118b,c</td>
</tr>
<tr>
<td>20:5n-3</td>
<td>13a</td>
<td>15a</td>
<td>14a</td>
</tr>
<tr>
<td>22:5n-3</td>
<td>23a,b</td>
<td>24b</td>
<td>20a</td>
</tr>
<tr>
<td>22:6n-3</td>
<td>1.9</td>
<td>1.8</td>
<td>1.5</td>
</tr>
<tr>
<td>n-6n-3</td>
<td>2.27a</td>
<td>2.02b</td>
<td>2.00b</td>
</tr>
<tr>
<td>P:S</td>
<td>0.07a</td>
<td>0.18b</td>
<td>0.20b</td>
</tr>
</tbody>
</table>

(iii) Fish oil protected from ruminal biohydrogenation (Richardson, Hallett et al., 2004)

Control | PFO (g/d) | ED | Significance |
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>4698</td>
<td>4092</td>
<td>3858</td>
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<tr>
<td>18:2n-6</td>
<td>88</td>
<td>81</td>
<td>87</td>
</tr>
<tr>
<td>18:3n-3</td>
<td>25</td>
<td>23</td>
<td>23</td>
</tr>
<tr>
<td>20:5n-3</td>
<td>14a</td>
<td>14a</td>
<td>15c,b</td>
</tr>
<tr>
<td>22:5n-3</td>
<td>23b</td>
<td>21a,b</td>
<td>20a</td>
</tr>
<tr>
<td>22:6n-3</td>
<td>3.4a</td>
<td>7.0b</td>
<td>9.8c</td>
</tr>
<tr>
<td>n-6n-3</td>
<td>1.70b</td>
<td>1.55a</td>
<td>1.61a</td>
</tr>
<tr>
<td>P:S</td>
<td>0.06</td>
<td>0.06</td>
<td>0.07</td>
</tr>
</tbody>
</table>

A PLS = protected lipid supplement.
B PFO = protected fish oil.
of bulls and lambs. Avoiding increases in trans isomers when attempting to decrease SFA and/or enhance PUFA is important. In this respect, it is important to note that grass and pasture based approaches result in lower effects on trans-fatty acids relative to supplementation with plant oils or fish oils (Noci, O’Kiely, et al., 2005; Noci et al., 2006; Scollan et al., 2001).

3.4. Dietary effects on CLA in beef

Conjugated linoleic acids consist of a collection of positional and geometric isomers of octadecadienoic acid. Ruminant meats and milk and their products are the main natural source of CLA in the human diet. CLA has been linked to a multitude of potential health benefits, including inhibition of carcinogenesis, reduced rate of fat deposition, altered immune response, reduced serum lipids, antidiabetic and antiatherogenic effects (Bauman, Baumgard, Corl, & Griinari, 1999; Belury, 2003; Kritchevsky, 2003; Pariza, Park, & Cook, 2001). Most research has focused on two isomers: CLA cis-9, trans-11 and CLA trans-10, cis-12 (Belury, 2003; Kritchevsky, 2003; Pariza et al., 2001). Studies on pure single isomers showed that they have differences in biological activities as reported in recent reviews by Banni, Heys, and Wahle (2003), Khanal (2004) and Martin and Valeille (2002).

CLA cis-9, trans-11 is the major CLA isomer in ruminant milk and meat products and is mainly deposited in the triacylglycerols (Dannenberger et al., 2004). CLA cis-9, trans-11 is formed during biohydrogenation of linoleic acid in the rumen and it was initially assumed that this was the source of CLA cis-9, trans-11 in milk and intramuscular fat (Harfoot & Hazelwood, 1998). However, Griinari et al. (2000) and Palmquist (2001) showed that the primary source of CLA cis-9, trans-11 is endogenous synthesis from TVA formed during ruminal biohydrogenation and involving Δ⁹-desaturase (Khanal & Dhiman, 2004; Song & Kennelly, 2003). There appears to be a linear relationship between muscle TVA and CLA content (Enser et al., 1999). The CLA content can be increased by different

![Fig. 2. Distribution of trans 18:1 isomers in ruminant fat and industrially hydrogenated vegetable oil (§ Stender and Dyerberg (2003) and Dannenberger et al. (2004)).]
dietary strategies (De La Torre et al., 2006; Schmid et al., 2006). Diets containing a proportionally high level of linolenic acid in the fat, such as fresh grass, grass silage, and pasture feeding during the finishing periods, resulted in increased deposition of CLA cis-9, trans-11 in muscle (Enser et al., 1999; French, O’Riordan, Monahan, Caffrey, & Moloney, 2003; Scollan et al., 2001; Shanta, Moody, & Tabedini, 1997). French et al. (2003) reported a significant increase in CLA cis-9, trans-11 in muscle of crossbred steers grazed for 85 days on pasture compared to concentrate, averaging 1.08% and 0.37% of total fatty acids, respectively. Dhiman (2001) and Poulson et al. (2001) observed a significant increase in CLA cis-9, trans-11 in muscle of crossbred steers on forage and pasture without grain supplementation. Similarly, Steen and Porter (2003) reported that the content of CLA cis-9, trans-11 in muscle and subcutaneous fat from steers finished on pasture was three times higher than that from steers finished on concentrate. Nuernberg et al. (2005) reported, that pasture feeding resulted in a significant increase of CLA cis-9, trans-11 from 0.50% to 0.75% in muscle lipids of German Holstein and German Simmental bulls compared with concentrate-fed bulls. Furthermore, adding oil seeds, vegetable oils and fish oil to the diet have proved to be efficient strategies to increase the CLA content in muscle lipids (Schmid, Collomb, Sieber, & Bee, 2002). The authors reviewed the available data on intramuscular CLA content in meat and meat products originating from different animal species. However, the amount of CLA found in meat is small, relative to the recommended daily intake for health benefits in human, which is 3500 mg/d (Ha, Grimm, & Pariza, 1997). It is important to consider the net CLA yield to the consumer rather than only the concentration in the dietary lipids. Values for CLA cis-9, trans-11 concentrations (mg/100 g fresh muscle) in beef are sparse in the literature and a selection is summarised in Table 4. Certain breeds of cattle that have a tendency to deposit high amounts of IMF in muscle (i.e. Wagyu or Wagyu × Limousin steers) will deliver a greater amount of CLA cis-9, trans-11 to the consumer (Table 4; note the data in this Table does not take into account conversion of TVA to CLA in human tissue). Bauchart, Gladine, Gruffat, Leloutre, and Durand (2005) and De La Torre, Gruffat et al. (2006) have shown that not only does lipid supplementation affect the proportion of CLA produced, but this also depends upon basal diet, breed, age and sex of the animals.

Furthermore, there are only a few publications dealing with the CLA isomer distribution in different beef tissues using silver-ion HPLC (Ag⁺-HPLC). This is particularly important because the individual CLA isomers show different biological activities (Banni et al., 2003; Pariza et al., 2001; Khanal, 2004). Additionally, the distribution pattern in the tissue lipids will be affected by the composition of the ration consumed (Dannenberger et al., 2004; Dannenberger et al., 2005; De La Torre, Gruffat et al., 2006; Nuernberg et al., 2002; Table 5). There is a lack of information on the metabolic pathways of individual trans 18:1-isomers and CLA isomers in muscle and their different biological activities and further research is needed.

4. Fatty acids and meat quality

4.1. Meat flavour

The flavour of red meats is derived from the Maillard reaction between amino acids and reducing sugars and the thermal degradation of lipid. The former produces roasted/meaty flavours and the latter the species differences in flavour (Gandemer, 1999; Mottram, 1998). Strategies which alter the fatty acid composition of the lipid fraction of meat could also alter the amount and type of volatiles produced and hence its aroma and flavour (Elmore, Mottram, Enser, & Wood, 1999; Elmore et al., 2004). In a study comparing grass- and concentrate-finished animals, the concentrate-fed animals had higher concentrations of linoleic acid in their meat and on cooking produced seven compounds at over three times the level found in meat from grass-fed animals, which had much higher concentrations of 18:3n-3 and produced a higher amount of only two compounds, phy-t-1-ene (10-fold) and phy-t-2-ene (three-fold), derivatives of chlorophyll (Elmore et al., 2004). These are similar results to those of Larick et al. (1987) who found that phy-2-ene, produced from cooking subcutaneous fat, was a good marker of forage feeding and that nine other compounds were useful in a discriminant analysis to predict the length of time an animal had been fed on grass or grain. Lorenz et al. (2002) quantified meat odour volatiles formed after pressure-cooking meat from cattle fed forage or con-

Table 4
Concentration of CLA cis-9, trans-11 (mg/100 g fresh muscle) in longissimus muscle of different beef genotypes

<table>
<thead>
<tr>
<th>Breed</th>
<th>Diet</th>
<th>CLA cis-9, trans-11</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wagyu, steers</td>
<td>Sunflower oil</td>
<td>134</td>
<td>Mir et al. (2002)</td>
</tr>
<tr>
<td>Wagyu × Limousin, steers</td>
<td>Sunflower oil</td>
<td>76</td>
<td>Mir et al. (2004)</td>
</tr>
<tr>
<td>Limousin, steers</td>
<td>Sunflower oil</td>
<td>59</td>
<td>Mir et al. (2004)</td>
</tr>
<tr>
<td>Charolais, steers</td>
<td>Grass silage whole linseed</td>
<td>36</td>
<td>Enser et al. (1997)</td>
</tr>
<tr>
<td>Crossbred steers</td>
<td>Grass silage</td>
<td>35</td>
<td>Steen and Porter (2003)</td>
</tr>
<tr>
<td>German Holstein, bulls</td>
<td>Pasture</td>
<td>17</td>
<td>Dannenberger et al. (2005)</td>
</tr>
<tr>
<td>German Simmental, bulls</td>
<td>Pasture</td>
<td>12</td>
<td>Dannenberger et al. (2005)</td>
</tr>
<tr>
<td>Double-muscled Belgian Blue, bulls</td>
<td>Crushed linseed</td>
<td>4.3</td>
<td>Raes et al. (2004)</td>
</tr>
<tr>
<td>Double-muscled Belgian Blue, bulls</td>
<td>Extruded linseed</td>
<td>4.2</td>
<td>Raes et al. (2004)</td>
</tr>
</tbody>
</table>
centrate. ‘Green’ odour from meat of grass-fed animals was connected with compounds (hexanals) derived from oleic acid (18:1\textit{n}-9) and 18:3\textit{n}-3, and “soapy” odours (octanals) from 18:2\textit{n}-6 (concentrate fed).

Campo et al. (2003) used a trained sensory panel to study the flavour of the individual fatty acids 18:1\textit{n}-9 and 18:3\textit{n}-3, and “soapy” odours (octanals) from 18:2\textit{n}-6 (concentrate fed).

4.2. Lipid and colour stability

In bovine animals given lipid supplements rich in PUFA, lipid oxidation can first occur in the plasma lipids, if the level of antioxidant is limiting, compared to the amounts of PUFA absorbed from the intestine (Scislowski, Bauchart, Grafft, Laplaud, & Durand, 2005). Lipid oxidation produces free radicals and, therefore, may impair the health of animals (Durand et al., 2005) In muscle tissues it can promote myoglobin (colour) oxidation and leads to the formation of rancid odours and flavours. Meat with more PUFA may be more oxidisable, but when these PUFA are derived from pasture feeding, they are associated with more antioxidant in the form of \( \alpha \)-tocopherol,
carotenoids and flavonoids (Wood & Enser, 1997), which stabilise the fatty acids and make the meat more desirable (Gatellier et al., 2005; Moloney et al., 2001; Richardson et al., 2004). Charolais cows finished on pasture had higher vitamin E content in their meat than those finished on silage and a cereal concentrate and this reduced lipid oxidation (Mercier, Gatellier, & Renerre, 2004). Aberdeen Angus cross and Holstein–Friesian steers were fed either perennial ryegrass silage (with 0.15 sugar beet pulp) or concentrates (0.6 barley, 0.2 sugar beet pulp, 0.125 full fat soya and barley straw) and slaughtered at 14, 19 or 24 months of age. The vitamin E content of the longissimus muscle was 1.3 and 3.4 mg/kg meat for the concentrate and silage-fed animals, respectively. When 10 d aged meat was packed as steaks in a modified atmosphere, this resulted in TBARS values at 7 d of simulated retail display of 3.8 and 0.6 mg malonaldehyde equivalents/kg meat, respectively (Richardson et al., 2004). Colour shelf life of the meat from silage fed animals was extended by 2 d. Hereford cross steers finished on pasture or a sorghum-based feedlot ratio \( n \), each with or without a 2500 IU/head/day supplementation of vitamin E had more vitamin E in their meat than those fed in the feedlot. Supplementation did not increase the vitamin E content of the grazed animals but brought that of the feedlot animals up to the level of the grass-fed animals and reduced the rate of fat and colour oxidation (Yang, Lanari, Brewster, & Tume, 2002). Interestingly, supplementation of the grass-fed animals with vitamin E reduced the content of \( \beta \)-carotene in plasma, liver, fat and muscle (Yang, Brewster, Lanari, & Tume, 2002). When animals were sampled throughout the year from an Irish abattoir, those overwintered indoors had better colour stability than those slaughtered from pasture. The vitamin E content of the muscle was not significantly different between slaughter periods, but overwintered animals had more vitamin E in their adipose tissue (Lynch et al., 2002). As the content of vitamin E in the muscle of many animals was less than the recommended 3.0–3.5 IU for optimum stability (Liu, Scheller, Arp, Schaefer, & Williams, 1996) then fatty acid composition may have been more critical. Meat from pasture finished animals had more PUFA than overwintered animals and would thus produce a greater oxidative stress in the meat. O’Sullivan et al. (2003) studied the effect of six diets varying from 100% forage through combinations of forage and concentrate allowances to a zero-forage with concentrates and straw ration. The high herbage diet produced the most lipid and colour stable meat and the high concentrate diet the least with other diets being intermediate. For production systems in Uruguay and Argentina, beef finished off grass had higher vitamin E concentration and better lipid stability than those finished on concentrates (Descalzo et al., 2000; Reulini, Duckett, Brito, Dalla Rizza, & De Mattos, 2004).

The type of forage in a silage-based diet can also affect lipid and colour stability. Charolais-cross heifers were fed \textit{ad libitum} on either maize silage, grass silage or a 50:50 mixture of these. Vitamin E concentration was 2.1, 3.8 and 3.0, respectively, and meat from the animals fed the maize silage had the worst lipid and colour stability, grass silage the best and the 50:50 mix being intermediate (O’Sullivan et al., 2002). Animals fed red clover silage, grass silage, or a 50:50 mix of the two, at 0.7 of intake, had an increasing content of PUFA in muscle with increasing red clover silage content but vitamin E concentration decreased and colour and lipid oxidative stability decreased. When a fourth group of animals were fed the red clover silage supplemented with vitamin E, vitamin E content of muscle, colour and lipid stability was the same as that in the muscle of 100% grass silage-fed animals (Fig. 3; Richardson, Costa, Nute, & Scollan, 2005).

When animals are fed a similar basal diet, but fatty acid composition is altered by the addition of different oils to the diet, lipid and colour stability can be expected to be more related to the fatty acid composition than the antioxidant concentration. Steers were fed linseed oil, fish oil or a...
linseed oil/fish oil mix at 30 g oil/kg diet and supplemented with vitamin E at 345 mg α-tocopherol-acetate/kg feed. The vitamin E concentration in the forequarter meat of animals receiving the fish oil was reduced 20% but at 5.7 mg/kg muscle was still well above that recommended for optimum stability, yet *longissimus* steaks and minced forequarter muscle were less oxidatively stable than the other treatments (Vatansever et al., 2000). Feeding a ruminally protected lipid supplement (PLS; see Table 3) rich in n-6 and n-3 PUFA increased the concentration of total lipid 18:2*n* - 6 from 120 to 305 mg/100 g and 18:3*n* - 3 from 29 to 139 mg/100 g, vitamin E was reduced 20% to 4.6 mg/kg and colour and lipid oxidative stability were reduced. This also significantly increased sensorial abnormal flavour and rancidity scores (Scollan, Enser, Richardson, Gulati, Hallett, Wood et al., 2004). Feeding protected fish oil (rich in DHA) (PFO) at three levels in combination with free fish oil (rich in EPA and DHA) increased EPA from 13 to 19 mg/100 g muscle and DHA from 3 to 12 mg/100 g total muscle lipid, did not affect vitamin E concentration at >5 mg/kg or colour stability, but increased TBARS at the highest level fed. It also produced some abnormal flavours but these were insufficient to affect overall acceptability (Richardson, Hallett et al., 2004). As the PLS contributed 295 mg extra PUFA and the PFO only 15 mg and whilst the instability of the meat was not as great for the PFO as PLS, nevertheless the extra double bonds in EPA and DHA made meat with elevated concentrations of these fatty acids more unstable. If ruminant meat is to be modified through dietary manipulation it will be necessary to define a strategy which protects these lipids from the pro-oxidative environment.

5. Conclusions

It is evident that nutritional value is an important dimension of beef quality and this is reflected with the efforts to improve the fatty acid composition of beef. Increasing the content of n-3 PUFA and CLA and reducing SFA with the net effect of increasing P:S and reducing n-6:n-3 ratio are important priorities. Nutrition is the major factor influencing fatty acid composition of beef whereas both nutrition and genetics affect the level of fat. Feeding grass and or concentrates-containing linseed or fish oil results in important beneficial responses in the content of n-3 PUFA, SFA and CLA in beef. Feeding the forage legume, red clover, results in further enhancements in PUFA content relative to grass feeding. Studies using ruminally protected lipids have revealed that muscle does have a high capacity to deposit n-3 PUFA but strategies to address the high degree of biohydrogenation of dietary PUFA in the rumen must be developed.

Knowledge of the relationships between the fatty acid composition of meat (and other chemical components such as amino acids and carbohydrates) and sensory attributes and colour shelf life is increasing. As the content of n-3 PUFA in the meat are increased, sensory attributes such as “grassy”, “greasy” and “fishy” score higher and colour shelf life may be reduced. Novel approaches (antioxidants) are required to protect n-3 PUFA from oxidation in muscle lipids (especially when higher levels of n-3 PUFA are achieved >3% n-3 PUFA).

The development of foods with functional properties is a major growth area and this is likely to continue as consumers demand more foods which offer scope in helping to promote health and prevent disease. In this respect, meat and meat products (including beef) have an important role to play. The meat industry has been the slowest section of the food industry to embrace the functional trend and incorporate functional ingredients into their products. However, this is changing as the industry seeks new opportunities to improve sustainability and improve competitiveness with other foods. However, as discussed by Verbeke (2006) consumers are unlikely to compromise on the taste of functional foods for health benefits and hence these foods must seek to deliver health benefits with neutral or positive impact on taste.

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