

Opportunities and Implications of Pasture-Based Lamb Fattening to Enhance the Long-Chain Fatty Acid Composition in Meat

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Abstract: Health-conscious consumers following dietary fat recommendations require meat that is low in saturated fat with preferably high levels of long-chain omega-3 fatty acids. This review summarizes the influence of dietary lipids from red meat on human health and examines the potential to enhance lipid composition through pasture-feeding. The role of fatty acids in plant and ruminant metabolism is discussed to highlight the complexity of ruminal digestion when trying to enhance fatty acids in meat. Generally, ruminants that consume pasture diets have been shown to produce a more desirable fatty acid composition than those fed grain and offer potential to be further enhanced by using specific plant species. Elevated polyunsaturated fat content in meat, however, tends to increase susceptibility to oxidation, which influences other meat quality characteristics including shelf-life and color. The use of specific plant species may mitigate these negative effects due to vitamin E or other antioxidants in these plants, which protect polyunsaturated fats from oxidation. When assessing the potential of plants as a natural dietary fat source, consideration must be given to environmental influences on plant fatty acid composition to ensure consistent production of meat products with high nutritive value under a range of management practices. This review also explores the potential impact of climate change on plant fatty acid composition, and the potential implications of this for meat quality.

Keywords: agriculture, antioxidant effect, diet, fatty acids, meat quality

Introduction

In the Western world, cardiovascular disease (CVD) is the main cause of mortality (Astrup and others 2011). The relationship between CVD and the quality of dietary fat intake has been established (WHO 2004; Scollan and others 2006) with further studies linking the incidence of developing colorectal cancer to red meat consumption (Corpet 2011). This has resulted in the development of dietary guidelines, which emphasize the need to reduce fat and specify recommended dietary fat intakes for each class of fatty acid (Table 1). Reports published by a panel of leading scientists on behalf of the World Cancer Research Fund and the American Inst. of Cancer Research (2007) further recommend ingesting no more than 500 g of red meat per week with limited processed meats.

Although public awareness has improved, the message regarding meat consumption is often misleading (Li and others 2005; McNeill 2014). Health professionals recommend moderate red meat consumption, because of its highly saturated fatty acid (SFA) content. This has had a negative impact on the red meat sector

with continual declines in red meat consumption over the past 3 decades (Li and others 2005; McNeill 2014) despite the known nutritional benefits of meat as it provides high-quality protein and important minerals including iron and zinc (Williams 2007). The perceived negative impact of red meat consumption has been derived largely from epidemiology studies, conducted in the 1980s, that correlated SFA intake indirectly with meat and CVD (Luciano 2009) and reports by the World Cancer Research Fund that link meat consumption with higher incidences of colorectal cancer (Oostindjer and others 2014). Oostindjer and others (2014) suggest there are too many confounding factors in previously reported meta-analyses, which found significant but weak incidences in epidemiological terms for the risk associated with developing colorectal cancer due to high meat consumption.

Considerable research has been conducted aimed at altering the fat composition and content of meat (Cooper and others 2004). However, it is important to note that fat dictates several sensory properties and is very important for the delivery of important nutrients such as Vitamins A, D, E, and carotenoids (Williams 2007). It is therefore in the producers' and consumers' interests to investigate to establish balanced views on dietary fat (Simopoulos 1999). Furthermore, it is important that these views take into consideration current and potential environmental changes that could impact the nutritional properties of pastures, and the impact that this could have on dietary fat composition and availability.

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Table 1—Dietary fat recommendations for healthy adults.

	% of Total caloric intake					Reference
	Total fat	SFA	Total PUFA	<i>n</i> -6 PUFA	<i>n</i> -3 PUFA	
World Health Organization	20 to 35	<10	6 to 11	2.5 to 9 LA	0.5 to 2 total >0.5 ALA	Elmadfa and Kornsteiner (2009)
U.S.	20 to 35	<10		5 to 10 LA	0.25 to 2 EPA+DHA 0.6 to 1.2 ALA	U.S. Dept. of Agriculture and U.S. Dept. of Health and Human Services (2010)
Britain	33	10	6 to 10	>1 LA	12	British Nutrition Foundation (2004)
Australia and New Zealand	33	10		8 to 13 g (1% to 4% LA)		Natl. Health and Medical Research Council (2006)

FA, fatty acid; LA, linoleic acid; SFA, saturated fatty acid; PUFA, polyunsaturated acid; MUFA, monounsaturated fatty acid; EPA, eicosapentaenoic acid; DHA, docosahexaenoic acid.

This review investigates the potential of red meat as a naturally produced, high-quality nutritional product and the relationship between fatty acid composition and the meat quality of grazing animals. Consideration will also be given to the physiological roles of fatty acids in plants and animals and the potential influence of environmental factors on plant fatty acid composition. The importance of other nutritional components obtained from plants and how these could influence consumer perception and meat quality is also discussed. For instance, some forage species enhance the antioxidant content in meat, which ameliorates the negative effects of oxidation on important meat quality characteristics (Warren and others 2008).

The Effects of Type of Dietary Fat on Human Health

Saturated fatty acids

Replacing 1% of dietary SFAs with polyunsaturated fatty acids (PUFAs) is thought to lower low-density lipoprotein (LDL) cholesterol by 2% or 3% (Astrup and others 2011) and has led nutritionists to recommend a minimum PUFA:SFA ratio of 0.4 (Wood and Enser 1997). Red meat is recognized to be a primary source of SFAs and typically has a PUFA:SFA ratio of around 0.1 (Geay and others 2001; Luciano 2009). However, not all SFAs negatively influence human cholesterol levels and research has demonstrated stearic acid (18:0) does not influence cholesterol levels (Hu and others 2001; Hunter and others 2010). This fact has been recognized by several regulatory authorities, including the U.S. Departments of Agriculture (USDA) and Human Health Services (HHS) (2010), which have defined cholesterol-raising fatty acids as SFAs from C12:0 to C16:0, including the *trans*-fatty acids except for those found in products from ruminants.

Meat produced from grass-fed ruminants was thought to contain more stearic acid than grain-fed animals (Duckett and others 2009, 2013; Daley and others 2010; Van Elswyk and McNeill 2014), but Ponnampalam and others (2014a) carried out a large study on 5726 lambs, involving 8 production sites, and found correlations between stearic and palmitic acid contents and feeding regimes. In particular, animals with feedlot or grain-based diets produced higher levels of stearic acid and palmitic acid than those with pasture-based diets with minimal amounts of grain.

Polyunsaturated fatty acids

Omega-6 (*n*-6) and omega-3 (*n*-3) fatty acids are metabolically diverse with different physiological functions (Simopoulos 2002). Omega-3 fatty acids are important for regulating immune responses (Simopoulos 2002), aiding brain and vision development

in fetuses, maintaining neural and visual tissues, and have recently been linked to reduced cancer, type-2 diabetes, and CVD (Benatti and others 2004). However, *n*-6 fatty acids, which account for most PUFAs in Western diets (Simopoulos 2002), are thought to have roles in the development of many diseases, including coronary heart disease, major depression, aging, and cancer, which are all distinguished by elevated levels of interleukin 1 (IL-1), levels of which can be increased by elevated levels of *n*-6 fatty acids (Simopoulos 2002, 2008).

Simultaneous increases in dietary *n*-3 and reductions in *n*-6 fatty acids lowers the *n*-6:*n*-3 ratio and has been shown to reduce CVD mortalities by up to 70% (Simopoulos 2008). Consequently, it has been suggested that the *n*-6:*n*-3 ratio should be below 4.0 in a healthy diet (Simopoulos 2004). Although α -linolenic acid is the most common *n*-3 fatty acid in food, and is mainly derived from higher plants, its longer-chain counterparts eicosapentaenoic acid (EPA, 20:5*n*-3) and docosahexaenoic acid (DHA, 22:6*n*-3), have been given much attention due to their biological potency and claims that they are beneficial to health (Simopoulos 2002). Fish is considered the main dietary source of EPA and DHA (Wolmarans and others 1999), but studies have also demonstrated that red meat is an alternative source of EPA and DHA (Ponnampalam and others 2014a, b). Although reports suggest that foods containing moderate levels of EPA and DHA are beneficial to human health, global standards associated with these claims vary. For example, the European standard requires a minimum of 40 mg/100 g cooked serving whereas Australia and New Zealand require at least 30 mg/100 g (Ponnampalam and others 2014b). In ruminants, docosapentaenoic acid (DPA, C22:5*n*-3) can also be present in high concentrations, yet DPA is not considered beneficial to human health, possibly due to the fact that DPA is produced from the elongation of EPA, or the retro-conversion of DHA (Knight and others 2003; Raes and others 2004).

Conjugated linoleic acid

Numerous studies have focused on the conjugated linoleic acids (CLAs) found in meat and their effects on human health. Rumenic acid (*cis*-9,*trans*-11 C18:2) is naturally abundant in the products of ruminants, such as milk, milk products, and meat, and is thought to represent about 75% of the CLA found in beef fat (McGuire and McGuire 2000). Daily intakes of CLA vary greatly, containing between 50 and 260 mg/d in the United States to between 350 and 420 mg/d in Germany, presumably due to differences in dietary fat consumption (McGuire and McGuire 2000). CLAs have

anticarcinogenic, antiatherogenic, antidiabetic, and antiadipogenic properties (Geay and others 2001; Khanal and Olson 2004; Meřuchová and others 2008). It has also been claimed that high levels of CLA supplementation enhances muscle growth, but there are limited data supporting this claim (McGuire and McGuire 2000).

Ruminant Fatty Acid Metabolism

The diets of most ruminants contain between 2% and 5% lipids, of which about half consist of fatty acids (Doreau and Ferlay 1994; Bauman and others 2003). However, biohydrogenation in the rumen reduces PUFAs to SFAs and monounsaturated fatty acids (MUFAs) (Doreau and Ferlay 1994). Biohydrogenation requires microbial lipases to hydrolyze ester linkages to free a carboxyl group so that isomerization and hydrogenation can occur (Sinclair 2007). For example, linoleic acid is 1st hydrolyzed to *cis*-9, *trans*-12 and then isomerized to rumenic acid (*cis*-9, *trans*-11 18:2 CLA). The *cis*-9 double bond is then preferentially reduced to form vaccenic acid (*trans*-11-18:1) (Demeyer and Doreau 1999). Vaccenic acid is then either subjected to ruminal hydrogenation to form stearic acid or endogenously desaturated via Δ 9-desaturase to reproduce CLA. Studies on CLA production have therefore focused on the production of CLA precursors and also the activity of Δ 9-desaturase (Raes and others 2004; Manso and others 2009).

The CLA content of meat varies greatly depending on an animal's diet, but usually ranges from 0.2% to 2% of tissue fat (Khanal and Olson 2004). French and others (2000) suggested grass diets could favor the growth and activity of the bacteria *Butyrivibrio fibrisolvens*, which aids protein breakdown, fiber and hemicellulose degradation, and biohydrogenation, which subsequently influences the production of CLA. Shifts in bacterial populations may favor the production of CLA (Cabiddu and others 2009).

Several methods have been developed to improve *n*-3 and *n*-6 fatty acid uptake that rely on protecting lipids from biohydrogenation in the rumen (Wood and others 2008). These methods have been successful to varying degrees and have included reducing the nitrogen content of the diet, reducing feed particle size, feeding with more mature forages, and using calcium salts (Seabrook and others 2011). However, the most successful method involved encapsulating PUFAs in formaldehyde-treated protein (Scott and others 1971; Cook and others 1972; Dewhurst and others 2003c). Scott and others (1971) discovered a significant increase in PUFAs in adipose, plasma, and milk triglycerides (TAGs), from 2% to 5% to 20% to 30%, when animals were fed megalac. This protected lipid supplement contains high levels of palmitic acid, and consumption resulted in a large improvement in the PUFA:SFA ratio (Scollan and others 2001, 2003).

Stearic acid is the most common fatty acid entering the duodenum and is absorbed in the jejunum region of the small intestine. Before absorption can occur, lipids must be adsorbed onto particulate matter in order to be solubilized in the aqueous environment, which requires micelle formation. Fatty acids are re-esterified into TAG and phospholipids in the epithelial cells of the small intestine and are transported by the lymphatic system into the circulatory system as chylomicrons and very-low-density-lipoproteins (VLDL) (Doreau and Ferlay 1994; Demeyer and Doreau 1999). Medium- and long-chain fatty acids are minimally absorbed or modified in the omasum or abomasum, which means the composition of lipids remain similar to that leaving the rumen. The lipid medium consists of 80% to 90% free fatty acids (FFAs) that

are adsorbed on to feed particles, which is markedly different to nonruminants where 90% of fatty acids are esterified. The remaining fatty acids include microbial phospholipids, a small proportion of TAGs, and glycolipids that exist in residual feed and are later hydrolyzed by pancreatic and intestinal lipases (Lock and others 2006).

Adipose tissue is comprised of approximately 90% neutral lipids, with the majority TAG (Wood and others 2008). The TAG content of sheep meat varies from 10 to 300 g/kg of tissue but rarely exceeds 50 g/kg in intramuscular fat (IMF), in the United Kingdom (Wood and Enser 1997). This may be due to IMF deposition being much slower than fat deposition in subcutaneous tissue, during the finishing period (Demeyer and Doreau 1999). Although phospholipids comprise a lesser proportion of adipose tissue than TAGs, they tend to reflect changes in diet more rapidly than TAGs (Aurousseau and others 2007a) and due to their regulatory role in maintaining cell stability (Faria and others 2012) the tissue composition is less variable, ranging from 5 to 10 g/kg of muscle (Wood and Enser 1997). Long-chain *n*-3 fatty acids, including EPA and DHA, are restricted to membranous phospholipids and are therefore almost exclusively limited to muscle tissue (Wood and others 1999), but physiological differences in muscle fiber characteristics also mean fatty acid composition varies with different muscle fiber types (Wood and others 2003). For example, type 1 (red, slow twitch) muscle fibers have a greater proportion of phospholipids, and thus contain higher proportions of PUFAs, than type II (white, fast twitch) muscle fibers (Wood and others 2003).

When IMF levels are higher, the contribution of the TAGs increases, which consequently reduces the contribution of the PUFAs as a proportion of the total fatty acids (TFAs) content (Fisher and others 2000; Lourenço and others 2007a). Scollan and others (2003) suggested that there is a negative exponential correlation between the amount of IMF and the PUFA:SFA ratio, and as a positive relationship between oleic acid and IMF has been acknowledged (Itoh and others 1999; Lourenço and others 2007a; Faria and others 2012), it is likely that this is a contributing factor toward this. Oleic acid levels are thought to be determined by the activity of stearoyl-CoA desaturase, which aids in the conversion of myristic, palmitic, and stearic acids to oleic acid, but could also result from higher rates of *de novo* synthesis (Faria and others 2012). Genetic variation between breeds may be the primary cause for differences in TAG composition and may also explain why limited differences have been found across genders at similar adiposity (Bas and Morand-Fehr 2000; Arsenos and others 2006).

Lipids and Meat Quality

Although research has focused on producing more nutritious meat products, that meet nutritional recommendations, scientists have remained cautious regarding the effects of manipulation of lipid composition on meat quality. This cautious approach is important when considering the necessity of producing high-quality products to attract consumers and retain their confidence in the products.

Color, shelf-life, and oxidation

Lipid peroxidation is an undesirable process in meat that occurs continuously during storage and leads to the development of rancid odors and off-flavors. The rate and extent of lipid peroxidation is determined by the amount of vitamin E within the muscles (Ponnampalam and others 2014c) and increases with increasing unsaturated chain length (Scisłowski and others 2005; Li and Liu 2012). Linoleic acid, for instance, is oxidized 10 times

faster than oleic acid, and 20 to 30 times faster than linolenic acid (Li and Liu 2012). Oxidative potential constrains the strategies that can be used to improve the levels of PUFAs in meat, as an increase in oxidative potential could limit shelf-life and hence acceptability.

Although some studies have suggested that meat from pasture-fed animals is darker than that from animals fed concentrates (Priolo and others 2001; Sheath and others 2001; Realini and others 2004b; Ripoll and others 2008), others have shown no difference during the early postmortem period (O'Sullivan and others 2003; Lind and others 2009). This could be due to the fact that pasture-fed animals are thought to be more susceptible to preslaughter stress compared to concentrate-fed animals, because they are less accustomed to handling and confinement that results in lower glycogen stores at slaughter and thus higher ultimate pH values (Muir and others 1998; Muchenje and others 2009). However, this effect can be alleviated when grass-fed lambs from mountainous regions are grazed on lowland for 2 to 3 d prior to transport for slaughter (Lind and others 2009). Also, differences in color attributed to higher ultimate pH for pasture-fed animals have not always been found to be true (Varela and others 2004; Faria and others 2012). An alternative suggestion for why pasture-fed meat is darker, is that pasture-fed animals are more physically active resulting in a higher myoglobin content, which is associated with a darker color (Muchenje and others 2009).

When displayed for retail sale, most consumers select meat based on color, with preference for the bright red "bloom" color that is produced from the initial oxidation of myoglobin to oxymyoglobin. However, further oxidation produces metmyoglobin, as the loss of an electron converts heme iron from ferrous to ferric state, that results in an undesirable brownish color (Geay and others 2001; Li and Liu 2012). Since the conversion of oxymyoglobin to metmyoglobin is reliant on electron transfer, the oxidation potential due to the level of fatty acid unsaturation can greatly influence color stability (Min and Ahn 2005). Color was initially thought to be determined by the total amount of *n*-3 fatty acids, because the negative characteristics associated with lipid and myoglobin oxidation are only seen once α -linolenic acid approaches 3% of total lipid content (Wood and others 1999, 2003). However, further studies have suggested that the level of *n*-3 fatty acids has a more important indirect relationship with heme iron and α -tocopherol (Ponnampalam and others 2012b). Manipulation of α -tocopherol levels in muscle tissues, via controlling diet, has shown a stronger relationship between α -tocopherol levels and lipid peroxidation than the level of heme iron or PUFAs present in the meat. However, to process is complex and the influence of PUFAs or heme iron on lipid peroxidation can vary (Ponnampalam and others 2014c). As human diets require high levels of PUFAs and iron and in combination these may affect meat color and color stability (Li and Liu 2012; Bekhit and others 2013), there may be an opportunity to overcome problems associated with high PUFAs and iron contents by ensuring high levels of α -tocopherol are present in muscle tissues prior to slaughter.

The generic term "vitamin E" includes the most common, α -tocopherol, which is present as 8 different isomers and is most commonly referred to when discussing meat antioxidants (Röhrle and others 2011). Recent studies suggest vitamin E can prevent lipid oxidation when there are high levels of PUFA, provided it is present above 2.95 mg/kg of muscle (Hopkins and others 2013; Ponnampalam and others 2014c). An increased antioxidant capacity within cell membranes can be achieved by feeding animals a diet rich in vitamin E (Gobert and others 2010). Vita-

min E is known to accumulate in tissues over time (Lee and others 2007a) and remains in tissues postmortem (Litta and others 2013). Increased vitamin E levels in pastures have been shown to reduce lipid peroxidation in meat from pasture-fed animals that typically have high PUFA contents (Descalzo and others 2007; Warren and others 2008; Lee and others 2009; Ponnampalam and others 2010). However, while cattle fed on pastures have been suggested to consume up to 3 g of vitamin E per day (Sheath and others 2001), the dietary intake of vitamin E from plants is dependent on the plant species being grazed. Leguminous species are thought to have reduced vitamin E contents compared to grasses (Tramontano and others 1993; Lee and others 2009), which can be evident when measuring meat color stability and shelf-life. Lee and others (2009) found beef from cows that were fed red clover silage produced a higher PUFA:SFA ratio and lower *n*6:*n*3 ratio compared to those fed a grass silage diet, but color declined more rapidly and was correlated with higher thiobarbituric acid-reactive substances (TBARS) levels (6 mg/g) and lower levels of vitamin E (2 mg/g) (Lee and others 2009). Fraser and others (2004) observed a similar trend when they compared meat from lambs grazed on *Trifolium pratense* (red clover), *Medicago sativa* (alfalfa), or *Lolium perenne* (perennial ryegrass). Lambs grazed on alfalfa produced TBARS 6 mg/g higher than those grazed on perennial ryegrass, but the only significant differences in color were observed at day 13 and were attributed to a higher color saturation score for the red clover compared to alfalfa.

Consumers are currently interested in naturally sourced antioxidants from plants because there is concern about the toxicity of synthetic antioxidants (Bekhit and others 2003, 2004; Gobert and others 2010). Synthetic antioxidants and natural extracts with high antioxidant capacities have been used as dietary supplements for animal to improve vitamin E contents. Recent studies investigating the relationship between polyphenols and antioxidant status have found that polyphenols reduce vitamin E breakdown (Gobert and others 2010), with 14% more vitamin E in muscle tissues from animals that were fed a high polyphenol diet. Vitamin E preservation was thought to arise from the antioxidant capacity of polyphenols that reduced the levels of reactive oxygen species (ROS), thus sparing vitamin E (Gobert and others 2010). There lies an opportunity to improve meat quality by feeding forages rich in natural antioxidants, which are known to stabilize fatty acids to make meat more desirable (Turner and others 2002; O'Sullivan and others 2003; Pearce and others 2005; Scollan and others 2006; Ponnampalam and others 2014c). However, not all authors have found elevated Vitamin E in meat when animals grazed on plants that are typically high in Vitamin E (Mercier and others 2004; Gatellier and others 2005; Petron and others 2007) and further work is needed in this area.

Vitamin E also has a synergistic relationship with ascorbic acid (vitamin C), but ascorbic acid levels are not always quantified in studies on meat. Ascorbic acid is able to scavenge ROS directly, but because it is not lipid soluble relative isolation from lipophilic radicals means that ascorbic acid functions indirectly by reducing, and thus regenerating the oxidized form of vitamin E, known as tocopheroxyl. The presence of ascorbic acid in the cytosol in close proximity cell membranes may assist with vitamin E recycling and help reduce membrane lipid oxidation (Descalzo and Sancho 2008). It is also important to note that the formation of ascorbyl radicals, which have powerful metal reducing capabilities, during some reactions can increase lipid and protein oxidation (Descalzo and Sancho 2008). Realini and others (2004a) found that color stability was improved in ground beef that was treated with ascorbic

acid postmortem, regardless of grass or grain-feeding treatment, but lipid oxidation was only improved in meat from animals that were grain-fed.

Meat texture and succulence

IMF positively influences meat quality through its effect on characteristics such as flavor, juiciness, and tenderness. Sheep meat requires at least a 5% IMF to achieve adequate consumer satisfaction (Hocquette and others 2010). Fatty acid types are strong determinants of fat softness (Banskalieva and others 2000), with high levels of linolenic acid in combination with low levels of stearic acid tending to produce a softer fat (Wood and Enser 1997; Sheath and others 2001; Smith and others 2009). Oleic acid is also associated with softer fat, but is linked to other palatability aspects of meat such as flavor (Smith and others 2009). Unsaturated fatty acids and fatty acids with *cis*-isomers tend to have lower melting points than the more highly saturated fats or those containing *trans*-isomers and similarly branched chain fatty acids have lower melting points than those with straight chains of the same carbon number (Wood and others 2003). Texture characteristics associated with fat softness and melting points for TAGs are also determined by the structure of the fatty acids involved, and also their position on the glycerol molecule (Gandemer 2002).

Vitamin E may also positively influence juiciness by reducing drip loss (Wood and Enser 1997; Geay and others 2001), as it is required to stabilize cell integrity, which in turn improves retention of cytoplasmic fluid (Pearce and others 2005). When lambs grazed on saltbush, which is naturally high in Vitamin E, drip and cooking losses remained the same, even though the lamb meat was found to be juicier by a sensory panel (Pearce and others 2005).

Flavor

Sensory preferences for flavor significantly vary across the world depending on what flavors the consumer is accustomed to. However, although consumer perception varies depending on experience, there are some trends that occur irrespective of cultural differences, such as oleic acid content, which has been reported to score well for flavor (Varela and others 2004; Woodfield and Easton 2004). Alternatively, meat with a high PUFA content produces unpleasant odors and flavors associated with oxidation (Wood and Enser 1997; Scollan and others 2006). Since there are large differences in the acceptability of meat from grain-fed and grass-fed animals, this area is very subjective to assess and will vary significantly depending on other characteristics including the presence of IMF and subcutaneous fat. Although research on lamb suggests IMF should be at least 4% to 5% to produce acceptable flavor characteristics, results from 3 y of Australian progeny tests found the average to be only 4%. These findings suggest that genetic selection for lean growth has reduced IMF deposition and may detrimentally affect eating quality (Pannier and others 2014).

When meat has a high myoglobin content in combination with elevated PUFA, without enough antioxidant capacity to protect against oxidation, meat is more susceptible to lipid peroxidation. Strong livery flavors were found for lambs that grazed on native mountainous pastures due to a combination of factors that were thought to contribute to lipid peroxidation, including minimal adipose tissue, elevated PUFA and a high myoglobin content (Fisher and others 2000). Similarly, lambs fed algae also produced high scores for rancid and abnormal flavors (Elmore and others 2005). However, since unacceptable flavors and odors are generally associated with high levels of oxidation, it seems these prod-

ucts could be improved by ensuring sufficient antioxidants, such as vitamin E, are present in the muscle. Ponnampalam and others (2014c) demonstrated that the level of lipid oxidation could be kept below 2.4 mg malondialdehyde (MDA)/kg muscle for up to 4 wk of storage, provided the vitamin E concentration was above 3.45 mg/kg muscle.

Regardless of the subjective nature of flavor scoring, there are quantitative measures of oxidation that can be used to indicate off-flavors. These include measuring levels of TBARS, in which off-flavors and rancidity can be detected by sensory panelists at levels of 0.5 mg MDA/kg of lean muscle (Berruga and others 2005). However, Greene and Cumuze (1982) found that detection of MDA by untrained panelists varied from 0.2 to 2 mg MDA/kg and did not necessarily relate to flavor acceptability. Campo and others (2006) found sigmoidal relationships between TBARS, rancidity, and beef flavors, and further determined a saturation or adaptation point of approximately 2, beyond which higher levels of oxidation could not be perceived. Other measures of rancidity include chemical assays of volatile compounds, although these compare 1 product to another when there could be a number of contributing factors to the rancid flavor (Campo and others 2006). Calkins and Hodgen (2007) carried out assays for the hexanal that was released from heating and subsequent oxidation of linoleic acid. They found increasing hexanal was associated with proportionate increases in TBARS and proportionate decreases in flavor acceptability (Calkins and Hodgen 2007).

Supplementary Sources of Dietary PUFAs Lipid supplementation

In many parts of the world, the nutritional quality of meat has been improved by the addition of supplementary oils or specific mixed ration diets that are fed to animals raised indoors or under feedlot conditions. By studying a range of lipid supplements, researchers have learned that dietary inclusion of fatty acids beyond 60 g/kgDM (consumed) impairs rumen function (Scollan and others 2006). However, numerous studies show that levels of *n-3* fatty acids can be improved in muscle and adipose tissues by lipid supplementation, although often the PUFA:SFA ratio is only marginally affected (Ponnampalam and others 2001; Wachira and others 2002; Demirel and others 2004; Webb and O'Neill 2008). The use of lipid supplements, including rapeseed, soybean, linseed, and fish oils have produced variable results due to differences in rumen biohydrogenation. Often addition of these oils into the diet increases the quantity of oleic, linoleic, and linolenic acids, and very-long-chain PUFAs, including DHA and EPA, that are renowned for their anticarcinogenic activities (Dewhurst and others 2003c; Raes and others 2004).

Fats, oils, and oilseeds vary greatly in their fatty acid compositions and thus have varying effects on the fatty acid profiles of meat (Khanal and Olson 2004). Rapeseed and soybean contain approximately 11% and 7% linolenic acid, respectively and also contain large proportions of linoleic acid, which unfavorably raises the *n-6:n-3* ratio (Raes and others 2004). Linseed oil is more commonly used because it contains approximately 53% linolenic acid (Raes and others 2004). When Elmore and others (2005) compared oil supplements, they found unprotected linseed oil contained the highest PUFA:SFA and lowest *n-6:n-3* ratios compared to other oils, but incorporation into the *longissimus dorsi* muscle of lamb was poorest. This was primarily due to the level of biohydrogenation that occurred in the rumen, which reduced the amount of PUFAs available for incorporation into other tissues. In comparison, protected lipid supplements (PLS) in the form of

linseed oil encapsulated in a formaldehyde-treated protein resulted in much higher levels of PUFA in muscles, due to protection from biohydrogenation (Elmore and others 2005; Scollan and others 2007).

When determining the influence of dietary lipids on muscle fatty acid profiles, most studies found no effect on animal performance (Nürnberg and others 1998; Scollan and others 2001, 2007; Cooper and others 2004; Demirel and others 2004; Noci and others 2007). Cosgrove and others (2004) reported no improvement in growth rates, but found feed efficiency improved by 33% (determined as carcass gain/kgDM intake) for lambs supplemented with linseed oil or sunflower oil, compared with a control grass diet. In contrast, studies using fish oil decreased dietary intake and consequently also detrimentally affected lamb performance (Wachira and others 2002; Chow and others 2004). Bacterial suppression could explain why elevated levels of biohydrogenation intermediates were found, as fish oil did not directly affect lipolysis or apparent biohydrogenation (Chow and others 2004). This may be an inverse relationship, where increases in the proportion of fish oil within the rumen disrupts the biohydrogenation process, particularly for long-chain fatty acids, EPA, and DHA (Dewhurst and others 2003c; Chow and others 2004).

Supplementation with algae

Algal supplementation has considerable potential as a means to improve fatty acid composition as it elevates DHA in ruminant products, which positively influences the $n-6:n-3$ ratio (Elmore and others 2005; Givens and others 2006) and appears to meet global health recommendations (Boeckaert and others 2007; Petrie and others 2010; Cox and others 2011). PUFAs derived from algal consumption are better incorporated into muscle and adipose tissues than fish oil (Cooper and others 2004), due to reduced biohydrogenation in the rumen that is thought to arise from either bacteria or enzyme inhibition (Vlaeminck and others 2008). Just 20 g of algae per day for 8 wk elevated $n-3$ fatty acid levels in lamb meat by 240%. Consequently, a 135 g serve of algal-supplemented lamb would provide 129 mg of long-chain $n-3$ fatty acids including EPA, DHA, and DPA (Ponnampalam 2012). Other studies have shown that high levels of long-chain $n-3$ fatty acids from algal supplementation could benefit other aspects of production, for example, fewer lamb mortalities due to increased transfer of immunoglobulins from colostrum thus increasing immunity (Keithly and others 2011). It has also been suggested that long-chain $n-3$ fatty acids may improve reproductive performance, as EPA and arachidonic acid (AA) are precursors of eicosanoids such as prostaglandin (Gulliver and others 2012).

The use of supplements has been thoroughly researched for many decades and has played a crucial role in understanding rumen function, particularly biohydrogenation. Formaldehyde treatments have been a useful tool to enhance $n-3$ fatty acid composition for the feedlot market, but they could largely be superseded by novel supplements, such as algae, in the future. Researchers continue to investigate the importance of fatty acid profile for meat quality and other aspects of production, such as immune function and reproduction. However, it is important to acknowledge that supplements are not readily accessible by all livestock finishers, particularly those that raise animals outdoors on pasture. Numerous comparisons have been made between grass-fed and grain-fed ruminants, but fewer studies have focused on specific pasture comparisons and whether opportunities exist to enhance $n-3$ fatty acid contents to meet consumer requirements, under natural pasture-based systems.

Plants as a Dietary Source of PUFAs

Pastoral grazing systems

In the meat industry, production varies globally and is reliant on factors that influence the cost and efficiency of rearing an animal from birth to slaughter. With contrasting diets across continents and even within countries, it is vital that we understand the effects of management practices on the nutritional value, consistency and palatability of meats, and the environmental sustainability of production (McCartney and others 2008).

Feeding and finishing systems influence growth characteristics, carcass quality, and meat quality, including fatty acid composition. In some regions the accessibility and cost of feeding supplements is uneconomical (Cosgrove and others 2004; Kenyon and Webby 2007), but can be compensated for by the ability to grow high-quality forages (Kenyon and Webby 2007). Climate and topography tend to dictate plant selection, which may range from high-performing species on fertile developed land, or alternatively consist of native species that thrive on steep undeveloped hill country (Ådnøy and others 2005; Lind and others 2009).

When evaluating alternative methods to improve the nutritive value of meat, it is crucial that production characteristics such as growth and carcass yield are not compromised. Under ordinary grass-based systems, animals often grow slower than those fed concentrates (O'Sullivan and others 2003; Webb and O'Neill 2008; Winichayakul and others 2008). However, this can be improved by strategically using plant varieties that more appropriately meet seasonal nutrition requirements (Brown 1990). The use of high-value forages such as *Brassica rapa* (turnip), *Brassica napus* (rape), *Cichorium intybus* (chicory), red clover, *Trifolium repens* (white clover), *Lotus corniculatus* (birdsfoot trefoil), *Onobrychis viciifolia* (sainfoin), *Hedysarum coronarium* (sulla), *Plantago lanceolata* (plantain), and alfalfa can achieve high postweaning live-weight gains in lambs, often in excess of 250 g/d throughout summer and autumn (Fraser and others 2004; Golding and others 2011). Furthermore, legumes are of increasing interest for sustainable farming in terms of nitrogen utilization (Humphreys 2005; Høgh-Jensen and others 2006) and are particularly relevant for areas subject to leaching (Høgh-Jensen and others 2006).

Lambs grazing on legumes typically grow faster than grass-fed lambs, partially due to a more rapid rate of digestion, which allows for higher feed intakes (Fraser and Rowarth 1996; Fraser and others 2004; Speijers and others 2004). As legumes have a higher ratio of crude protein (CP) to water-soluble carbohydrates (WSC), dietary protein utilization is more efficient than for lambs grazing on grass (Fraser and others 2004; Merry and others 2006). Furthermore, some forage species contain condensed tannins (CTs), which reduce protein degradation in the rumen, resulting in enhanced nitrogen utilization as more dietary proteins are absorbed in the intestinal tract of the host animal. Additionally, forages containing CTs have a direct anthelmintic effect that has reduced worm burdens in lambs grazing on plantain and chicory (Woodfield and Easton 2004).

The high nutritional value of legumes also impacts on other aspects of production including ewe lactation and lamb survival. Ewes were found to produce 25% more milk when grazing on legumes compared to grass, which consequently improved lamb weaning weights (Kenyon and others 2010; Hutton and others 2011) and is associated with improved triplet survival (Keithly and others 2011). Interestingly, lamb survivability is related to PUFA content as thermogenesis, which uses brown adipose tissue (BAT) as an energy source, is mainly fueled by linoleic acid. Grazing ewes on forages high in linoleic acid, throughout the latter stage

of gestation and during early lactation, could influence the amount of BATs present in their lambs. This is thought to improve lamb survivability, because the transfer of linoleic acid from the ewe to its lamb via the placenta or milk could be used as an energy source within BATs. This could enable lambs to withstand harsher environmental conditions during the early stages of life due to the use of BATs during thermogenesis (Keithly and others 2011).

Nutritional quality of meat using grass or grain-feed

To achieve the recommended daily adult intake in New Zealand and Australia, red meat needs to contain 30 mg of EPA and DHA per 100 g cooked serving (or 135 g raw) (Ponnampalam and others 2014b). A trial conducted at Massey Univ., determined that grass-fed beef supplies approximately 2% of this, or 4% to 5% at maximum EPA and DHA levels. If 100% conversion of DPA is assumed, this increases to 7% to 11%. Knight and others (2003) suggested typical genetic selection and management practices would not improve the quantity of *n*-3 fatty acids that significantly contribute to the daily requirement (greater than 20%). Yet, a number of trials conducted in Australia, suggest this can be achieved when animals are grazed on high-quality pastures (Ponnampalam and others 2006).

Dietary source can influence the fatty acid profiles of animals more significantly than genotype (Bas and Morand-Fehr 2000; Garcia and others 2008). In general, the more concentrate in the diet, the more SFAs that will be present in meat. This is especially evident during the later stages of growth when animals deposit more adipose tissue (Arsenos and others 2006). Pasture finishing produces higher quantities of *n*-3 fatty acids than concentrate-fed animals, which improves both the PUFA:SFA and *n*-6:*n*-3 ratios (Wood and Enser 1997; Gatellier and others 2005; Rochfort and others 2008). For example, Kasapidou and others (2012) found an *n*-6:*n*-3 ratio of 8.9 in the meat of concentrate-fed animals, compared to a more desirable 0.9 for grass silage-fed animals (Table 2).

Health recommendations suggest that PUFA:SFA ratios should be at least 0.4, which is a challenge to achieve in ruminants, even with forage-based diets. Some studies have achieved a more desirable PUFA:SFA ratio by increasing PUFAs levels, which consequently decreased SFAs as a proportion of TFAs (Mir and others 2002; Aurousseau and others 2004; Noci and others 2007). In contrast, other studies have reported minimal changes to the PUFA:SFA ratio when PUFAs were elevated, because SFA levels remained unchanged (Santos-Silva and others 2002; Realini and others 2004b).

CLA production has also been reported to rise with grass-finishing (Table 3), but this is not routinely measured and findings have been inconsistent (Knight and others 2003). Since CLA isomers differ in structure and function, these findings may not be directly comparable, and could depend on the isomer found.

Species and cultivar variances in fatty acid content

Although many studies have explored the influence of grass and clover on the PUFA contents of meat, alternative finishing species such as herbs and legumes (except clover) have been studied to a lesser extent. As herbage can be a cheap and sustainable source of fatty acids, there may be an opportunity to breed plants that have increased levels of desirable fatty acids. However, when doing this, it is important to note that the PUFA content is significantly reduced in muscle and adipose tissues, due to biohydrogenation in the rumen. However, intermediates of the biohydrogenation process also have useful properties for improving human health (Dhiman and others 2005; Dewhurst and others 2009).

Lipids make up 8% of leaf dry matter and 22% to 25% of chloroplasts on a dry matter basis. Most leaf tissues are composed of complex lipids such as phospholipids and glycolipids. Esterified lipids contribute two-thirds of total lipids and represent 5% of leaf dry matter. The esterified lipids in forages are approximately one-third simple lipids, half galactolipids, and the remaining portion is phospholipids (Boufaïed and others 2003). The building block of *n*-3 PUFAs, linolenic acid, is synthesized by *de novo* plants (Dewhurst and others 2003c) and contributes 55% to 66% of the TFA content of grasses (Elgersma and others 2003a). The combination of palmitic, linoleic, and α -linolenic acids contributes 75% to 93% of TFAs (Meřuchová and others 2008). Although these remain the predominant fatty acids in most forage plants, their concentrations vary between species. Dewhurst and others (2001) noted minor compositional differences between the fatty acids found in grasses such as *Festuca arundinacea* (fescue). However, in other plant species, such as chicory which has high TFA contents, the fatty acid compositions were highly variable. Boufaïed and others (2003) also found individual fatty acids varied greatly between cultivars, with some variation attributed to differences in maturity date.

Although forages are naturally high in linolenic acid, biohydrogenation means this is not necessarily reflected in muscle tissue. In addition, differences in fatty acid concentrations are more obvious in phospholipids than in TAGs, when comparing grass- and concentrate-fed lambs (Bas and Morand-Fehr 2000; Aurousseau and others 2004; Sinclair 2007). Aurousseau and others (2004) found lambs grazing on pasture had up to 3 times more linolenic acid than those fed concentrate, which was evident in the neutral lipids and even more so in the phospholipids. Relationships between fatty acid content in pastures and the rate of biohydrogenation are still being determined, so it is unknown whether improvements in the lipid compositions of plants would be replicated in muscle tissue.

Recent studies have investigated the influences of grazing animals on botanically diverse pastures on the fatty acid composition of meat (Sinclair 2007). "Botanically diverse" typically refers to mixed pastures of native origin and can include a range of grass, legume, and herb species. Differences in composition are especially apparent when animals graze on diverse pastures in mountainous areas, compared with those grazed in monoculture lowlands (Ådnøy and others 2005). Lourenço and others (2007a) found botanically diverse pastures accumulated more biohydrogenation intermediates in the rumen and an elevated PUFA content in the IMF. This suggests rumen biohydrogenation was partially inhibited and PUFAs were further desaturated and elongated. This could also have been due to the lower IMF levels that were found in the botanically diverse treatment group (Lourenço and others 2007a).

Compared to composite grass swards, mixed leguminous pastures produce significantly higher proportions of linoleic and α -linolenic acids in the abomasum and subcutaneous fats, but not in the rumen (Lourenço and others 2007a, b). This suggests that there may be greater duodenal flow of PUFAs, which agrees with other findings suggesting that reduced lipolysis occurs (Lourenço and others 2008). Lourenço and others (2008) found higher PUFA contents in IMF of lambs grazed on pastures that contained high quantities of white clover and alfalfa, compared to those on perennial ryegrass. Similarly, Ponnampalam and others (2012a) indicated that alfalfa has the potential to improve the linolenic acid and vitamin E contents in the muscles of lambs, compared to lambs fed senescent ryegrass pasture, or concentrate

Table 2—Comparison of the ratio of omega-6 to omega-3 (n6:n3) and the ratio of polyunsaturated fatty acids (PUFA) to saturated fatty acids (SFA) (PUFA:SFA) for pasture-fed and concentrate-fed animals.

Diet	Species	Muscle	n6:n3	n6:n3	PUFA:SFA	PUFA:SFA	Reference
			pasture	concentrate	pasture	concentrate	
Grass-fed lambs; grass-fed steers compared to barley/soybean/straw-fed bulls	Lambs	<i>Longissimus dorsi</i>	1.68	—	0.12	—	Enser and others (1998)
	Cattle		1.98	15.6	0.08	0.21	
Sulfolk x Mule finished on lowland grass compared to those on concentrate	Lambs	<i>Semimembranosus</i>	1.78	5.69	—	—	Fisher and others (2000)
Steers on alfalfa and tall fescue compared with steers on feedlot (corn, alfalfa hay, soybean)	Cattle	<i>Longissimus dorsi</i>	1.72	10.38	0.21	0.27	Garcia and others (2008)
Entirely concentrate diet supplemented with α -tocopherol acetate, compared to lambs fed grass silage supplemented with concentrate to provide varying levels of α -tocopherol	Lambs	<i>Semimembranosus</i>	0.9	8.9	—	—	Kasapidou and others (2012)
Grass (perennial ryegrass, white clover, and tall fescue) fed steers compared to concentrate (corn silage, wheat hulls, corn, Rumensin [®] + urea)	Cattle	<i>Longissimus</i>	1.44	3.00	0.20	0.13	Realini and others (2004b)
Feedlot diet (corn ear, corn grain, soybean, wheat + minerals) compared to lambs raised on <i>Cynodon dactylon</i> (Bermuda grass)	Lambs	<i>Longissimus dorsi</i>	—	—	0.10	0.10	Rowe and others (1999)
Merino Branco lambs either reared with dams on pasture <i>Lolium multiflorum</i> (Italian ryegrass) or weaned and fed concentrate (maize, soybean meal, and wheat straw)	Lambs	<i>Longissimus thoracis</i>	1.85	5.47	—	—	Santos-Silva and others (2002)
Perennial ryegrass + white clover diet compared to a maize silage + concentrate diet	Cattle	<i>Longissimus thoracis</i>	1.822	4.061	0.291	0.313	Varela and others (2004)

Table 3—Conjugated linoleic acid (CLA) concentrations for grass-fed and concentrate-fed ruminants as a proportion of total fatty acids (TFAs).

Diet	CLA (% TFAs)		Reference
	Grass	Concentrate	
Ile-de-France lambs of high growth rates grazing grass with their dam compared to those with their dam indoors, with high growth rates fed with on a concentrate diet (barley, wheat, sugar beet + soybean meal)	1.7	0.7	Aurousseau and others (2004)
Steers on alfalfa and tall fescue compared with steers on feedlot (corn, alfalfa hay, soybean)	0.72	0.31	Garcia and others (2008)
NZ grass-fed cattle compared to U.S. grain-fed cattle (at same age)	0.50	0.37	Purchas and others (2005)
Grass (perennial ryegrass, white clover, and tall fescue)-fed steers compared to concentrate (corn silage, wheat hulls, corn, Rumensin [®] + urea)	0.53	0.25	Realini and others (2004b)
Merino Branco lambs either reared with dams on pasture <i>Lolium multiflorum</i> (Italian ryegrass) or weaned and fed concentrate (maize, soybean meal, and wheat straw)	0.71	0.32	Santos-Silva and others (2002)

supplements during the finishing period. However, Dierking and others (2010) found no significant differences when steers grazed on leguminous species were compared to those grazed on tall fescue, tall fescue + red clover, or tall fescue + alfalfa. These conflicting findings were thought to occur due to a short feeding duration and lower percentage of clover in the sward (Dierking and others 2010).

There is considerable interest in red clover due to its ability to forgo rumen biohydrogenation, which increases the proportion of PUFAs in animal tissues (Dewhurst and others 2003a, 2003b; Lee and others 2003a, 2003b; Lourenço and others 2007b; Dierking and others 2010; Faria and others 2012). High consumption of red clover tends to inhibit lipolysis as a result of elevated activity of the enzyme polyphenol oxidase (PPO) in the rumen (Lee and others 2007b, 2009; Lourenço and others 2008). PPO converts phenols into quinones, which reduces proteolysis by binding to proteins (Faria and others 2012) and prevents lipolysis by forming complexes with polar lipids (Lee and others 2004).

Biohydrogenation may also be influenced by the presence of tannins or other secondary compounds and has led some researchers to investigate the influence of CTs on fatty acid profiles (Ponnampalam and others 2012a). Although CTs are present in a number of plant species, research has mainly focused on the supplementation of tannins in concentrate diets. High dietary concentrations of CTs reduce the activity of ruminal bacteria, which limits biohydrogenation (Vasta and others 2007, 2008, 2009a; Patra and Saxena 2011). Furthermore, *in vitro* studies have established high CTs levels can cause a reduction in *Butyrivibrio proteoclasticus*, a bacterium commonly found in the gastrointestinal systems of animals, which are known to convert vaccenic acid to stearic acid in the final step of biohydrogenation (Vasta and others 2010). However, if replicated *in vivo*, animal performance would be limited at such high CT levels, thus further work is required to measure the effects of CTs at levels below 4.5% dry matter (Vasta and others 2010). Studies have also evaluated the impact of CTs on CLA production, but this is difficult to measure because CLA can

be synthesized endogenously in muscle via Δ -9 desaturase (Vasta and others 2007, 2009b), the levels of which vary across muscle types (Poulson and others 2004).

Pastures such as red clover or others that contain CTs are of considerable interest for pasture-based finishing, as significant compositional differences can be created in meat and milk, by selecting specific plant species for animals to graze. However, further studies are required to evaluate the effectiveness of this approach in the field as many of the studies to date have been carried out *in vitro*, or with ensiled forage, and therefore little is known about the variability within a species, especially under different grazing conditions. It is also possible that there are other plant species that could have unique characteristics with the potential to influence biohydrogenation and the uptake of PUFAs.

When assessing the impacts of animal diet on fatty acid composition, time on the diet is also an important factor to consider. Studies suggest that the composition of fatty acids in lamb muscle will continue to change until about 42 d after the change in diet and not change markedly thereafter (Griswold and others 2003; Arousseau and others 2007a, b; Bessa and others 2008). With short feeding durations, the fatty acid profile of lamb still resembles that resulting from the pretreatment diet (Scerra and others 2011). While short feeding durations would be advantageous for some lamb finishing systems in terms of the costs associated with feeding, a sufficiently long duration is required for tissue deposition to occur and hence significant changes in muscle and adipose tissue fatty acid composition.

Livestock Feeding Strategies to Improve PUFA Content of Meat

The impact of pasture management on PUFAs

Fatty acid content not only varies among plant species, but is also affected by growth stage, nitrogen application, water status, and ensiling (Boufaïed and others 2003). It is widely recognized that some plant species do not undergo biohydrogenation in the rumen, which suggests that significant benefits could be made in meat fatty acid composition if these plant species were managed in a way that promoted higher levels of *n*-3 fatty acids.

As plant lipids are primarily derived from leaf tissue, fatty acid changes across a season can coincide with changes in the leaf-to-stem weight ratios, that can also correspond to fluctuations in the levels of cell wall, components such as cellulose, hemicellulose, and lignin (Clapham and others 2005). Individual fatty acid and TFA levels increase significantly during summer regrowth when compared to spring irrespective of yield (Elgersma and others 2003a), particularly for orchard grass, timothy (Boufaïed and others 2003), and ryegrass (Dewhurst and others 2001; Elgersma and others 2003a). Elgersma and others (2003a) demonstrated an increase in α -linolenic acid during grass regrowth in summer, but TFA levels were the same for both grasses and legumes. The same authors reported no increase in fatty acid levels during the autumn period, regardless of increased leaf area, which occurred irrespective of a constant temperature and light intensity.

Recent studies have suggested that fatty acid composition of plants also changes at different times of the day. The chemical composition of a pasture is known to change throughout the day as simple sugars accumulate due to photosynthesis, increasing the WSC:CP ratio. However, studies of changes in fatty acid and other aspects of chemical composition have given inconsistent results (Vasta and others 2012). Linolenic acid has been reported to increase in afternoon pasture samples (Avondo and others 2008; Vasta and others 2012) but others have reported no change

(Gregorini and others 2008). Since linolenic acid is involved in the regulation of membrane fluidity, variations could be attributed to environmental differences such as changes in temperature (Vasta and others 2012).

Vasta and others (2012) were the 1st to investigate the impact of grazing period on meat composition, while similar studies had already been carried out for dairy products. Vasta and others (2012) measured the fatty acid contents of plants and lambs subjected to 4-h morning, 4-h evening, or 8-h (all day) grazing treatments for 35 d, after a 20-d adaptation period. Pastures had 6% higher linoleic acid and linolenic acid during afternoon grazing, which corresponded to higher PUFAs and increased CLAs, at the cost of stearic acid, and subsequently lowered the levels of SFAs in the meat of lambs from this treatment. However, an increase in biohydrogenation intermediates at the expense of stearic acid was not found by Avondo and others (2008) and could not be explained by herbage composition alone. The combination of increased CLAs and reduced stearic acid have generally been produced when animals grazed forages that contained CTs (Vasta and others 2009a, b), but CTs were not present in the study detailed above. Regardless of these differences, lambs produced similar ratios of *n*6:*n*3 fatty acids, with values ranging from 3.01 to 3.21 and therefore meeting human dietary recommendations. These findings are especially relevant for the Mediterranean environment because outdoor grazing can be limited to afternoons, with desirable carcass weights and fatty acid profiles that have reduced SFAs, still achievable (Vasta and others 2012).

As a feed source, silages contain high levels of readily fermentable sugars and soluble fiber, compared to fresh forages, which produces an ideal environment for biohydrogenation (Warren and others 2008), thus resulting in reduced PUFA and elevated SFA levels (French and others 2000; Elgersma and others 2003b; Lee and others 2006). Elgersma and others (2003b) found 98% of the lipid content in fresh grass constituted esterified fatty acids, but when ensiled this was substantially reduced to a broad range between 27% and 73%. Ensiled forages typically have less TFAs (Dewhurst and others 2003a, b; Elgersma and others 2003b), fewer phospholipids, and elevated FFAs from lipolysis of lipid bilayers (Lee and others 2006). In plants this can occur naturally in response to stress and senescence (Lee and others 2006), which increases the oxidation of unsaturated fatty acids (van Ranst and others 2009). However, in red clover much more gradual decline in linolenic acid proportions occurs during wilting (van Ranst and others 2009). Therefore, using ensiled forages to improve fatty acid composition and CLAs in meat may not be as effective as using fresh sources, although it is unknown how much variation may be attributed to differences due to wilting of the timing of harvest. These factors largely impact on silage quality and would therefore also play a role in the preservation of fatty acids.

Harvest trials typically measure fatty acid composition of regrowth once plants have been cut to a specific height. Although this is applicable for many regions where forage is machine-harvested, it does not represent grazing situations (Mir and others 2006). Unlike practices of feed conservation, which are based on mechanical harvest determined by plant maturity, animal grazing is more continuous. It is recognized that fatty acid composition changes over time, thus it is important to evaluate these differences by replicating the grazing environment.

Since lipids in vegetative plants are mainly found in membranes, the ability to increase fatty acid content in plants is constrained by a lack of physical space. However, when developing seeds and pollen, plants preferentially synthesize and store TAGs, which may

provide an opportunity to enhance and alter fatty acid composition. In New Zealand, plant breeders are progressing toward elevated TAG biosynthesis in the leaves of forage plants to deliver protected PUFAs in the form of oil bodies. Encouraging results suggest a 40% increase in lipid accumulation for 1st-generation hemizygous plants (Winichayakul and others 2008).

Lipids and Climate Change Influence of environmental stressors on PUFAs

Plants provide an economical and sustainable renewable resource (Cox and others 2011). It has been well established that forage diets produce desirable effects on meat quality in terms of PUFA content and reduced *n-6:n-3* fatty acid ratio. Thus, there may be an opportunity to raise the total lipid contents of plants and further modify fatty acid profiles, and improve nutritional value (Cosgrove and others 2004). However, before beginning a plant breeding programme, we need to thoroughly understand the role of fatty acids in plants and how they impact animal productivity. The complex nature of fatty acid metabolism means environmental and genetic factors are likely to influence the responses of plants and ruminants.

Plants are frequently subjected to a range of stresses including, low or high temperatures, salt, drought, water logging, and insect attack. Even agricultural lands with high fertility and best management are likely to be affected by 1 or more of these stresses (Upchurch 2008). The impact of environmental stressors on crop productivity is significant for agriculture and can be financially burdensome. Sheep and beef farmers at present can not only suffer from diminishing returns as a result environmental fluctuations, but are also subject to pressure from local governmental with respect to sustainable farming practices, and hence are becoming more vulnerable to the impending effects of climate change. For these reasons, it is vital that research assesses the impact of environmental stress on crop performance and the consequent effects on meat quality.

Although plants are exposed to occasional elevated temperatures throughout their life cycles, increased temperatures in the future may limit agricultural crop production (Ahuja and others 2010). The stability of cellular membranes will be crucial for plants to maintain functionality with increasing temperatures. Impaired membrane function at high temperatures usually occurs when there is reduced strength of hydrogen bonds and electrostatic interactions between polar groups of proteins within the aqueous phase of the membrane. This modification of membrane composition often results in ion leakages that consequently inhibit processes including photosynthesis and respiration (Shanklin and Cahoon 1998). Excessive fluidity of membranes is correlated with loss of physiological function and, therefore, plants that have membrane lipids with higher SFAs tend to be less fluid at high temperatures and display improved heat tolerance (Falcone and others 2004).

The physical properties of membrane lipids also influence the activities of membrane bound proteins including H^+ -ATPases, carrier, and channel-forming proteins, which are crucial for the regulation and transport of ions and other solutes. In chilling-sensitive plants, for instance, there is a high percentage of SFAs in the lipid bilayers, that can result in solidification of membranes into a semi-crystalline state at temperatures above 0 °C. Since SFAs have no double bonds they solidify at higher temperatures than membrane bilayers composed of unsaturated fatty acids, which inhibits H^+ -ATPase activity, solute transport, energy transduction, and enzyme-dependent metabolism (Shanklin and

Cahoon 1998). Thus, plants with high proportions of PUFAs tend to have greater chilling tolerance, and during acclimatization to cooling will respond physiologically by increasing the activity of desaturase enzymes, which further increases their degree of unsaturation (Upchurch 2008).

Lambs are often fattened during warmer times of the year using pasture species that are better adapted to warmer, drier weather. This infers that SFAs would contribute more significantly to the membrane lipids of these plants compared to PUFAs, but it is unknown to what extent this might influence the fatty acid composition of lamb meat. In contrast, lambs that are finished during cooler months are grown on forages that are adapted to cool, and potentially wet environments, which could contribute to a higher PUFA content. To the best of our knowledge, no research has investigated the effects of seasonality on meat fatty acid composition, especially with an emphasis on the plant species being used. This would also be of interest when climatic conditions contrast those that are typically found at a particular time of year, which may not only affect pasture production, but also influence the nutritional value of the plants.

Literature supporting the positive impact of increasing CO_2 on plant performance is typically based on C_3 plants produced under conditions with optimal nutrient supply. Under conditions with limited nitrogen availability, these responses decline from a 14% improvement in dry matter yield to approximately a 4% improvement. Leguminous plants are the most responsive of pastoral species, with an improvement of 17% in yield for clover compared to 7% for ryegrass, when grown under high CO_2 for 3 y. This response is thought to further improve with pasture diversity because of the larger range of plant functional traits affecting carbon and nitrogen cycling. Increased CO_2 not only enhances dry matter production, but has shown promising results for root growth. Improved root characteristics enable plants to more efficiently obtain nutrients and water from the soil (Lee and others 2013).

Elevated CO_2 promotes photosynthesis by increasing the rate of carboxylation and inhibiting the oxygenation of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Elevated CO_2 is also thought to ameliorate water stress by reducing stomatal opening and hence reducing transpiration losses. Reduced stomatal conductance, associated with partial stomatal closure, is also associated with increased photosynthesis due to improved light interception. Such improvements in photosynthetic efficiencies are also likely to promote more effective nitrogen use (Lee and others 2013) that may alter forage characteristics such as fiber levels (Owensby and others 1996). Although this may reduce plant digestibility and slow passage rates (Owensby and others 1996), it has been predicted that the effects of 10 y of elevated atmospheric CO_2 may elevate long-chain fatty acids in plants by 20% to 100% (Wiesenberg and others 2008), which would positively impact on PUFA intake for grazing animals.

The potential impacts of multiple environmental stressors

Higher plants have diverse metabolic functions to overcome fluctuating environments, but many studies only expose plants to single stressors in controlled environments that do not represent field situations (Shao and others 2008). Although it is necessary to understand the effects of temperature, water-availability, and CO_2 on plant productivity, it is also imperative to understand the consequence of these in combination as interactions between stressors become complex. For example, high CO_2 concentrations were found to compensate the negative effects of drought for wheat. The high CO_2 environment facilitated improved drought

tolerance because osmoregulation was enhanced and drought avoidance was improved as a result of lower stomatal conductance, reduced transpiration, and enlargement of root structures (Lee and others 2013).

The overall effects of elevated temperature, adjusted rainfall, and elevated CO₂ have been predicted using a variety of models (Hopkins and Del Prado 2007; Lee and others 2013). Recent studies suggest New Zealand will see an increase in herbage production, but with much seasonal and regional variability. Tasmania, in southern Australia, will experience significant production increases associated earlier production during spring (Lee and others 2013). Hopkins and Del Prado (2007) described the practical implications and benefits of climate change for farm production systems in Europe. They summarized there may be increased use of legumes for livestock production that are likely to have higher WSC and lower nitrogen concentrations at any given dry matter yield, compared to the present day. More frequent water-logging could also be expected during wet periods, which will impede grazing and increase the risk of leaching, but this may be overcome by more efficient nitrogen utilization. Farm systems will need to adapt to changing climatic conditions and a number of aspects will need to be considered including plant species, feed conservation, irrigation, feed budgeting, and effluent storage and application (Hopkins and Del Prado 2007). Nevertheless, it is important to acknowledge there may be many detrimental effects on animals. For example, elevated temperatures may create problems with heat stress (Nardone and others 2010).

Climate change is predicted to benefit and challenge agriculture globally, primarily through its effects on plant productivity, which may positively influence fatty acid compositions in plants and, therefore, meat lipid composition. Selecting plant species with increased tolerance to drought, flooding, cold, and disease may be essential in the future (Humphreys 2005). Even under present-day conditions, research on climate change is of significant interest for plant breeders because it provides valuable information regarding the ability of plants to adapt to different environments. This is also important to consider when trying to strategically manage plants to promote changes in fatty acid composition of forages and meat. Until now, knowledge has been gathered on the regulation of plant metabolic pathways with a limited focus on practical implications. Understanding the practical implications is essential for agricultural production, especially when global industries are challenged with sustainable food security (Ahuja and others 2010).

Conclusions

Complex metabolic processes in the rumen constrain the ability to improve fatty acid content in meat products to meet recommendations for daily fat intake. Although an animal's diet significantly influences the composition of meat, most success has been achieved through encapsulation and protection against rumen biohydrogenation. However, in many areas this is not profitable and livestock are more economically finished on pasture. Pasture naturally enhances the proportion of long-chain fatty acids in meat and often enriches the meat with antioxidants, which is especially important for meat quality characteristics when there are high levels of PUFA. Red clover has been identified as a promising dietary source to elevate long-chain fatty acids in meat, as it does not undergo significant biohydrogenation in the rumen. However, studies on plants have demonstrated that fatty acid composition is largely determined by species, cultivar, climate, and management, which may or may not confound the effects seen in grazing animals. Therefore, it would be beneficial to assess whether there

are other plant species that have the potential to favorably alter the fatty acid composition of meat, and to determine whether the effects of environment and seasonality on plant fatty acid contents are replicated in meat.

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Author Contributions

Howes researched prior studies, interpreted the results, and drafted the manuscript. Bekhit, Burritt, and Campbell contributed material, provided feedback, and edited the manuscript.

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