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Review Article

Fat deposition and partitioning for meat production in cattle and sheep

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ABSTRACT

In markets for beef and sheep meat, an appropriate level of intramuscular fat (IMF) is highly desirable for meat-eating quality, but strategies to improve it usually lead to an undesirable excess in carcase fat, presenting a major challenge to livestock producers. To solve this problem, we need to understand the partitioning of fat among the major fat depots: IMF, subcutaneous fat (SCF) and visceral fat (VF). In most genotypes of cattle and sheep, the rate of accretion is lower for IMF than for SCF and VF, so genetic selection for a high level of IMF, or the use of an increased dietary energy supply to promote IMF deposition, will increase overall fatness and feed costs. On the other hand, feeding postnatal calves with excessive concentrates promotes IMF deposition, so a nutritional strategy is feasible. With genetic strategies, several problems arise: 1) positive genetic correlations between IMF, SCF and VF differ among genotypes in both cattle and sheep; 2) genotypes appear to have specific, characteristic rates of accretion of IMF during periods of growth and fattening; 3) most breeds of cattle and sheep naturally produce meat with relatively low levels of IMF, but IMF does vary substantially among individuals and breeds so progress is possible through accurate measurement of IMF. Therefore, an essential prerequisite for selection will be knowledge of the genetic correlations and fat accretion rates for each genotype. Currently, selection for IMF is based on existing technology that directly measures IMF in the progeny or siblings, or estimates IMF in live animals. New technology is needed to permit the simultaneous measurement of SCF and IMF in the field, thus opening up the possibility of accurate selection, particularly for fat partitioning in live animals. Specifically, there would be great value in detecting individuals with an IMF advantage at an early age so the generation interval could be shortened and genetic gain accelerated. Genetic gain would also be greatly aided if we could select for genes that control adipogenesis and lipogenesis and are also differentially expressed in the various depots.

1. Introduction

Consumers are increasingly demanding better eating quality in beef and sheep-meat. Among the primary attributes of meat-eating quality is intramuscular fat (IMF) because it is closely correlated with consumer preferences for juiciness, flavour and tenderness (Motoyama et al., 2016; Pethick et al., 2021). These preferences are driving producers to develop sheep and cattle with high levels of IMF, either by genetic selection or by manipulation of diet and nutrition. However, both strategies present problems: (1) genetic selection to improve one fat depot, such as IMF, will lead to simultaneous increases in other fat depots because of positive

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genetic correlations, as has been documented for most cattle and sheep genotypes; (2) feeding animals with high-energy density diets can increase deposition of IMF, but also accelerates deposition in the other fat depots. Both strategies can increase in overall fatness, resulting in reduction of carcass quality, as well as increases in feed costs.

This conflict is the focus of the present paper, in which we analyse the literature with a view to shedding light on ways to produce cattle and sheep that have favourable levels of IMF while avoiding overall fatness.

2. Total fat content in the body and feed utilization efficiency

During the growth, animals deposit minerals into bone tissues, and protein, fat and water into the other tissues. It has long been known that the protein and mineral content, as percentages of the body weight, are relatively constant during growth, or even over a lifetime, although protein content per unit of body weight does decline slightly as body weight increases (de Sousa Barcelos et al., 2020). By contrast, total fat content as a percentage of body weight increases with body weight and with maturity, while the percentage of water declines (Honig et al., 2022; Tedeschi, 2019). Therefore, the amounts of protein and fat deposited per unit of weight gain will show the same trends: protein content declines slightly while fat content increases with overall weight.

Adipose tissue in sheep and cattle contains 39.3 kJ/g energy, much more than the 23.1 kJ/g attributable to fat-free organic matter (ARC, 1984). Thus, if weight gained contains a high percentage of fat, more dietary energy is required, leading to a high feed conversion rate (feed intake/body weight gain; kg/kg). For example, for an extra 1% of fat content per kilogram of body weight gain, 10 g fat containing 393 kJ energy is deposited. In fattening young sheep, the efficiency of utilization of dietary metabolizable energy (ME) for adipose synthesis ranges from 60% to 80%, and the theoretical value for the synthesis of triglyceride from acetate is 72% (Jones et al., 2004; Rattray et al., 1974). Using 72% as the efficiency of utilization, 545 kJ ME is required to deposit the 10 g fat, equivalent to 55 g of a diet that contains 10 MJ ME per kilogram dry matter (e.g., 50% barley grain and 50% lucerne hay; dry matter basis). In Dorper cross ewe lambs, Deng et al. (2014) showed that the total body fat percentage increased from 17.9% at 35 kg liveweight to 22.9% at 50 kg liveweight, and the deposition of this extra 5% fat per kilogram of liveweight required extra 275 g of feed, leading to a markedly poorer feed conversion rate. In cattle, the efficiency of utilization for fat deposition was estimated to vary between 54% and 69% (Geay, 1984; Owens et al., 1995), so depositing an extra 1% body fat demands extra 570 to 727 MJ ME, equivalent to an extra 57 to 73 g of a diet that contains 10 MJ ME per kilogram dry matter.

Table 1 summarizes the change of total percentage fat in the whole body or carcass for sheep and cattle from the literature. Clearly, the percentage body fat is highly correlated with body weight. Based on the published data for mean body weight or carcass weight and the corresponding total fat weight, we calculated the regression and correlation coefficients presented in Table 1. The regression coefficient indicates the change in total fat percentage per kilogram gain in body weight (or carcass weight), and the correlation coefficient indicates the fit in the linear relationship between total fat percentage and body or carcass weight.

The regression coefficients range from 0.29 to 0.73 (% fat/kg) with the average of 0.52 for sheep, indicating that, with every kilogram increase in body weight, the total fat increases by 0.52%. For cattle, the regression coefficients range from 0.026 to 0.064 (%/kg), with the average of 0.05 (%/kg), so total fat increases by 0.05% with every kilogram increase of body weight. Clearly, the change in the total fat percentage per unit gain in body weight (kg) is 10-fold greater in sheep than in cattle. Thus, compared to cattle, sheep show a greatly accelerated fat deposition rate with increase in body weight, and a more marked increase in feed conversion rate with heavier body weight.

The functions of lipids in the body depend on their chemical form and location. At the cellular level, the most important function is the formation of membranes in cells and organelles, and the storage of energy, mainly as triglyceride droplets (Beltz and Allen, 1984). Beyond the cellular level, lipids are found mainly in adipose tissue (fat) where they serve as energy storage and as thermal insulation for the body. When energy intake does not meet the energy demand, body fat reserves can be mobilized to cover the deficit.

Table 1
Linear regression analysis of relationships between the total fat percentage and body weight (BWt, kg) or carcass weight (kg) in sheep and cattle.

Animals	Linear regression coefficient, %/kg	Correlation coefficient	Source
Sheep			
Clun, Colbred, Suffolk, Hampshire (14 to 21 kg carcass weight)	0.726	0.97	Wood et al. (1980)
Clun (birth to 415 d old)	0.709	0.96	Butler-Hogg (1984)
Southdown (birth to 415 d old)	0.527	0.99	
Merino (15 to 45 kg empty BWt)	0.625	0.994	ARC (1984)
Non-Merino (15 to 45 kg empty BWt)	0.428 to 0.564	0.994	
German Merino (18 to 55 kg BWt, males)	0.288	0.999	Bellof and Pallauf (2004)
German Merino (18 to 55 kg BWt, females)	0.471	0.999	
Merino (20 to 40 kg carcass)	0.490	0.83	Ponnampalam et al. (2008)
Border Leicester × Merino (20 to 40 kg carcass)	0.593	0.93	
Poll Dorset × Merino (20 to 40 kg carcass)	0.608	0.93	
Poll Dorset × Border Leicester Merino (20 to 40 kg carcass)	0.527	0.93	
Merino, Merino × Poll Dorset, and Merino × Border Leicester (15 to 46 kg carcass weight)	0.658	0.95	McPhee et al. (2008)
Dorper × Thin-tail Han (28 to 45 kg empty BWt, female lambs)	0.428	0.999	Deng et al. (2014)
Cattle			
Charolais and Friesian (125 to 579 kg empty BWt)	0.026	0.975	Robelin (1981)
Castrated male (300 to 500 kg empty BWt)	0.048	0.999	ARC (1984)
Holstein steers (216 to 326 kg empty BWt)	0.064	0.977	Waldo et al. (1990)
Dairy (562 to 640 kg empty BWt)	0.058	0.640	Gibb et al. (1993)
Growing (300 to 500 kg empty BWt)	0.053	0.999	Tedeschi (2019)
Simmental bulls (87 to 752 kg empty BWt)	0.049	0.990	Honig et al. (2022)

Under natural conditions in many regions, grazing animals usually source energy from forages, but plant growth shows an annual cycle. To cope with that challenge, the animals evolved processes for depositing fat in seasons when forage availability exceeds requirements, and then mobilizing the fat so they can survive during, say, cold and dry seasons, when forage availability is inadequate to meet requirements. However, in modern farming systems, supplementary feeding has been adopted when forage availability is limited, so a capacity for fat deposition may not be essential for survival, allowing the processes that evolved to control fat deposition to be ignored so genetic pressure can be diverted towards meat quality and towards an increasingly important trait, efficiency of feed utilization. Low feed-efficiency sheep deposit more body fat than high feed-efficiency sheep at the same rate of gain of body weight (Zhang et al., 2021). Total body fat percentage can influence the price of sheep meat, and the lean weight and economic value of the carcass, but extra subcutaneous fat (SCF) can reduce the economic value of the carcase in the UK and New Zealand (Jones et al., 2004).

3. Fat partitioning

In research on animal nutrition and production, the term "fat" usually refers to either the lipid in tissue that is extractable by solvents (e.g., ether) or to adipose tissue that can be physically dissected after slaughter. For both approaches, the quantities of fat measured can vary with the procedures of sampling and analysis.

Total body fat includes adipose tissues and lipids in the abdominal cavity (visceral fat [VF]), thoracic cavity, below the skin (SCF), between the muscles (intermuscular fat [IntMF]), within muscle (IMF, adipocytes present between muscle fibres), and within muscle fibres or myocytes (intramyocellular fat [IntMCF], usually present as triglyceride droplets), in the bone marrow (Abdallah et al., 1982; Kempster, 1981; Kiefer et al., 2021), and in the tail of fat-tail sheep breeds (Shao et al., 2020). After sheep and cattle are slaughtered, VF, thoracic fat, and tail fat are trimmed off, leaving carcass fat, which includes SCF, IntMF, IMF and IntMCF. Fat in the bone morrow is not included. Thoracic fat accounts for a small fraction of total body fat (Afonso et al., 2019) and, in most cases, it is not reported. Neither IMF nor IntMCF can be dissected.

If lipids in a cut of meat are quantified accurately, using chemical extraction, or estimated using technologies such as computed tomography (CT) (Lambe et al., 2017) or near-infrared spectroscopy (Perry et al., 2001), the resulting value for fat content will include both IMF and IntMCF, and probably IntMF. This value is usually termed IMF by the meat industry. Research on IntMCF content in sheep and cattle is very rare because the research is complex and IntMCF is not directly related to marbling score. By contrast, in research on human health, IntMCF is currently very topical because it is linked to insulin resistance and the development of diabetes (Savage et al., 2019; Thamer et al., 2003). In the abdominal skeletal muscles of normal-weight humans (psoas major, quadratus lumborum, autochthonous back muscles, rectus abdominis), IntMCF accounts for 59% of the total muscle fat content whereas extramyocellular fat (ExtMCF) accounts for 41% (Kiefer et al., 2021). In obese humans, the total fat content increased to 13.4%, but the proportions of both IntMCF and ExtMCF did not change. In the soleus muscle, both IntMCF and ExtMCF were about 3-fold greater in obese adolescents than in lean adolescents (Sinha et al., 2002). For lamb and beef, there seems to be no data about IntMCF content or about its relationship with meat eating quality, although Pethick et al. (2004) suggested that IntMCF is unlikely to be a major component of the 12% to 30% of IMF (primarily as adipocytes) that is present in fattening cattle.

In the lamb and beef industries, in most regions, VF and tail fat add no economic value to the product but increase the cost of feed. A high level of SCF decreases the economic value of the carcass (Jones et al., 2004) and increases the cost of feed. By contrast, the importance of IMF for meat-eating quality, including juiciness, tenderness, flavour, and palatability, has long been clear (Park et al., 2018; Pethick et al., 2004) and an IMF level of 5% seems to be optimal (Hopkins et al., 2006). In China, the popular Tan sheep breed has 2.0% to 3.8% IMF in the longissimus dorsi (Wang et al., 2015), and many cattle breeds have usually <4% IMF (Huang et al., 2020).

The beef industry often uses a marbling score (or marbling grade) to indicate the level of IMF (Emerson et al., 2013; Stewart et al., 2021) and there is a strong linear correlation between the marbling score and measures of IMF percentage. For example, in the loin of 982 cattle carcasses (mean weight of 268 to 461 kg), chemical IMF varied from 2.3% to 13.4% while marbling score (Meat Standard Australia) varied correspondingly from 291 to 524 (Stewart et al., 2021). Similarly, the marbling degree in longissimus dorsi of Red Angus cattle was highly correlated to the corresponding IMF percentage which ranged from 2.19% to 35.24% (Emerson et al., 2013; McAllister et al., 2011).

Therefore, under farming conditions, feed supplementation strategies for sheep and cattle should be designed to ensure continuous body weight gain while reducing VF and SCF, and maintaining or even increasing IMF percentage. If this combination of outcomes can be achieved, there will be improvements in feed efficiency, the economic value of carcasses, meat quality. These feeding strategies can be accompanied by genetic selection that targets the same goals.

To develop such nutritional and genetic and strategies, we need to understand the dynamics of fat deposition in the different regions of the body during growth. The dynamic changes in a given body component can be best described using the allometric growth curve, $Y = aX^b$, where Y is the weight of a body component, such as protein or fat, and X is liveweight or empty body weight (ARC, 1984). The allometric growth efficient, b in this equation, indicates the growth rate of the component in relation to the body growth rate. A b value greater than 1.0 suggests that this component is growing at a greater rate than the whole body. Kempster (1981) used data for dissected fat content from slaughtered cattle and sheep in a number of studies and determined the allometric growth coefficients for the fat components: in cattle, the coefficients were 1.20 for SCF, 0.87 for IntMF, and 0.99 for perinephric and retroperitoneal fat (close to VF); in sheep, the coefficients were 1.81 for SCF, 0.79 for IntMF, and 1.17 for perinephric and retroperitoneal fat. It is therefore clear that, in both cattle and sheep, that the growth of SCF is faster, the growth of IntMF is slower, and the growth of VF is close to the rate of gain of body weight. Moreover, during the growth, the rate of deposition of IntMF is much lower than the rates of deposition of SCF and VS. With the deposition of IntMF being slower than the deposition rates of SCF and VF, the proportion of IntMF in total body fat (the sum of IntMF, SCF, and VF) will decline as body weight increases. A lower rate of accretion of IMF, compared to VF and SCF, was also observed in adult Serra da Estrela ewes that were being fattened to different body condition scores (Caldeira and Portugal, 2007), as well as in buffalo and Friesian-cross cattle (Abdallah et al., 1982). Indeed, in five genotypes of lambs, the ratio of IMF to the total body fat declined with age or body weight (they are closely related in growing animals, McPhee et al., 2008). However, for cattle, there are some data showing that the rate of accretion of IMF percentage in longissimus was the same as the accretion rate for total fat (SCF plus IMF) throughout a carcass range of 304 to 417 kg (Pethick et al., 2004), suggesting that IMF and SCF are deposited at the same rate as carcass weight increases, perhaps because of the relatively small range of the carcass weights, particularly at the lighter end. Given

the differences in rates of deposition of the various fat components, selection of animals for an overall low body fatness will lead to different outcomes for fat deposition in different parts of the carcass, and selection for fatness in one depot is unlikely to provide the same effect in other depots.

The slower accretion rate of IMF, compared to SCF and VF, infers that the initial or pre-fattening level is an important determinant of the final IMF percentage (Pethick et al., 2004). In young sheep and cattle, there are only small phenotypic differences between breeds in IMF percentage (Gotoh et al., 2009; McPhee et al., 2008). Subsequent expansion of IMF will depend on the rates of proliferation and hypertrophy of adipocytes, an aspect investigated by Duarte et al. (2013) who found that Wagyu had more preadipocytes and adipocytes in the sternomandibularis muscle than Angus cattle, explaining the faster rate of accretion IMF in the Wagyu genotype (Gotoh et al., 2009).

Dietary regimes for early growth in cattle also influence the IMF percentage when the animals are mature. Scheffler et al. (2014) studied Angus calves and compared those weaned at 105 d of age and then transitioned to a high-protein and high-energy diet ("metabolic imprinting"), with control calves that remained on their dams until 253 d of age. Both groups were then grazed under the same conditions until slaughter. In the carcasses of the steers, backfat thickness was not affected but the marbling score was increased by metabolic imprinting, suggesting that combining early weaning with a high concentrate diet before grazing is a viable strategy for increasing the deposition of IMF. This conclusion was confirmed in a study of early-weaned Augus × Simmental heifers (Wertz et al., 2001). These observations appear to be consistent with the studies of adipocytes mentioned above, and with diet-induced changes molecular processes in adipocytes that were explored in a study with Wagyu steers, comparing a 650 g/kg concentrate diet with a 90% concentrate diet during the entire fattening period. With the high-concentrate diet, there were increases in the expression of CCAAT/enhancer-binding protein (*C/EBP*) β and α, two adipogenic transcription factors in the C/EBP family, as well as peroxisome proliferator-activated receptor γ (*PPARγ*) in SCF and IMF adipocytes, and these effects were associated with an increase in IMF percentage from 23% to 32% (Yamada and Nakanishi, 2012).

However, the outcome is not consistent across all studies. For example, Greenwood et al. (2015) studied Angus, Hereford, and Wagyu × Angus genotypes. They observed a reduction in the depth of subcutaneous rib fat, but no effect on IMF, when they substituted forage grazing with a high-energy concentrate (50% of dietary energy requirements of weaned steers, average body weight of 212 kg) for 168 d, with both dietary groups following the same fattening regime until slaughter at 585 d. The inconsistent effects on IMF of post-weaning diets could be related to the proportion of concentrate in the diet and on the feeding regimes, particularly the duration.

4. Genetic variations in fat partition

The importance of genetics on fat partitioning and IMF has long been evident from the differences among genotypes. For example, four decades ago, Abdallah et al. (1982) determined the allometric regression coefficients for SCF, IntMF and VF (kidney and channel fat) and found lower values in buffalo than in Friesian crosses, for both IntMF (0.795 vs. 0.839 to 0.862) and VF (1.148 vs. 1.265 to 1.310). On the other hand, the coefficient for SCF was greater in buffalo (1.347) than in Friesian crosses (1.072 to 1.242). Clearly, as they grow, Friesian cross bulls deposited relatively more fat in the muscle, and less fat underneath the skin, than do buffalo. In Hereford bulls of liveweight 612 kg, the carcass contained 21.5 kg IntMF and had an SCF:IntMF ratio of 1.20:1, whereas, in double-muscled bulls of liveweight 532 kg, the carcass contained 13.7 kg IntMF and had an SCF:IntMF ratio of 0.72:1 (Shahin and Berg, 1985). Clearly, compared with the Hereford, the double-muscle breed had a lower level of body fat in general, and its SCF depot was proportionally much smaller than its IntMF depot.

The Wagyu genotype is well-known for its strongly marbled meat, with IMF in the longissimus muscle (6th to 8th rib position) reaching 30% or 40% (Motoyama et al., 2016). Gotoh et al. (2009) studied the longissimus in 24-month-old animals, and reported IMF values of 23.3% in Wagyu, 0.6% in double-muscled Belgian Blue, and 4.4% to 4.7% in German Angus and Holstein-Friesian. Interestingly, at age 6 to 8 months, IMF was less than 5% for all breeds, so the Wagyu has a much greater IMF accretion rate than the other genotypes; in fact, in the double-muscled breed, there was little change in IMF percentage during the growth (Gotoh et al., 2009). Albrecht et al. (2011) also studied IMF percentage in longissimus in steers and found 14% greater values in Wagyu than in Holstein, although, in Wagyu, the percentages of SCF and VF were much lower than the IMF percentage.

Within genotypes, there is also variation in fat partitioning among individual steers that have substantial differences in IMF percentage, as reported by Underwood et al. (2008) who studied Angus × Gelbvieh steers and compared animals with longissimus IMF 5.71% and IMF 2.09%. The high-IMF and low-IMF steers had similar levels of kidney, pelvic, and heart fat (5.09% vs. 5.05% of hot carcass weight), and similar back-fat thickness (1.52 mm vs. 1.03 mm). The ratio of IMF to kidney-pelvic-heart fat was 1.12:1 in high-IMF and 0.41:1 in low-IMF steers, and the ratio of IMF percentage to back-fat thickness (%/mm) was 3.75:1 in high-IMF and 2.03:1 in low-IMF steers. The low-IMF steers had much greater proportions of SCF and VF depots. This large variation among individuals within genotype provides a solid foundation for genetic selection.

In sheep, there seems to be little variation among genotypes. In a comparison of carcasses (14.7 to 21.4 kg) from Clun, Colbred, Suffolk, and Hampshire breeds, IntMF% only ranged from 17.2% to 17.6%, whereas SCF percentage varied greatly from 11% to 16% of carcass weight (Wood et al., 1980). The IMF percentage in longissimus lumborum from carcasses (12.7 to 46.1 kg) of Merino, Border Leicester × Merino, and Poll Dorset × Merino genotypes ranged from 3.8% to 4.8%, whereas carcass fat ranged from 15% to 38% (McPhee et al., 2008). In a massive study of 5867 lambs from a dozen of sheep breeds in Australia (Pannier et al., 2014), the average IMF in longissimus lumborum was 4.23% ± 0.01%. The authors of the present paper used the data in McPhee et al. (2008) for a regression analysis of mean carcass weight against IMF and carcass fat percentages, and found that, as carcass weight increased, IMF percentage increased only gradually (0.012%/kg; $R^2 = 0.14$) whereas carcass fat increased rapidly (0.66%/kg; $R^2 = 0.95$). Moreover, the variation in IMF percentage among breeds was much smaller than the variation in carcass fat percentage. As carcass fat is the sum of SCF and IMF, the results suggest the SCF depot accumulated substantially faster than the IMF depot as the sheep grew.

It seems that, for sheep, liveweight is the primary driver of SCF, followed by genotype, and that IMF is influenced little by body weight or genotype under the normal conditions. This situation seems to differ between sheep and cattle.

In conclusion, there is considerable variation among genotypes, in both IMF percentage and IMF accretion rate, during growth in both cattle and sheep (Fig. 1) and, within genotype, there is also considerable variation among individuals in IMF percentage. Fat partitioning and the process of maturation of each fat depot appear to be specific to genotype. Consequently, to improve the success of breeding, we need to understand the breed-specific characteristics of IMF accretion rate.

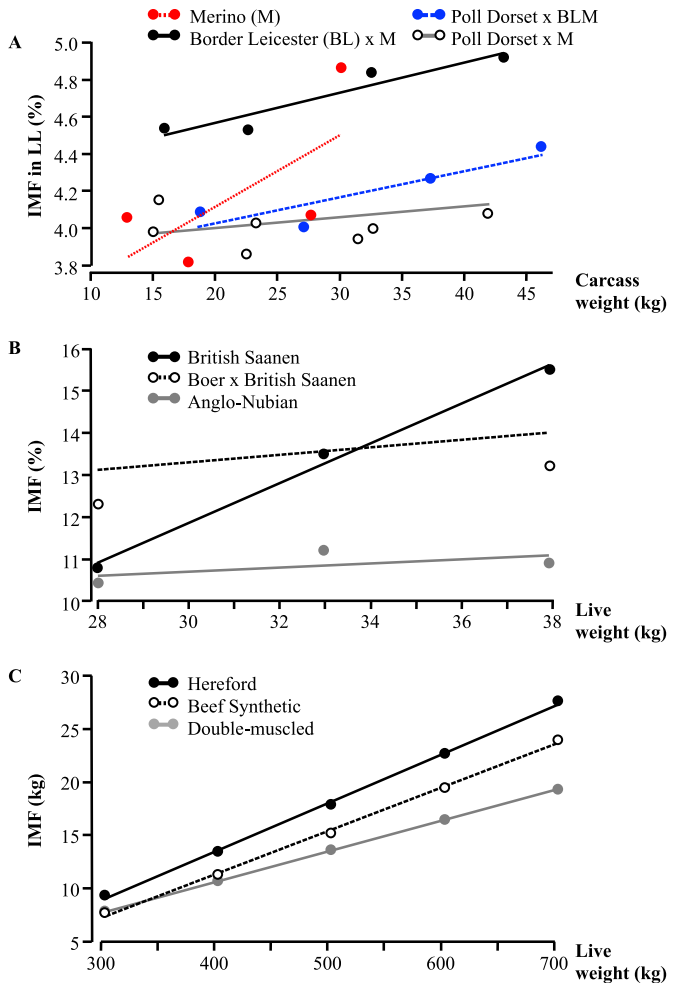

Fig. 1. The relationships between intramuscular fat (IMF) and carcass weight or liveweight in various breeds of sheep, goats and cattle. Mean IMF is plotted against carcass weight or animal body weight, with data taken from publications as follows. (A) The IMF (%) in longissimus thoracis et lumborum (LL) muscle was determined by near-infrared spectroscopy and carcass fat content was determined by dual energy X-ray absorptiometry in sheep slaughtered at 4, 8, 14, and 22 months of ages (McPhee et al., 2008). (B) Dissected intermuscular fat (IntMF, %) in carcasses of three goat breeds slaughtered at 18, 33, and 38 kg liveweight (Gibb et al., 1993). (C) Dissected IntMF (kg) in three cattle breeds, recalculated from the means of the allometric growth coefficients of the regression of IntMF (kg) against liveweight (Shahin and Berg, 1985).

Despite the variation among genotypes and among individuals within a genotype, the evidence suggests that fat deposition is only moderately heritable in both cattle and sheep. Table 2 summarizes the heritability data for some fat traits measured in large numbers of cattle and sheep. For IMF, the heritability ranges from 0.17 to 0.40 in cattle and 0.28 to 0.88 in sheep. The heritability for marbling score appears to be greater than that for IMF. The variation in heritability is large for both IMF and marbling, but it is clear that selection for an appropriate level of IMF can improve meat-eating quality in both cattle and sheep.

The problem is that selection to improve one fat depot will also lead to changes in other depots (Bennett, 1990). In theory, the partitioning of fat among depots is determined by genetic correlations among those depots, and those correlations are critical for avoiding overall fatness. As shown in Table 2, genetic and phenotypic correlations between fat traits (IntMF, IMF, SCF, VF, c-site fat thickness, g-site fat thickness, marbling score) are positive in both cattle and sheep, and vary markedly among genotypes within species. In Southdown sheep selected for high backfat (21 mm), backfat increased by 60% compared to the low backfat line (13 mm) at the same carcass weight, while SCF increased by 5%, VF increased by 17%, and IMF percentage increased by 48% (Kadim et al., 1989). Clearly, selection on the basis of a single measure, such as backfat depth, increases overall fatness, and the outcome of selection for backfat thickness will differ with site of fat depot. In Australian sheep, selection for low c-site fat depth will reduce IMF percentage; However, this strategy seemed to have little effect (Pannier et al., 2014). In conclusion, genetic correlations, which vary among breeds of cattle or sheep, suggest that deposition of back fat and IMF is regulated by different genes, so it is possible that sheep and cattle could be bred to increase IMF levels without increasing overall fatness.

It is important to note that, in contrast to sheep or other cattle breeds, in Wagyu cattle, there is a negligible genetic correlation (−0.06 to −0.03) between marbling score and SCF (Kahi and Hirooka, 2005; Oyama, 2011). An explanation might be found in the unique production system, established over a long history, that includes small herds (national average of 45 cattle per farm), a calf registration system, a beef traceability system, a nationwide unified grading system, and specialized techniques for cutting meat (Motoyama et al., 2016). The origin, breeding history and breeding process of Wagyu cattle can be traced back to the 'improved Japanese cattle' established in 1912 and fixed as the new Wagyu breed in 1944 (Motoyama et al., 2016). With decades of continuous selection for large amounts of IMF, Wagyu cattle are now accepted as the genotype that produces beef with the highest marbling score. In recent times, modern technology, such as controlled breeding and ultrasound scanning of IMF in live animals, has accelerated progress. In Japan, marbling is scored at the 6th to 7th rib with values from 1 to 12, with 12 indicating the greatest degree of marbling (Hirooka and Groen, 1999). The annual genetic gain for marbling score varies from 0.20 to 0.46, depending on the selection schemes applied (Hirooka and Groen, 1999; Kahi and Hirooka, 2005). These annual gains show that IMF or marbling score can be increased through long-term continuous selection. The genetic disassociation between marbling score and SCF in Wagyu cattle enables the selection for increasing IMF, with SCF change not at the same rate of genetic gain. Clearly, in other breeds and species, the genetic association/disassociation between IMF and SCF needs to be considered when establishing a breeding program for a high marbling score.

5. Differential expression of genes involved in adipogenesis and lipogenesis with fat distribution

Adipose tissue contains adipocytes, the stromal vascular fraction of cells including preadipocytes, fibroblasts, vascular endothelial cells, and a variety of immune cells (Hausman et al., 2014). Most myocytes, adipocytes and fibroblasts in the fetus are derived from the same pool of mesenchymal stem cells. In cattle, myogenesis is initiated in the embryonic stage and continues until the later stage of gestation, whereas adipogenesis is initiated in mid-gestation, and the number of adipocytes increases from before birth until 1 year of age (Bonnet et al., 2010; Du et al., 2010). Adipogenesis involves several genes and transcription factors. For example, the transcription factor zinc-finger protein 423 (Zfp423) commits progenitor cells to become preadipocytes (Gupta et al., 2010), after which C/EBP triggers the expression of *PPARγ* to promote the conversion of preadipocytes into mature adipocytes (Du et al., 2010, 2013). The importance of *PPARγ* is clear from the fact that its expression is greater in adipose tissue than in all other tissues in goats (Li et al., 2013), and greater in adipose tissue than in skeletal muscle in cattle (Martínez del Pino et al., 2017).

Variations in these differentially expressed genes (DEG) appear to explain differences in adipose development. For example, expression

Table 2
Heritability and genetic and phenotypic correlations of fat traits in cattle and sheep.

Animals	Traits and measurement	Heritability, h^2	Genetic correlation	Phenotypic correlation	References
Cattle					
Angus, Charolais, Hereford, Simmental, Limousin, Blonde d'Aquitaine, Gelbvieh ($n = 2172$)	Dissection of 10th to 12th rib sections	IntMF: 0.40 SCF: 0.42 VF[1]: 0.26 Marbling: 0.43	IntMF and SCF: 0.32 SCF and VF: 0.05 IntMF and VF: 0.50 IntMF and marbling: 0.28	IntMF and SCF: 0.30 SCF and VF: 0.10 IntMF and VF: 0.15 IntMF and marbling: 0.28	Bergen et al. (2006)
Angus ($n = 38,296$)	Ultrasound scanning live animals	IMF: 0.17 to 0.30 Marbling: 0.34 SCF[2]: 0.011 to 0.012	IMF and marbling: 0.51 to 0.83		MacNeil and Northcutt (2008)
Cattle		Marbling: 0.30 to 0.57			Park et al. (2018)
Korean cattle		Marbling: 0.57 to 0.64			
Wagyu cattle	Slaughter and dissection	Marbling: 0.56 SCF[3]: 0.46	Marbling and SCF thickness: −0.03	Marbling and SCF thickness: 0	Kahi and Hirooka (2005)
		Marbling: 0.55 SCF[3]: 0.39	Marbling and SCF thickness: −0.06		Oyama (2011)
Sheep					
Texel ($n = 3534$)	CT and ultrasound scanning live animals	IMF[4]: 0.28 to 0.40 SCF[4]: 0.33 to 0.37	IMF and SCF: 0.67 to 0.73		McLaren et al. (2021)
Suffolk ($n = 2357$)		IMF: 0.21 to 0.23 SCF: 0.33 to 0.39	IMF and SCF: 0.60 to 0.61		
Charolais ($n = 2013$)		IMF: 0.87 to 0.88 SCF: 0.32 to 0.39	IMF and SCF: 0.61 to 0.66		
Australian sheep ($n = 183$ sires and 7176 progeny)	Ultrasound scanning live animals, slaughter and carcass measurements	IMF[5]: 0.39 SCF[5]: 0.15 C-site fat thickness: 0.23 G-site fat thickness: 0.50	IMF and SCF: 0.12	IMF and SCF: 0.10	Mortimer et al. (2010)
Australian sheep ($n = 91$ sires, 7846 progeny)	Slaughter and carcass measurements	C-site fat thickness[6]: 0.44 G-site fat thickness[6]: 0.47	C-site fat and g-site fat: 0.60	C-site fat and g-site fat: 0.70	Ingham et al. (2007)
New Zealand sheep ($n = 19,446$)	Ultrasound scanning live animals, slaughter and carcass measurements	Marbling[7]: 0.30 C-site fat thickness: 0.28 G-site fat thickness: 0.21	Marbling and c-site fat thickness: 0.43 Marbling and g-cite fat thickness: 0.44		Brito et al. (2017)
New Zealand sheep ($n = 33,457$)	Slaughter and carcass measurements	IMF[8]: 0.57 Marbling: 0.35 Carcass fat: 0.32	IMF and carcass fat: 0.35 IMF and marbling: 0.93	IMF and carcass fat: 0.46 IMF and marbling: 0.61	Johnson et al. (2023)

IMF = intramuscular fat; IntMF = intermuscular fat; SCF = subcutaneous fat; VF = visceral fat; CT = computed tomography.
[1] VF, body cavity fat (Bergen et al., 2006).
[2] SCF, fat thickness at the 12th rib (0.6) + rump fat thickness (0.4) (MacNeil and Northcutt, 2008).
[3] SCF, fat thickness at the 6th to 7th rib section (Kahi and Hirooka, 2005).
[4] IMF measured by CT scanning and SCF thickness measured by ultrasound scanning live animals (McLaren et al., 2021).
[5] SCF thickness measured by ultrasound scanning and IMF measured by near infrared procedure in longissimus muscle (Mortimer et al., 2010).
[6] C-site, fat thickness at the 12/13th rib, 5 cm from the midline; g-site, tissue thickness at the 12th rib, 110 cm from the midline (Ingham et al., 2007).
[7] Marbling score: 1, little or no marbling; 5, about 30% visual IMF on slices of loin taken from the lumbar region (Brito et al., 2017).
[8] IMF measured by both chemical analysis and near infrared scanning (Johnson et al., 2023).

of *C/EBPα*, *PPARγ*, and *Zfp423* in the sternomandibularis were greater in Wagyu cattle (liveweight 585 kg) than in Angus cattle managed under the same conditions, whereas *C/EBPβ* expression did not differ (Duarte et al., 2013). The expression of *PPARγ* and *C/EBPβ* in the longissimus was greater in Wagyu × Hereford heifers than in Piedmontese × Hereford contemporaries, when the animals were 7 months old; when animals reached 25 months of age, *PPARγ* expression had increased substantially, as had the expression of adiponectin C1Q, fatty acid synthase and stearoyl-CoA desaturase (Wang et al., 2009). In another study, the expression of *PPARγ2*, *C/EBPα*, and *Znf423* in longissimus was greater in Wagyu cross than in Holstein steers at 26 months of age, but the two breeds showed no difference in SCF (Liu et al., 2021). On the other hand, the use of *PPARγ* as an indicator to IMF deposition has been questioned because its expression in longissimus did not differ significantly between Wagyu and Holstein steers (Albrecht et al., 2011). In adult Korean Hanhoo cattle, the expression of *PPARγ* in longissimus was greater in high IMF (23.5%) animals than in low IMF (7.4%) counterparts, but there was no difference in the expression of *PPARα* or *PPARδ* (Lim et al., 2015). In cell culture, there was less expression of *PPARγ* and *C/EBPα* in intramuscular preadipocytes than in subcutaneous preadipocytes isolated from 18-month old, Chinese Luxi Yellow steers (Wan et al., 2009), perhaps explaining the low IMF and high SCF typical of this breed. Clearly, there is a need for more exploration of the contribution of these genes to genotype differences in adipogenesis and IMF.

In sheep muscle, the patterns of these DEG are not consistent with those seen in cattle. The expression of *PPARγ* and *C/EBPδ* in longissimus dorsi of male lambs (liveweight 14 to 24 kg) did not differ significantly among four Brazilian genotypes (Morada Nova, Somali, Santa Ines, Dorper × Morada), despite IMF varying from 3.0% to 5.9% (Lôbo et al., 2012). By contrast, in SCF, DEG were highly enriched in PPAR signalling and in adenosine monophosphate-activated protein kinase (AMPK) signalling pathways; these two pathways might contribute to the marked differences in total body fat (5331 g vs. 1265 g), tail fat (3252 g vs. 49 g) and backfat thickness (8.29 mm vs. 4.43 mm) in Kazakh and Texel sheep (Shao et al., 2020). Despite the inconsistencies, it does seem that differences between genotypes in adipose-specific DEG are associated with the magnitude of phenotypic divergence in fat content.

Dietary nutrition is another determinant of gene expression, and thus IMF, in cattle and sheep. Adipocyte determination and

differentiation occurs during the early stages of life, so Du et al. (2010) suggested an order of effectiveness of nutritional manipulation of IMF deposition for cattle: fetal > neonatal > early weaning > post-weaning and older stages (up to 250 d of age). However, levels of fat are very low in the fetus and very young animals, and body fat is laid down much more rapidly with progressive maturity, so the effects of nutritional manipulation during gestation are often masked by responses to postnatal nutrition (Bell and Greenwood, 2016). Compared with ewes fed at the normal plane of nutrition, over-feeding pregnant ewes from 60 to 135 d of gestation (150% of the NRC nutrient requirements) upregulated the expression of *PPARγ* in the fetal semitendinosus, suggesting an increase in adipogenesis in the muscle (Yan et al., 2010). At 22 months of age, the offspring retained the *PPARγ* upregulation, and had more intramuscular adipocytes and a higher level of triglycerides (Yan et al., 2011). Du et al. (2013) suggested that supplementation of nutrients or other bioactive compounds to enhance adipogenesis, from early post-weaning to about 250 d of age in cattle, would specifically enhance intramuscular adipogenesis, thus maximising adipose hypertrophy during 'fattening' and improving marbling. Indeed, in Angus and Angus × Simmental steers, early weaning (141 d of age) followed by feeding a high-starch diet upregulated the expression of *PPARγ*, *C/EBPα*, and *Zfp423*, accelerated pre-adipocyte differentiation and increased the marbling score (Moisá et al., 2014).

The effect of high-starch or high-concentrate diets on IMF in cattle can also be attributed to a greater rumen production of propionate that is then used in gluconeogenesis. This favours intramuscular adipocytes because they preferentially use glucose/lactate carbon for lipogenesis, whereas subcutaneous adipocytes mainly use acetate (Hocquette et al., 2010). However, this hypothesis is not supported by studies of the incorporation of isotope-labelled acetate and glucose into palmitate in SCF, IMF and VF in finishing steers – the fractional rate (%/h) of palmitate synthesis from glucose as the substrate was less than one tenth of the rate of synthesis from acetate (Nayananjalie et al., 2015). If there is any effect of increasing glucose supply on fat depots, it seems to be limited.

Caution is also required when manipulating nutrition to increase IMF because there can also be disproportional changes in other fat depots. Compared with grazing on pastures, feeding crossbred heifers with grains increased adiposity in the body, the magnitude of which was associated with the length of grain feeding (99 d and 218 d; finished at about 600 d of age). Marbling score increased by only 27%, whereas backfat thickness increased by 770% and VF increased by 260%. The expression of *PPARγ* in SCF was upregulated by grain feeding, as was the expression of the genes involved in lipogenesis, such as fatty acid synthase and stearoyl-CoA desaturase (Key et al., 2013).

The fat content of the carcass is determined by both the number (hyperplasia) and volume (hypertrophy) of adipocytes. During the growing process in cattle, the rate of increase in volume is greater than the rate of cell number increase (Robelin, 1981). Kadim et al. (1989) proposed that variation in the fatness of meat-producing animals at a set weight is explained to a greater extent by variation in the size of the adipose cells rather than by variation in the number of cells, although the number of adipocytes in each depot was greater in high-fat individuals than in low-fat contemporaries. Du et al. (2013) agreed on a sequential formation of adipocytes during the period from embryonic development until slaughter in cattle, with VF first, followed by SCF, IntMF, and IMF, and proposed a nutrient supplementation strategy during the late fetal-neonatal stage to about 250 d of age to particularly promote IMF deposition.

The literature shows that increases in adipocyte volume are primarily driven by lipogenesis, so DEG associated with lipogenesis in the various fat depots, particularly during 'fattening', can contribute significantly to fat partitioning and fat content. In beef cattle with phenotypically high or low backfat thickness, a recent study that aimed to identify candidate genes for deposition of SCF found that the acetyl-CoA carboxylase (*ACACA*) gene, which functions to provide malonyl-CoA substrate for fatty acid synthesis, is most likely a key contributor to SCF deposition (Du et al., 2022). Guo et al. (2014) screened out the top 30 DEG expressed in longissimus that were correlated with IMF percentage, in both cattle and sheep, and found that the top 5 were all involved in lipogenesis: cell death-inducing DFFA-like effector a (*CIDEA*), thyroid hormone responsive (*THRSP*), acyl-CoA synthetase medium-chain family member 1 (*ACSM1*), diacylglycerol O-acyltransferase 2 (*DGAT2*) and fatty acid binding protein 4 (*FABP4*). In addition, Huang et al. (2020) reported, for 20- to 30-month-old beef cattle (Angus, Hereford, and Wagyu × Angus), that genes involved in lipogenesis in IMF from longissimus dorsi (fatty acid synthesis, elongation, desaturation, esterification) were down-regulated compared to SCF (over the rump). This observation could explain the low accretion rate of IMF compared to other fat depots.

Campos et al. (2016) reviewed other molecular markers for fat deposition and partitioning, and focussed on preadipocyte factor-1 (pref-1), a membrane protein in preadipocytes that prevents adipogenesis, and perilipin 1 (*PLIN1*), a major protein residing on the surface of mature adipocyte lipid droplets that plays an integral role in triacylglycerol storage and breakdown (Campos et al., 2016; Shirouchi et al., 2014). Another emerging marker is retinoic acid-induced 14 (*RAI14*), for which the expression in longissimus is always greater in Wagyu than in low-IMF Piedmontese cattle, and increases postnatally until 30 months of age (Hudson et al., 2015). This gene plays a role in the metabolism of retinoic acid, a factor that is involved in many physiological processes, including fat metabolism, can promote the differentiation of preadipocytes into mature adipocytes, and up-regulate the expression of genes involved in lipogenesis, thereby increasing fat deposition (Bonet et al., 2012). Indeed, the metabolism of vitamin A seems to be related to the high IMF characteristics of Wagyu cattle (Hirooka, 2014; Motoyama et al., 2016).

In summary, several DEG are statistically correlated with fat deposition in farm animals, and the numbers of such DEG are increasing rapidly with advances in the development of gene sequencing technology. Important DEG are usually identified by comparing groups of animals (individuals or bloodlines) that diverge substantially in their phenotypes for fat depots. One serious challenge is how we can use the increasing number of such DEG to select young and growing individuals for genetic selection. A second is the need to understand the molecular mechanisms that underpin the differential expression of these genes, including sequence variations in DNA (Shao et al., 2020), but this topic is beyond of the scope of the present review. From our perspective, the immediate goal should be direct measurement (or estimation) of the phenotype – fat content in live animals.

6. Quantification of phenotype in live animals – body fat and fat distribution

In farmed animals, body fat is measured traditionally after slaughter by dissecting and weighing fat and lean tissues. Usually, VF, including omental, mesenteric, kidney, and pericardial fat, are dissected and collected. A major limitation of this approach is that subcutaneous and intermuscular, but not IMF, can be dissected. Therefore, to quantify the total fat content of the whole-body of an animal, after removing pelage and gut content, the body must be minced and sampled so the fat can be extracted (e.g., with ether) and measured using chemical methods. Alternatively, this chemical

technique can be applied to individual tissues or organs and the individual values used to calculate total body fat. Obviously, this approach is not appropriate for animal breeding programs, so non-invasive methods are needed for live animals.

A number of non-invasive methods are available, including deuterium- or ^{18}O-labelled water, and imaging instruments such as dual-energy X-ray absorptiometry (DXA), CT, magnetic resonance imaging (MRI), ultrasound, and ultrawide-band microwave system. The application of imaging has been reviewed for farming animals (Scholz et al., 2015; Wells and Fewtrell, 2006) as well as humans (Seabolt et al., 2015). The various instruments acquire signals, based on a variety of mechanisms, which are then transformed to images that can be used to estimate the volumes or masses of adipose tissue, lean tissue, and bone. Importantly, total body content of adipose tissue can be estimated and the spatial distribution can be assessed.

6.1. Measuring total body water volume using deuterium- or ^{18}O-labelled water

To measure the total body water volume, known amount of water labelled with deuterium or ^{18}O is injected. A baseline sample before injection is taken to measure the natural abundance of the isotope. The labelled water is allowed to equilibrate fully in the body for 4 to 6 h (depending on the body size and total body fat) before a second blood sample is taken to measure the isotope enrichment using various instruments, such as mass spectrometry and nuclear magnetic resonance (Khaled et al., 1987). Total body water volume, calculated by the amount of label injected divided by the net increase of the label enrichment (from the natural abundance sample to equilibrated sample), is then used to estimate fat-free mass (FFM) with an assumption that water content in FFM is a constant at about 73% in animals and humans (ranged from 67% to 80%) (Duren et al., 2008; Schröder and Staufenbiel, 2006). Adipose tissue contains only a trivial amount of water, so total body fat is calculated as the difference between body weight and FFM (Duren et al., 2008). Obviously, this approach is not suitable for measuring fat distribution.

6.2. Dual-energy X-ray absorptiometry

With this technology, high- and low-energy X-rays are simultaneously pass through a body and the attenuation of energy is recorded. The energy loss differs among soft tissues (lean tissues and adipose tissue) and bones (Scholz et al., 2015), so the bone can be excluded, leaving estimates of fat and the proportion of fat to lean tissue (Seabolt et al., 2015). Dual-energy X-ray absorptiometry method assumes that the attenuation coefficients of fat and lean tissues do not vary greatly among individual animals, and that the hydration of lean tissue remains constant (Seabolt et al., 2015). The DXA scan provides an estimate of composition of the whole-body/carcass, but does not provide an accurate measure of the lean meat percentage in the whole body; with manual image analysis, the regional distribution of adipose tissue can be estimated (Scholz et al., 2015).

6.3. Computed tomography

The approach uses an X-ray generator that rotates around the body, emitting radiation at a single energy level. The attenuate of the X-rays at they pass through the body depends on the electron density of a tissue, differing among water, air, adipose tissue, lean tissue, and bone. Thus, tissue-specific attenuation coefficients can be used to distinguish and quantify the tissues, using tomographic reconstruction algorithms, thereby, producing tomographic images (Scholz et al., 2015). The CT scanner can be used to estimate muscle weight or eye muscle depth, total adipose, subcutaneous adipose or backfat thickness, visceral adipose, intermuscular and intramuscular adiposes, in humans (Seabolt et al., 2015) and in live sheep (Bünger et al., 2011; Clelland et al., 2014; Johnson et al., 2020; McLaren et al., 2021; Rosenblatt et al., 2017; Seabolt et al., 2015). Frisullo et al. (2010) used micro-CT for the rapid estimation of IMF in beef slices and for the description of the fat microstructure.

6.4. Magnetic resonance imaging

The whole body is rapidly scanned the computer-assisted diagnosis is used to automatically identify, localize, and measure body fat tissue (Brennan et al., 2005). This approach depends on tissue-specific magnetic-resonance properties, such as proton density, longitudinal relaxation time, and transverse relaxation time. The chemical characterises of the protons in water differ from those in fatty acid chains of triglycerides, leading to different proton nuclear magnetic resonance frequencies that can be used to estimate fat and water within tissues (Seabolt et al., 2015). After imaging, the raw data are transferred to a workstation and processed by algorithms that isolate adipose tissue (Brennan et al., 2005). Software designed for processing acquired image data allow the estimation of the volumes of total, visceral, and subcutaneous adipose, and lean tissue (Seabolt et al., 2015). However, MRI cannot differentiate the sources of lipid from intra- or extra-myocellular compartments due to limitations in resolution (McAllister et al., 2011). An interesting recent development is a portable magnetic resonance sensor for grading liver steatosis using diffusion-weighted multicomponent T2 relaxometry (Bashyam et al., 2021); it could be useful as a non-invasive tool for the measurement of IMF in live animals in the field.

6.5. Ultrasound scanning

Ultrasound scanner applies sound waves higher than the upper audible limit (>20 kHz), at the limit of human hearing, to various parts of a body, and then records the reflection of sound from body segments. Adipose, lean tissues, bone, and air, differ in acoustic reflection impedance, and therefore the amount of refection, allowing adipose tissue to be distinguished from lean tissue, the depth or volumes of the tissues to be estimated (Scholz et al., 2015; Wagner, 2013). Ultrasound scanners are portable so are readily deployed for assessment of live animals. They can provide estimates of VF, SCF, and IntMF, but not IMF (Afonso et al., 2019), as well as eye muscle depth, in a reference site (e.g., c-site, g-cite). The accuracy of the estimates seems to be lower than those from CT and MRI (Seabolt et al., 2015). Ultrasound scanning can measure the fat content in a whole tissue/organ, but not the entire body because the depth of penetration ultrasound waves is limited.

6.6. Ultrawide-band microwave

The system consists of a transmitter with an antenna that projects short pulses of low-power microwaves into biological tissues, with other antennae that collect the reflected electromagnetic signals. These reflected signals are processed using identification algorithms that create an image of a tissue and tissue components (Rafique et al., 2022). The dielectric properties differ among biological tissues – for example, muscles and the different types of adipose tissue, healthy and tumourous tissues – due to variations in water content, ion concentration, and cell structure (Sasaki et al., 2022). These characteristics permit tissue identification. Ultrawide-band microwave was recently used to predict the rump fat depth in cattle carcasses (Marimuthu et al., 2021), lamb carcase c-site fat

depth and GR tissue depth (Marimuthu et al., 2022), and muscle mass in humans (Vidhya et al., 2020).

Isotope dilution, DXA, and ultrasound are not suitable for phenotype measurement in genetic selection for fat partitioning in live animals, particularly with respect to IMF, the critical variable. The CT and MRI technologies can be used to estimate IMF, SCF, and VF, but the instruments are costly and large, and their operation is labour-intensive, preventing routine application on-farm in the large populations that needed for quantitative genetic selection. The industry urgently needs portable instruments that can be used in the field to measure SCF, IMF, and eye muscle depth simultaneously. Among the possibilities discussed above, portable ultrasound, MR sensor, and ultrawide-band microwave are the most promising, but further research and development are needed to validate the technologies in live animals and to establish working standards. In our view, success will be most likely with a combination of a physical parameter (such as water-fat frequency shift, transient elasticity, water diffusion rate) and images for types of fat visible to the relevant imaging resolution.

7. Concluding remarks

An appropriate level of IMF in meat is desirable for the favourable perception of meat quality by consumers. However, increasing IMF by increasing dietary energy supply also promotes rapid fat deposition in non-muscle depots, leading to an undesired increase in overall fatness as well as considerable extra costs in feed.

We therefore need to turn to genetic selection and IMF is a heritable trait. Unfortunately, most breeds of cattle and sheep produce meat with relatively low IMF content, so the simple solution of choosing a better genotype will not lead to rapid improvement. On the other hand, the genetic correlations among fat depots do vary substantially among genotypes, so it is essential to use breed-specific correlations for breeding programs.

Another impediment is detection of individual animals with a desired phenotype – a relatively high IMF score accompanied by a low SCF score. In the carcasses of progeny or siblings, IMF can be measured directly thus allowing assessment of the breeding value of the sire and dam. However, for the most rapid genetic gain, it is best to estimate IMF and SCF simultaneously in live animals so the generation interval can be shortened (Kahi and Hirooka, 2005). Various radiation-based technologies are available but the current instruments have several drawbacks that make them impractical for use on significant numbers of live cattle and sheep in the field. Detection of young individuals with a high-quality IMF phenotype is difficult because such animals have low levels of IMF. The technical challenge is confronting.

Finally, there is scope for the development of a molecular genetic approach because several DEG relating to adipogenesis and lipogenesis appear to diverge in relation to body fat patterns (Guo et al., 2014).

Author contributions

Shimin Liu: Conceptualization, Data Collection, and Writing Original Draft; **Yanyan Yang** and **Hailing Luo:** Review; **Wenjie Pang:** Writing and Review; **Graeme B. Martin:** Writing, Review and Editing.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors did not use any AI tool. All authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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