Genetics and breeding for intramuscular fat and oleic acid content in pigs

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ABSTRACT: The intramuscular fat (IMF) and oleic acid (OL) content have been favorably related to pork quality and human health. This influences the purchasing behavior of consumers and, therefore, also shifts the attention of breeding companies towards whether these traits are included into the breeding goal of the lines producing for high-valued markets. Because IMF and OL are unfavorably associated with lean content, a key economic trait, the real challenge for the industry is not simply to increase IMF and OL, but rather to come up with the right trade-off between them and lean content. In this paper we review the efforts carried out to genetically improve IMF and OL, with particular reference to the research we conducted in a Duroc line aimed at producing high quality fresh and dry-cured pork products. Based on this research, we conclude that there are selection strategies that lead to response scenarios where IMF, OL, and lean content can be simultaneously improved. Such scenarios involve regular recording of IMF and OL, so that developing a cost-efficient phenotyping system for these traits is paramount. With the economic benefits of genomic selection needing further assessment in pigs, selection on a combination of pedigree-connected phenotypes and genotypes from a panel of selected genetic markers is presented as a suitable alternative. Evidence is provided supporting that at least a polymorphism in the leptin receptor and another in the stearoyl-CoA desaturase genes should be in that panel. Selection for IMF and OL results in an opportunity cost on lean growth. The extent to which it is affordable relies on the consumers’ willingness to pay for premium products and on the cost to benefit ratio of alternative management strategies, such as specific dietary manipulations. How the genotype can influence the effect of the diet on IMF and OL remains a topic for further research.

Key words: growth, LEPR, meat quality, pork, SCD, selection
INTRODUCTION

Intramuscular fat (IMF) content and composition affect technological, sensorial, and nutritional quality attributes of pork. Intramuscular fat has been associated with improved drip loss, cooking yield, tenderness, texture, taste, flavor, juiciness, and eating quality (Wood et al., 2008; Font-i-Furnols and Guerrero, 2014). Likewise, saturated (SFA) and MUFA have been favorably correlated with flavor preference and overall acceptability (Cameron et al., 2000; Wood et al., 2003). The beneficial health effects of dietary MUFA over SFA (Hammad et al., 2016) has placed the focus on the substitution of SFA by MUFA, which also have the advantage of being less prone to oxidation and rancidity than PUFA.

The continued selection for increased leanness practiced for decades in most of commercial pig lines has led to producing pork with very low levels of IMF. This has been particularly disruptive for products intended for niche, traditional or premium markets. Such is the case of dry-cured products, where IMF and MUFA, notably oleic acid (OL), are critical. The influence of IMF and OL on color, texture, and intensity and persistence of aroma of dry-cured hams is well documented (Ventanas et al., 2007; Gandemer, 2009; Lorido et al., 2015). However, to remain competitive, the real challenge for the industry is not simply to increase IMF and OL, but rather to modify them with the right trade-off with lean growth efficiency. Several genetic, nutritional, and management approaches have been proposed to manipulate IMF and OL independently of the rest of fat depots, usually measured indirectly as backfat thickness (BT).

The objective of this paper is to review the research carried out to genetically improve IMF and OL, with particular reference to the results we obtained in a Duroc line aimed at producing high quality pork products. Results on genetic and DNA variation are presented before discussing opportunities for selection and breeding.
GENETIC VARIATION

The genetic variation in IMF and OL results from differences between breeds, lines within breed, individuals within line, and tissues within individuals.

Between Breed and Line Variation

The first approach used to increase IMF and OL was to exploit the differences between breeds. Wood et al. (2004) found that the relationship between marbling fat and BT is breed-dependent, with Duroc having greater IMF at low BT as compared with other traditional and modern breeds. Breed also affected the fatty acid composition of IMF, with high values for SFA in fattier traditional breeds and high values for PUFA in leaner modern breeds. The Iberian pig, with its high capacity to accumulate fat and MUFA, is considered the most adequate breed to obtain dry-cured pieces of high sensorial quality (López-Bote, 1998). However, the elevated production costs of purebred Iberian limit their market scope. Therefore, attention has turned to the Duroc as a convenient option to supply the increasing demand for quality pork products. Thus, Reixach et al. (2008) showed that purebred Duroc pigs had more IMF and OL (but less lean growth) than Large White × Landrace pigs but less IMF and OL (but greater lean growth) than Iberian × Duroc crossbreds (Figure 1). Those authors, in line with others (Cilla et al., 2006), also found that there exists substantial variation between Duroc lines. As with breeds, differences across lines indicate that IMF and OL are inversely related to lean growth.

Within-Line Variation

The estimates of within-line genetic (co)variances indicate that there is enough genetic variation for IMF and OL to respond to selection, but also that this variation is partly confounded with that for overall fatness (Ros-Freixedes et al., 2012; Table 1). The heritability for IMF in our Duroc reference line is relatively high, approximately 0.50. This estimate is in accordance with
values in literature, which range from 0.26 to 0.86, with an average of 0.50 (Sellier, 1998).

However, with the exception of the early work of Cameron (1990), it was not until the last
decade that genetic parameters of fatty acids were further studied. Although results in the
literature varied by genetic type, adipose tissue, and analytical methodology, the heritability of
OL is also approximately 0.50, with values ranging from 0.25 to 0.30 (Fernandez et al., 2003;
Sellier et al., 2010) to 0.55 to 0.70 (Sellier et al., 2010; Ntawubizi et al., 2010; Gjerlaug-Enger et
al., 2011). Some of these studies, however, used few and heterogeneous data, and they were
designed for other purposes than estimation of genetic parameters, which makes some of the
estimates not sufficiently conclusive.

In our Duroc line, the genetic correlation between IMF and OL in muscle is positive
(0.47), but both traits, although favorably correlated with BW (0.11 to 0.27), present an
unfavourable correlation with BT (0.22 to 0.37). Reported estimates from other lines vary around
these values (Suzuki et al., 2005a; Ntawubizi et al., 2010; Schwab et al., 2010). The correlation
structure of IMF (and OL) with BW and BT indicates that there is room for independent
manipulation of IMF (and OL) and lean growth. In fact, there are selection strategies leading to
expected response scenarios in which IMF, OL, BW and BT can be simultaneously improved
(Solanes et al., 2009; Ros-Freixedes et al., 2012). Yet, the responses in one trait can be very
sensitive to small genetic changes in the others. Successful strategies require records on either
IMF or OL, since there is little chance for a favorable correlated response in IMF and OL to
selection for increased lean growth, particularly if lean content (i.e., BT) is emphasized over
growth rate (i.e., BW) in the selection objective.

There is scarce literature on the genetic correlations of IMF and OL with other economic
traits. Small effects are expected on IMF if litter size is included in the selection objective
(Solanes et al., 2009), a circumstance that was confirmed experimentally by Estany et al. (2002) who did not observe a correlated response in IMF after an intense cycle of selection for number of piglets born alive. The correlation pattern of IMF with ham weight, loin thickness, and carcass length observed by Ros-Freixedes et al. (2013), together with previously reported estimates in Iberian (Fernández et al., 2003) and Duroc pigs (Suzuki et al., 2005a; Solanes et al., 2009), indicate that selection for IMF may have a negative impact on the proportion of primal cuts in the carcass but not necessarily on their final weight. Because feed efficiency for fat is less than for lean, selection for increased IMF is expected to impair feed efficiency. In line with this hypothesis, estimates of the genetic correlation of IMF with feed efficiency were negative (Suzuki et al., 2005a; Cai et al., 2008) and selection for reduced residual feed intake resulted in less IMF in loin (Cai et al., 2008; Smith et al., 2011). However, IMF as such is not a large factor associated with differences in feed efficiency (Cai et al., 2008). Although there are almost no estimates for OL, published results show that the genetic correlation of OL with litter size, primal cuts and feed efficiency should follow a similar pattern as IMF (Fernández et al., 2003; Hofer et al., 2006).

**Within-Individual Variation**

There is not only a single measure of IMF and OL that represents an individual, since both traits can be determined at different ages and within different muscles and tissues at a given age. During the growing-finishing period, the evolution of IMF with age is linear, but not that of OL, BT and BW (Bosch et al., 2012), a circumstance that may lead to changes in the correlation pattern among them with time. For a given production scenario, pigs are slaughtered at around the same age and, therefore, the muscle, the tissue, or even the location within a muscle or tissue where IMF or OL are determined remains as the main source of individual variation. The genetic
correlations of IMF and OL across muscles and fat tissues, although positive, are variable enough to produce uneven responses across them (Table 2). For instance, Ros-Freixedes et al. (2014) estimated that the expected correlated response in IMF or OL in the gluteus medius muscle to selection for IMF or OL in LM, and vice versa, were 55% to 71% of direct responses. The responses of OL in these two muscles when using OL in the subcutaneous fat as selection criterion were less (27% to 45%).

DNA VARIATION AND GENETIC MARKERS

Genetic variation can be analyzed at the DNA level. Thus, during the last two decades, much effort has been placed into the detection of QTL affecting IMF and fatty acid composition. Using low-density microsatellite linkage maps, several QTL and candidate genes have been reported for IMF (as summarized by Gao and Zhao, 2009). On the whole, many of the reported QTL regions for IMF co-localize with QTL for fattening traits, such as BT, in agreement with the positive genetic correlation that exists between them. Selection for most of these markers would then increase IMF and overall fatness at the same time. In addition, these QTL effects are breed-specific and show little positional coincidences across muscles (Quintanilla et al., 2011). The development of high-density porcine marker panels and automatic genotyping platforms has revolutionized the search for genomic regions in terms of speed and mapping accuracy. Moreover, the assembly and public release of the pig genome (Archibald et al., 2010) has provided a valuable tool to select candidate genes underlying these genomic QTL effects. However, locating causal mutations has proved to be challenging even with very high density marker maps. Approaches to downsize the list of candidate genes for IMF content and composition have most frequently combined genome-wide association studies (GWAS) and QTL mapping information with functional transcriptional data (e.g., Ramayo-Caldas et al.,
2014). With this approach, a number of mutations have been described in candidate genes, albeit most of them had a rather small effect over IMF and OL or the associations only held for a small subset of breeds (reviewed in Switonski et al., 2010), denoting that they are not causal, but in linkage disequilibrium with the causal mutation. Three of the genes with a more consistent effect on IMF across studies are the melanocortin 4 receptor (\textit{MC4R}), the (heart) fatty acid binding protein 3 (\textit{FABP3}), and the leptin receptor (\textit{LEPR}).

Of particular relevance, a missense mutation in the exon 14 of the \textit{LEPR} (g.1987C>T) shows the most consistent effect on fat deposition across breeds (Óvilo et al., 2005; Lopez-Buesa et al., 2014; Ros-Freixedes et al., 2016). The \textit{LEPR} encodes for a receptor of leptin, a (mainly) adipose-secreted hormone with endocrine and paracrine activity that regulates satiety and food intake through receptors in the hypothalamus. Leptin also interacts with other hormonal mediators and regulators of energy status and metabolism such as insulin or glucagon to regulate growth and reproduction processes (Margetic et al., 2002). In skeletal muscle, leptin increases fatty acid oxidation. The \textit{LEPR} g.1987C>T mutation results in a less functional receptor, which reduces leptin clearance (Ros-Freixedes et al., 2016), increases feed intake (Rodríguez et al., 2010) and promotes fat accumulation. Based on data from 987 Duroc pigs, we showed that the TT genotype, which was at a frequency of approximately 20%, resulted in greater BT (14% of the mean), IMF (13% of the mean), and SFA (4% of the mean) but not MUFA as compared with the CT and CC genotypes (Figure 2).

Overall, markers associated with IMF affect overall fatness, which does not allow specific selection for IMF. The exception to this general rule is the missense \textit{PCK1} c.2456C>A polymorphism, which is the first marker described that increases IMF (up to 20.4%) while decreasing BT by 9.9% (Latorre et al., 2016). The PCK1 enzyme plays a regulatory role in
gluconeogenesis and, in tissues where it does not occur, PCK1 provides glycerol-3-phosphate as a precursor for the esterification of fatty acids into triglycerides (glyceroneogenesis). The favorable A allele is the major allele in fattier pigs such as wild boar, Iberian, and Duroc, whereas it is less frequent in breeds selected for high lean content such as Pietrain (Latorre et al., 2016). Although these results need to be validated in further studies and causality is yet to be proven, this remains a very exciting marker to be incorporated in selection schemes.

Changes in fat content entail correlated changes in fat composition, with SFA and MUFA increasing with the amount of fat (Bosch et al., 2012), in line with the positive correlation between IMF and OL. There are a couple of genes, however, affecting fatty acid composition but not fat content. One of them is that encoding the fatty acid elongase 6 (ELOVL6), which has substrate preferences for C12-C18 SFA and MUFA. Although it needs to be further validated in other pig populations, results by Corominas et al. (2015) with Iberian × Landrace crossbreds point to the c.-394G>A SNP in the promoter of ELOVL6 as the causal mutation affecting palmitic and palmitoleic acid contents. Interestingly, the mutation is lying in the binding site for the estrogen receptor alpha.

To date, the most promising marker for OL is the stearoyl-CoA desaturase (SCD) gene. The SCD enzyme has a direct role in the MUFA biosynthesis pathway as it is responsible for catalyzing the desaturation at the Δ⁹ position of stearoyl-CoA and palmitoyl-CoA into oleoyl-CoA and palmitoleoyl-CoA, respectively. The SCD gene co-localizes with some previously detected QTL for C16 and C18 SFA and MUFA in pigs with Duroc background (Quintanilla et al., 2011; Uemoto et al., 2011). Findings thus far support that there is genetic variation in the SCD gene affecting MUFA and OL in muscle and adipose tissue. A haplotype of three SNP in the SCD promoter has been associated to C16 and C18 SFA and MUFA content both in IMF and
subcutaneous fat (Estany et al., 2014), with evidence supporting causality for the g.2228T>C SNP. Results from 1,087 Duroc pigs confirmed that the TT pigs had 1% more MUFA (and 1% less SFA) than the CT pigs and the CT pigs had 1% more MUFA (and 1% less SFA) than the CC pigs (Figure 2). The effect of the mutation did not affect BT or IMF. The favorable effect of the allele T has been validated in several Duroc crossbreds including Duroc × Iberian (Estany et al., 2014), throughout the growing-finishing period (Henriquez-Rodriguez et al., 2016) and in dry-cured hams (Henriquez-Rodriguez et al., 2015). A GWAS undertaken in our Duroc reference line singled out SCD and LEPR as the genes most influencing IMF and OL (Ros-Freixedes et al., 2016). These two genes give rise to a compelling micromodel for fatty acid deposition, with LEPR affecting (dominantly) the quantity and SCD (additively) the quality of fat (Figure 2). For instance, while LEPR increases IMF but not MUFA, SCD increases MUFA but not IMF. Recently, van Son et al. (2016) confirmed the effects of SCD gene in Norwegian Duroc, where it explains more than 50% of the genetic variance of MUFA, and of ELOVL6 in Norwegian Landrace on palmitoleic acid. Both genes have also been identified in a White Duroc × Erhualian F2 intercross as strong candidate genes for fatty acid elongation and desaturation, respectively, (Zhang et al., 2016). Interestingly, these polymorphisms give genetic clues to interpret the correlation of BT with IMF and of IMF with OL and to unravel opportunities to select these traits independently of each other.

**SELECTION AND BREEDING**

In line with expected responses, realized responses indicate that, at best, selection for lean growth does not affect IMF. Thus, Solanes et al. (2009) found that IMF did not respond to selection for BW at fixed BT. This result is consistent with findings from studies conducted with Danish Landrace (Oksbjerg et al., 2000) and French Large White pigs (Tribout et al., 2004),
where long-term continuous selection for lean growth did not reduce IMF. In two studies with Duroc pigs, however, selection for lean growth resulted in less IMF (Lonergan et al., 2001; Schwab et al., 2006), likely because in these experiments pigs were more intensively selected for lean content than for growth. Cameron et al. (2000) showed that this is the case even when the selection criterion is designed to obtain equal correlated responses in lean content and growth rate. These results confirm the need for IMF data in order to change IMF irrespective of lean content.

**Phenotyping**

Collecting phenotypes for IMF and OL is difficult and costly, especially in the selection candidates. *In vivo* determination of IMF is based on non-invasive electronic and computer-driven techniques, such as real-time ultrasound (Newcom et al., 2002) or computed tomography (Scholz et al., 2015). Besides not being adequate for OL, these techniques are not fully applicable at large scale and have limited accuracy, even if BT is included in the prediction models. As a result, greater genetic responses in IMF are expected when using chemical IMF than ultrasound IMF (Newcom et al., 2005), particularly in the fraction of genetic variation of IMF that is not captured by BT. Therefore, *in vivo* measurements may be regarded more as complementary rather than alternative if individual traceability is ensured from farm to abattoir. If it is not, then *in vivo* recording in selection nucleus becomes critical.

In the abattoir, IMF and OL can be measured in different tissues, muscles, and locations using different methodologies. The optimal combination of location and method is critical and depends on the target trait, the cost and accuracy of sampling, and the cost and speed of the methodology used for the determinations. Our results showed that samples from gluteus medius muscle and LM can be used alternatively as a reference muscle (Table 2; Ros-Freixedes et al.,
As increasingly accurate equipment is developed, it could also become possible to implement cheap, speedy, and multiple-trait recording systems and then used to make more than one determination per pig. Near infrared spectroscopy has proved to be effective for recording data on fat content and composition in a breeding scheme (Gjerlaug-Enger et al., 2011).

**Selection based on Phenotypes**

Experiments so far provide evidence that IMF responds to selection, but at the expense of increasing fatness. After six generations of direct phenotypic selection based on IMF real-time ultrasound records, Schwab et al. (2009) found that IMF increased (47% of the mean) but also BT (40% of the mean). Growth performance was not affected. This line was used to identify signatures of selection associated with IMF. Although difficult to interpret, some of the signatures co-located with genes associated to overall fatness and, interestingly, one of them was *LEPR* (Kim et al., 2015).

Two selection experiments were undertaken in pigs to determine whether IMF and BT can respond independently. Suzuki et al. (2005b) selected a Duroc line, for which sib-records on IMF were available, for an index based on desired gains including BW, BT, and IMF during seven generations. Results indicated that they were able to increase IMF (+15% of the mean) while constraining but not reducing BT (+8.5% of the mean). The experiment in Ros-Freixedes et al. (2013) was designed to test the opposite, whether BT can be reduced at restrained IMF, thereby assuming that IMF was already at the optimum value. In this experiment, consisting of three one-generation selection rounds on the mid-parent predicted breeding value for BT and IMF, selected pigs had less BT (−7.8% of the mean), but less IMF as well (−3.2% of the mean), although the decrease in IMF was half of the expected if it had not been restricted (Table 3).

Incomplete restriction of IMF was due to limitations in accuracy of breeding values and selection
intensity. These results highlight the fact that selection is able to break the relation of IMF with BT, but also that it is not easy, requiring a right combination of predictive accuracy (i.e., phenotypes), population size (i.e., selection pressure), and time (i.e., generations). The genetic trends over a decade of selection in a commercial line would confirm that such goal is indeed feasible (Figure 3).

There is little experimental evidence on the changes in fatty acid composition due to selection. In line with their correlation, Burkett (2009) found that selection for IMF increased OL and MUFA. To our knowledge, the only experiment of selection for OL is that referred to in Ros-Freixedes (2014), for which two batches of pigs selected on the mid-parent predicted breeding value for OL were compared with contemporary pigs chosen randomly. Despite the limited size of each batch, there was enough evidence indicating that the selected pigs had +0.31% more OL in IMF than the control pigs (Table 4), a response explained by both the genetic change in the polygenic component (+0.24%) and in the SCD gene (+0.07%). The response in OL fell short compared with that expected (0.60%) because the limitations in selection accuracy and intensity were even more marked in this experiment. Further analyses showed that if the records from littermates had also been available, the response would have been much closer to that expected (Table 5).

**Marker and Genomic Selection**

The DNA markers with known associated effects to IMF and OL can be easily embedded into conventional BLUP of breeding values, even in situations of missing genotypes (Legarra and Vitezica, 2015). In addition to markers in candidate genes, today there are also available high-density panels of porcine SNP markers with up to 658,692 markers. The integration of this new genomic information into the prediction of breeding values is the basis of genomic
selection. A major advantage of genomic selection is that it can notably increase the accuracy of non-phenotyped individuals (Ibáñez-Escriche et al., 2014), which might be the case of selection candidates for IMF and OL. Results from a stochastic simulation study indicated that genomic prediction can improve the accuracy of traits such as IMF (from 39% to 58%; Tribout et al., 2012). Gjerlaug-Enger et al. (2014) confirmed the expectations with real IMF data (accuracy increased from 36% to 63%), but Jiao et al. (2014) did not, finding much lower values of accuracy than expected (22%). Genomic selection in pig breeding is a reality (Knol et al., 2016), although its benefits need to be carefully examined (Blasco and Toro, 2014). Genomic selection provides greater genetic gains than conventional selection, but when both approaches are compared at the same cost, the advantage of genomic selection becomes only apparent at high levels of budgetary expenditure (Tribout et al., 2013).

In terms of prediction accuracy, there is some evidence with Duroc pigs showing that markers at the SCD and LEPR loci have a predictive capacity similar or even superior to the 36k markers from the PorcineSNP60 Beadchip (Illumina Inc., San Diego, CA) that passed regular quality control. Using a Bayes B model and these 36k markers on a small training population, the correlations between genomic predicted breeding values and phenotypes in the testing population were high for total SFA and MUFA (0.48 and 0.50, respectively), moderate for OL (0.28), and low for IMF and PUFA (0.04 and 0.07, respectively) (Table 5; Ros-Freixedes et al., 2016). However, the correlations for these traits ranged from 0.38 to 0.49 when the SNP at the SCD and LEPR loci were used alone. In the absence of genotypic information, correlations were similar or even greater (from 0.38 to 0.67) if data on BT, BW, and littermates were included in the evaluation model. Combining phenotypes and markers at the SCD and LEPR loci, correlations as high as 0.47 to 0.70 can be achieved for IMF content and composition traits (Table 5).
Genomic selection reduces phenotyping needs at the expense of genotyping. Therefore, the benefits of genomic selection for IMF and OL must be assessed against the benefits that would be achieved in case of allocating these extra economic resources to improve phenotyping. According to Tribout et al. (2012), only a small set of animals needs to be phenotyped and genotyped annually to create a suitable training population for implementing genomic selection for traits such as IMF and OL. This offers the potential to explore intermediate scenarios, such as increasing phenotyping capacity while genotyping only a limited number of pre-selected candidates. The final decision will depend on the phenotyping and genotyping costs, on the weight of IMF and OL in the breeding goal and on the nucleus size (Tribout et al., 2013). A strategy to reduce genotyping costs is the imputation of genotypes of animals genotyped with low density panels using a reference subset of animals genotyped at higher density. Another alternative is to use a low-density marker panel designed with a subset of specific markers for meat quality. This is likely the best option for low budgets. Thus, in this situation, and as a first approach, genetic evaluations for IMF and OL can be based on a combination of data from relatives and genotypes at selected loci such as SCD and LEPR. Whole-genome sequences obtained with the new high-throughput sequencing platforms have great potential for the discovery of new variants associated with IMF and OL and for increasing the accuracy and persistency of breeding values predictions (Daetwyler et al., 2014; Hickey et al., 2014).

**Nutrigenetics**

In pig, fat deposition is greatly influenced by diet. Experimental results indicate that dietary fatty acid additions mainly affect subcutaneous fat and PUFA rather than IMF and MUFA (Wood et al., 2008). A frequently used approach to increase IMF is to reduce the amount of dietary protein (reviewed in Katsumata, 2011; Madeira et al., 2014). Under these conditions,
hypertrophy of already-existing adipocytes takes place as a result of enhanced lipogenesis. Still, low protein diets also have undesirable effects promoting slower growth rate, thicker BT, and smaller loin muscle area (e.g., Goerl et al., 1995; Madeira et al., 2014). Moreover, the extent of the effect depends on the genetic background of the pigs (Liu et al., 2016). Different dietary fat sources, such as conjugated linoleic acid, have been explored as an alternative to modify fat content and composition with results very much dependent on the breed (Gatlin et al., 2002; Morel et al., 2008).

Vitamin A also influences fat deposition by promoting adipogenic commitment of precursor cells and reducing lipid accumulation in mature adipocytes (Wang et al., 2016). Ayuso et al. (2015a,b) observed that vitamin A-restricted diets, particularly if restriction is made at early ages, increased IMF but not BT by developing an increased number of preadipocytes in muscle. The delayed pattern of adipocyte maturation in IMF allows targeting this depot at a critical period at the beginning of fattening, without enhancing fat deposition in other depots. Again, the extent of the gain is clearly affected by the genetic background of the pigs (Olivares et al., 2009).

The examples above show how the diet exerts a regulatory role on fat content and composition, which in turn, can be fine-tuned by genotype. Therefore, dietary and genetic factors can be combined to enhance IMF independently of BT. Because the SCD g.2228T>C SNP sits in a putative retinoic acid response element, it can be hypothesized that the response of the SCD gene to dietary vitamin A is genotype dependent. In a recent study, we have used varying amounts of dietary pro-vitamin A carotenoids in two groups of pigs differing in the SCD g.2228T>C SNP (Pena et al., 2016). At the end of the fattening period in this 4-wk trial, we observed important differences in IMF and liver fat content but not in BT. Activation of the putative retinoic acid response element is being tested by chromatin immunoprecipitation (ChIP)
in muscle and liver samples. The study aims at finding the optimal feeding conditions (in terms of (pro)vitamin A compounds) to maximize IMF and low BT. This is an interesting area of nutrigenetics that expands over the use of a small panel of markers to enhance selection decisions.

**SUMMARY AND CONCLUSIONS**

Duroc lines are a good choice for high IMF (and OL) at high lean growth, albeit there is substantial variation between lines. Although IMF and OL are inversely related to lean growth, there are within-line selection scenarios in which IMF and OL can be improved simultaneously with lean growth. Such scenarios involve regular recording of IMF and OL, so that developing a cost-efficient phenotyping system for these traits becomes a priority. Genomics offers an opportunity to discover new genetic markers and make additional improvements in selection accuracy. However, because it is costly, its genetic advantages are not directly translated into economic benefits. Thus, a critical issue, particularly in situations under limited economic resources, is to assess whether the cost of implementing genomic selection is worth the opportunity costs of not investing in phenotyping. At this stage, selection on a combination of pedigree-connected phenotypes and genotypes from singled-out genetic markers (or low density marker panels) is proposed as a convenient approach to improve IMF and OL in commercial lines. Selection for IMF and OL has also an opportunity cost on lean growth, with a value equal to the difference between the economic response with and without IMF (and OL) in the selection objective. The extent to which it is affordable relies on how much consumers are prepared to pay for premium products and on the cost to benefit ratio of alternative management strategies, such as specific dietary manipulations. The role of genetics in fine-tuning the effects of the diet on IMF and OL is an interesting topic for further research.
LITERATURE CITED


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Schwab, C. R., T.J. Baas, and K. J. Stalder. 2010. Results from six generations of selection for


Table 1. Heritability (bolded diagonal), genetic correlations (above diagonal), residual correlations (under diagonal) and additive genetic variance for BW, backfat thickness (BT), and intramuscular fat content (IMF) and oleic acid content (OL) in gluteus medius (GM) (adapted from Ros-Freixedes et al., 2012).\(^1\)

<table>
<thead>
<tr>
<th>Trait</th>
<th>BW</th>
<th>BT</th>
<th>IMF in GM</th>
<th>OL in GM</th>
</tr>
</thead>
<tbody>
<tr>
<td>BW at 180 d, kg</td>
<td>0.31</td>
<td>0.63</td>
<td>0.27</td>
<td>0.11</td>
</tr>
<tr>
<td>BT at 180 d, mm</td>
<td>0.60</td>
<td>0.45</td>
<td>0.37</td>
<td>0.22</td>
</tr>
<tr>
<td>IMF in GM at 205 d, %</td>
<td>0.08</td>
<td>0.15</td>
<td>0.56</td>
<td>0.47</td>
</tr>
<tr>
<td>OL in GM at 205 d, %</td>
<td>0.20</td>
<td>0.22</td>
<td>0.20</td>
<td>0.50</td>
</tr>
<tr>
<td>Genetic variance</td>
<td>29.8</td>
<td>4.1</td>
<td>1.9</td>
<td>2.2</td>
</tr>
</tbody>
</table>

\(^1\)Posterior SD were less than 0.12 for all heritabilities and genetic correlations.
Table 2. Genetic correlations of intramuscular fat content (IMF) and oleic acid content (OL) in gluteus medius (GM) with IMF and OL in LM and OL in subcutaneous fat (SF) (adapted from Ros-Freixedes et al., 2014).\(^1\)

<table>
<thead>
<tr>
<th>Trait</th>
<th>IMF in GM</th>
<th>OL in LM</th>
<th>OL in SF</th>
</tr>
</thead>
<tbody>
<tr>
<td>IMF in GM</td>
<td>0.68 (0.48, −0.87)</td>
<td>0.24 (−0.04, 0.50)</td>
<td>−0.03 (−0.30, 0.32)</td>
</tr>
<tr>
<td>OL in GM</td>
<td>0.51 (0.30, 0.71)</td>
<td>0.62 (0.41, 0.80)</td>
<td>0.29 (−0.06, 0.72)</td>
</tr>
</tbody>
</table>

\(^1\) Within parentheses, the highest posterior density interval at 95% of probability.

\(^2\) All traits were measured at 205 d of age.
Table 3. Direct and correlated responses (R) to selection for decreased backfat thickness (BT) at 180 d at restrained intramuscular fat (IMF) content in muscle gluteus medius at 205 d (adapted from Ros-Freixedes et al., 2013).

<table>
<thead>
<tr>
<th>Realized response</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trait</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>BT, mm</td>
</tr>
<tr>
<td>IMF, %</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>

1 BW was measured at 180 d and oleic acid and carcass traits at 205 d.

2 P(>0), posterior probability of having a negative response.
Table 4. Direct and correlated responses to selection for increased oleic acid content in muscle gluteus medius at 205 d (adapted from Ros-Freixedes, 2014).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Direct Response</th>
<th>Correlated response$^1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oleic acid, %</td>
<td>+0.31 &gt;0.99</td>
<td>Intramuscular fat, %</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+0.16 0.71</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Backfat thickness, mm</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−0.73 0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td>BW, kg</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−0.96 0.27</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lean weight, kg</td>
</tr>
<tr>
<td></td>
<td></td>
<td>−0.12 0.55</td>
</tr>
</tbody>
</table>

$^1$ BW and backfat thickness were measured at 180 d and intramuscular fat and lean weight at 205 d.

$^2$ P(>0), posterior probability of having a positive response.
Table 5. Correlation between predicted breeding values and adjusted phenotypes in a set of 70 pigs born in 2009 using different genomic, pedigree and phenotypic data collected since 2002 [adapted from Ros-Freixedes (2014) and Ros-Freixedes et al. (2016)].

<table>
<thead>
<tr>
<th>Method</th>
<th>IMF</th>
<th>SFA</th>
<th>MUFA</th>
<th>OL</th>
<th>PUFA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genomic-36k</td>
<td>0.04</td>
<td>0.48</td>
<td>0.50</td>
<td>0.28</td>
<td>0.07</td>
</tr>
<tr>
<td>SCD/LEPR</td>
<td>0.46</td>
<td>0.48</td>
<td>0.43</td>
<td>0.36</td>
<td>0.49</td>
</tr>
<tr>
<td>U-BLUP, NL</td>
<td>0.11</td>
<td>0.11</td>
<td>0.08</td>
<td>0.12</td>
<td>0.16</td>
</tr>
<tr>
<td>U-BLUP, L</td>
<td>0.31</td>
<td>0.15</td>
<td>0.32</td>
<td>0.32</td>
<td>0.39</td>
</tr>
<tr>
<td>M-BLUP, L</td>
<td>0.42</td>
<td>0.41</td>
<td>0.40</td>
<td>0.38</td>
<td>0.67</td>
</tr>
<tr>
<td>M-BLUP L, SCD, LEPR</td>
<td>0.47</td>
<td>0.62</td>
<td>0.55</td>
<td>0.48</td>
<td>0.70</td>
</tr>
</tbody>
</table>

1 IMF: intramuscular fat; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; and OL: oleic acid. All traits determined in muscle gluteus medius at 205 d.

2 Genomic-36k: prediction based on 36,432 SNP (PorcineSNP60 v2, Illumina, CA), whose effect was estimated with Bayes B using data from 65 pigs born in 2002; SCD/LEPR: prediction based on the SCD g.2228T>C SNP (MUFA and OL), the LEPR c.1987C>T SNP (IMF and PUFA), or both (SFA), estimated using data from 65 pigs born in 2002; BLUP: best unbiased linear prediction based on full pedigree and data either only on the target trait (U, univariate model) or also on BW and backfat thickness (M: multivariate model). BLUP models were solved including (L) or excluding (NL) the data on littermates, and the effect of genotypes at SCD/LEPR genes.
FIGURE CAPTIONS

**Figure 1.** Means for live body weight (BW) and backfat thickness (BT) at 200 d of age, carcass lean content and intramuscular fat (IMF) and oleic acid (OL) content in gluteus medius (GM) muscle by genetic type (LW × LS = Large White × Landrace; Duroc A and B are purebred Duroc pigs from different lines). Means with different letters differ (P ≤ 0.05) (adapted from Reixach et al., 2008).

**Figure 2.** Backfat thickness at 180 d (BT) and intramuscular fat (IMF), saturated fatty acid (SFA) and monounsaturated fatty acid (MUFA) content in muscle gluteus medius by SCD g.2228T>C SNP and LEPR c.1987C>T SNP genotypes (TT, CT and CC). Means with different letters differ (P ≤ 0.05).

**Figure 3.** Genetic trends (average predicted breeding value per year of birth, PBV, expressed in additive genetic standard deviation units, $\sigma_a$) for backfat thickness (BT), intramuscular fat (IMF), oleic acid (OL), body weight (BW), and lean weight (LW) in a commercial line during the last decade (adapted from Ros-Freixedes, 2014).
Figure 1
Figure 2