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Genetics of meat quality defects in broilers

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Context: Face to a growing demand, poultry meat should soon become the first meat produced and consumed in the world, with 37% of the total in 2023 (OCDE-FAO, 2014). Poultry meat is now mostly consumed as cut up parts or processed products, which has emphasized the importance of breast meat yield in addition to body weight and feed efficiency. Genetic selection, together with progress in nutrition and veterinary medicine, has led to an incredible increase of the efficiency of birds to produce meat in a reduced rearing time. While 8 weeks were needed to produce a bird of around 2 kg in the sixties, chickens are now reaching 2.2 kg at 5 weeks, with a proportion of breast meat higher than one fifth of live body weight (Petracci et al., 2015). Higher muscle growth has been accompanied by changes in histological and metabolic characteristics of breast muscle. Thus, muscle hypertrophy resulted in an increased fiber size as well as lower glycogen reserve and blood supply (Berri et al., 2001; Berri et al., 2007; Le Bihan-Duval et al., 2008). With the increased use of meat as cut-up parts and processed products, meat quality defects were also revealed. Metabolic defects due to abnormal post-mortem pH fall were first reported. In poultry as in pigs, rapid post-mortem decline (evidenced by low pH value measured 15 min post-slaughter) is responsible for PSE (pale, soft, exudative) meat that exhibits a pale aspect and reduced water-holding capacity (Owens et al., 2000). Variations in the extent of decrease in pH are also responsible for variations in meat quality. Low ultimate pH (measured 24h post-slaughter) results in "acid meat" which is often qualified as PSE-like since it presents similar defects (Barbut, 1997), while high ultimate pH leads to DFD (dark, firm, dry) meat with dark color and poor storage quality (Allen et al., 1997). More recently, a global attention was paid to the increasing incidence of structural defects described as myopathies. The two main defects are White Striping and Wooden Breast that are both characterized by myodegeneration, and regenerative events along with fibrosis and lipodosis (Kuttappan et al., 2016). As for metabolic disorders, they largely affect the sensorial and technological quality of the meat. As it was the case for meat quantity, genetics could be an efficient way to improve meat quality by reducing the occurrence of meat defects. This however depends on the role of genetics in the control of meat quality as well as on the possibility to develop tools such as biological or genetic markers that could improve the applicability and efficiency of selection against meat defects.

Genetic determinism of meat quality traits and defects: Genetic analyses conducted on different chicken lines, experimental or commercial, slow-growing or fast-growing, reared in controlled or commercial conditions, have revealed a significant role of genetics in the control of meat quality traits. Thus, the heritability of breast meat ultimate pH (pHu) ranged between 0.31 and 0.49, that of meat lightness (L^*) between 0.29 and 0.75 (Le Bihan-Duval, 1999, 2001, 2008; Chabault et al., 2012; Gaya et al., 2011). Two independent experiments proved the feasibility of a divergent selection on the two latter parameters and allowed to create useful

resource populations for the study of PSE- and DFD-like meat (Harford et al., 2014; Alnahhas et al., 2014). After six generations of divergent selection on breast meat ultimate pH, mean pHu was estimated at 5.67 in the pHu- line while it was equal to 6.16 in the pHu+ line. This implied that 61% of the breast meat in the pHu- line could be classified as acid or PSE-like ($\text{pHu} < 5.7$) and 63% of breast meat in the pHu+ line as DFD ($\text{pHu} > 6.1$). Divergent selection resulted in a higher glycolytic potential in the *Pectoralis Major* muscle of the pHu- line compared to the pHu+ line. Metabolic changes were also observed in the thigh with a difference of more than 0.3 pHu unit in the *Sartorius* muscle. Regarding meat quality, the divergence of pHu led to breast fillets less pale, less red and less yellow in the pHu+ than in the pHu- line. The reported divergence was also associated with higher curing-cooking yield and lower drip and cooking loss in the pHu+ compared to the pHu- line. Regarding the sensorial quality, the breast fillets of the pHu+ were tenderer and had a less pronounced acidic taste than those of the pHu- line (Alnahhas et al., 2015). After 8 generations of divergent selection on L*, this criterion was increased by 7 points in the High Muscle Color (HMC) line by comparison to the Low Muscle Color (LMC) line. Selection resulted in correlated responses on drip loss and post-mortem pH fall associated to PSE and DFD-like meat. As shown by these experiments, criteria such as lightness or ultimate pH can be efficiently selected. Although we know that genetic variability is partly dependent on the line, these results indicate that these two measurements could be used to monitor meat quality in the selected lines and to limit or prevent the incidence of PSE- and DFD- like conditions.

While divergent selection on breast meat pHu had no impact on abdominal fat or body weight, a favorable effect on thigh and breast meat yield was observed in the pHu+ line. The cross-sectional area of muscle fibers in the pectoralis major was not modified, but significant reduction of the number of capillaries per muscle fiber was observed in the pHu+ by comparison to the pHu- line. The structural and metabolic changes observed in the pHu+ line appeared to be predisposing factors to the development of White Striping (WS) whose incidence of moderate (MOD) and severe (SEV) cases was higher than in the pHu- line (Alnahhas et al., 2016). Regardless of the line, the MOD and SEV cases of WS were phenotypically characterized by increased body weight and breast meat yield compared to normal muscles, confirming the unfavorable relationship between muscle growth and susceptibility to myopathies (Kuttappan et al., 2012; Petracci et al., 2013). WS was found to be highly heritable ($h^2=0.65$), and highly positively genetically correlated with breast meat yield and body weight that appeared to be the major determinants of this defect ($rg = 0.68$ and 0.33 , respectively) in the pHu lines. The intramuscular fat content of the *Pectoralis major* was also strongly correlated with the defect ($rg = 0.64$), which was consistent with the presence of lipidosis described in affected muscles. Bailey et al. (2015) reported lower WS heritability in two commercial lines of broiler chickens characterized by high ($h^2 = 0.34$) or moderate ($h^2 = 0.18$) breast meat yield. Quite low heritability was also obtained for wooden breast ($h^2 < 0.10$). In this second study, the genetic correlations between myopathies and breast muscle yield were null to moderate (0 to 0.25). These differences in magnitude (for heritability and genetic correlations) may be related to differences of scoring, methods of genetic parameters estimation but also history of selection that affects the within line genetic variability and possibility of genetic progress.

New tools for breeding on meat quality and against defects: Current research programs are aiming to identify biological and genetic markers that could be useful for a more efficient selection on meat quality traits and against defects. High-resolution NMR was used to characterize the metabolic signature of the muscle and serum of the pHu+ and pHu- lines and

to look for predictive biomarkers (Beauclercq et al., 2016). Lowering or increasing muscle glycogen by selection affected several muscle and serum metabolites. Because of their high ability to store glycogen in muscle, pHu- birds were using carbohydrates as main source of energy. By contrast, pHu+ birds that are depleted in muscle glycogen, used amino-acid catabolism and lipid oxidation leading to oxidative stress and to an adaptative response of protection by releasing antioxidant molecules. Statistical analyses allowed identifying sets of muscle or serum markers able to discriminate clearly groups of birds with high (DFD) or low (PSE-like) ultimate pH. Serum biomarkers are of special interest since they require a less invasive sampling technique than muscle biopsy. The more parsimonious model established with serum metabolites still ensured a good level of discrimination. It included a set of 7 biomarkers among which xanthine and hypoxanthine were the most discriminant. It is worthwhile to note that the metabolomics analysis of muscle affected by wooden breast revealed some common metabolic characteristics and biomarkers with those evidenced in the pHu+ line (Abasht et al., 2016). Glycogen content was considerably lower in samples taken from Wooden Breast affected birds when compared with samples from unaffected birds. Affected tissues exhibited biomarkers related to increased oxidative stress, elevated protein levels, muscle degradation, and altered glucose utilization. Affected muscle also showed elevated levels of hypoxanthine, xanthine, and urate molecules (the generation of which can contribute to altered redox homeostasis). This suggested again a possible link between the deficit in muscle energy and the susceptibility to myopathies. The use of genetic markers as an alternative to sib-selection is of course a promising way of progress. Few studies have been conducted in order to look for QTL of meat quality and, among the 6633 QTLs reported in Animal QTL database, only 105 concern meat quality traits. The divergent lines selected for meat quality traits constitute relevant genetic materials to identify new genetic markers. The pHu+ and pHu- lines were recently used in order to look for selection signatures and pHu QTLs. Several regions of interest have been revealed and will be further investigated in order to look for candidate genes and mutations.

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