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REVIEW ARTICLE

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A review on pale, soft, and exudative (PSE)-like zones in pork: current knowledge on underlying factors and identification of knowledge gaps for further research

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ABSTRACT

This review examines the multi-factor problem of pale, soft, and exudative (PSE)-like zones in pork causing slicing losses in valuable cuts. Increasing slaughter weight, suboptimal chilling regime, effects of post-slaughter pH and temperature on glycolysis, and protein denaturation seem to be important factors connected to water-holding and colour attributes. The presence and expression of the *n* allele on the *RYR1* gene and the *RN* ⁻ allele on the *PRKAG3* gene increase PSE incidence. Studies involving tissue characterization of destructured muscles have associated oxidative stress and apoptotic processes with the progression of 'PSE-like zones'. Classical PSE meat shows many histological and biological similarities with PSE-like zones, particularly in protein characteristics, but there are differences in underlying physiological mechanisms limiting PSE-like zones to deep *semimembranosus* muscles. Developing early detection methods, efficient carcass handling, mapping underlying physiological mechanisms, and determining genetic background are important future measures to eliminate PSE-like zones and improve pork quality.

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Pork; PSE-like zones; oxidative stress; apoptotic processes; mapping; genetic background

Introduction

The presence of pale, soft, and exudative (PSE)-like zones in pig meat is a major concern due to the economic burden it imposes, and the incidence of PSE-like zones appears to be increasing in the pork industry globally (Balac et al., 1998; Barbut et al., 2008; Vautier et al., 2008). The undesirable classical PSE condition in meat is characterized as pale colour, soft texture, and excessive exudation. In the late 1990s, PSE-like zones began to emerge as a problem, especially in the industrial slicing of cooked hams, where they reduce sliceability. The condition was originally termed 'structureless meat', as sliceability is highly related to meat structure (Vautier et al., 2008). Different terms have been used since for this problem, e.g. PSE-like defect, PSE-like zones, destructured meat, two-toning, PSE-like muscle defect, etc. Causative factors in classical PSE, such as the *n* allele on the *RYR1* gene (Halothane gene; hal^n allele) and the *RN* ⁻ allele on the *PRKAG3* gene (Rendement Napole gene; *RN* ⁻ *200Q* allele), may still apply in the development of PSE-like zones, depending upon region or breed, e.g. presence of a hal^n mutation in Pietrain pigs in France (Schwob et al., 2018) and of an *RN* ⁻ mutation in Hampshire pigs in some European countries (Bertram et al., 2000; Josell, 2002; Lindahl et al., 2004). Therefore, the term 'PSE-like zones' is used in this review as a more inclusive term covering long-known defects, but mainly focused on recently emerging defects with similar features (pale, soft, exudative), but unknown origin.

PSE-like zones are now a widely discussed problem and in many aspects are comparable to classical PSE. Classical PSE has been studied for over 50 years in pigs subjected to intense genetic selection for fast growth, efficient feed conversion, and high lean meat content, which can lead to the development of pre-slaughter pig stress syndrome (PSS), resulting in PSE meat (Eikelenboom & Minkema, 1974; Lee & Choi, 1999; Adzitey & Nurul, 2011). The *n* allele on the *RYR1* gene causes halothane hypersensitivity and also escalates post-mortem glycogenolysis metabolism, leading to rapid pH fall, while the *RN*⁻ *200Q* allele on the *PRKAG3* gene prolongs the extent of post-mortem pH fall but without any change in its rate, but both produce classical PSE meat (Laville et al., 2005). PSE mainly affects white glycolytic muscles of hams and loin, while PSE-like zones are mostly limited to the *adductor* muscle

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and deep regions of the *semimembranosus* muscle, which constitutes a large part of the ham (Franck et al., 1999; Laville et al., 2003; Vautier et al., 2008). This indicates that there are differences in the underlying physiological mechanisms causing classical PSE meat and PSE-like zones. Another difference is that hams with PSE-like zones appear in some studies to be more related to ultimate pH value, rather than early pH value, and to be associated with a high rate of early post-mortem glycogenolysis (Vautier et al., 2008). There are many histological and biological similarities between classical PSE and PSE-like zones, e.g. the protein denaturation observed in PSE-like zones resembles that induced by the acceleration of post-mortem glycogenolysis (Laville et al., 2005), while muscle fibre alignment in PSE-like zones shows a significant increase in inter-fibre spacing and presence of extracellular fluid accumulation (Laville et al., 2005) and exhibits histological commonalities with classical PSE meat (Penny, 1977; Fialik, 1983).

Some previous studies have found that high slaughter weight is positively (unfavourably) correlated with the occurrence of PSE-like zones in muscles, while low ultimate pH value is negatively correlated (Franck et al., 1999; Le Roy et al., 2001). Biochemical studies have revealed a strong correlation between PSE-like zones and glycolytic potential (Minvielle et al., 2001; Laville et al., 2005), while mass spectrometry analysis has indicated the involvement of biological pathways, such as abnormal fast post-mortem glycolysis, in the determination of PSE-like zones in muscles (Laville et al., 2005). Fast post-mortem glycolysis leads to protein denaturation due to a rapid decrease in pH while carcass temperature is still high (Briskey & Wismer-Pedersen, 1961), causing decreased water-holding capacity (WHC) and increased water loss (Offer, 1991) and pale appearance due to light scattering (Goldspink & McLoughlin, 1964). Potential protein markers recently identified reflect oxidation–reduction processes and apoptosis in the internal part of ham muscles (Théron et al., 2019). Meat from PSE-like zones looks like extreme cases of classical PSE generated due to abnormally high carcass temperature and high rates of post-mortem pH fall, as can happen in halothane-sensitive pigs (Laville et al., 2005).

Overall, pork quality is governed by multiple factors, including animal production conditions, animal genetics, and conditions in the processing stages, including chilling, handling, and storage of carcasses (Wenk et al., 2000; Klont & Klont, 2010). Unappealing pale appearance, reduced juiciness, decreased processing yield during high-speed mechanical slicing, and increased cooking losses make meat with PSE-like zones an unpopular choice among customers. Thus, the development of efficient chilling methods and steps to reduce oxidative stress and apoptosis, monitored with potential biomarkers, could be important future measures to overcome problems with PSE-like zone disorder. This review paper summarizes current knowledge, focusing on dominant factors resulting in PSE-like zones, measures to minimize the incidence of this problem, and suggested future directions to eliminate the problem.

Factors important in the development of PSE-like zones

Slaughter weight

During the past few decades, pig carcass weight has increased worldwide, with Swedish pigs following a similar trend (Figure 1). This is due to improved genetic selection for reduced fat deposition, leading to increased growth and leanness and higher feed conversion, and to improvements in management and feeding regimes. Carcass weight is an important factor affecting pork quality (Kim et al., 2005).

The rate of lean gain decreases, and fat gain increases, with increased slaughter weight, and thus with slaughter age (Shields et al., 1983; Gu et al., 1992; Ellis et al., 1996; Povod et al., 2019). However, continuous genetic improvements in growth and carcass leanness in modern pig breeding have delayed the phase in which fat gain rapidly increases, leading to larger carcasses with less fat (Wu et al., 2017). Fat content is one of the criteria influencing economically optimal slaughter weight, and the genetic improvements in growth and carcass leanness have allowed increases in slaughter weight in commercial production. However, some recent reports on this gradual slaughter weight increase have raised concerns regarding effects on carcass and meat quality, i.e. increased weight and size of the

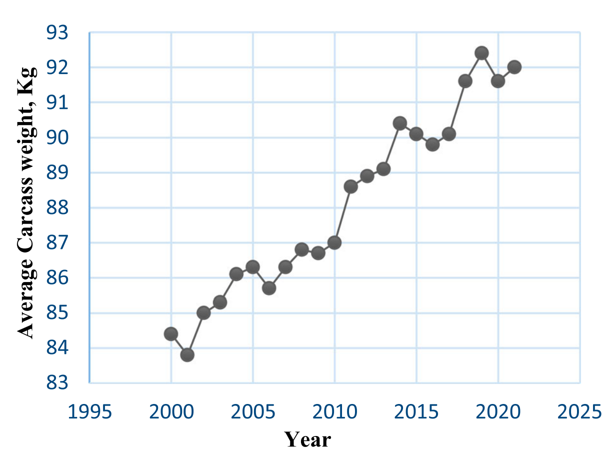

Figure 1. Change in average carcass weight of Swedish pigs over time, 2000–2022 (source: based on data from Gård & Djurhälsan, 2022).

carcass cuts and associated significant effects on meat, adipose tissue, and bone content (Peláez et al., 2017; Mykhalko et al., 2022). In particular, the development of PSE-like zones has been extensively associated with higher slaughter weight (Franck et al., 1999). Some previous studies have found a relationship between gender and slaughter weight, and between season and slaughter weight, in the prevalence of classical PSE, i.e. pigs gender with higher slaughter weight and pigs slaughtered in summer being more prone to develop the condition (Guàrdia et al., 2004; Djordjevi et al., 2016). A recent pilot study found similar results for PSE-like zones, where female pigs with higher slaughter weight compared with males developed more PSE-like zones (Mashood et al., 2023). Higher muscular mass and increasing carcass weight may slow down the post-mortem temperature decline in deeper muscle regions, with the temperature decline being significantly slower in larger hams compared with smaller hams. Further increases in carcass weight will lead to even larger hams and continue to boost the incidence of PSE-like zones in the core of hams (Kurt et al., 2020).

Carcass chilling

Post-slaughter carcass chilling rate is a frequently mentioned factor influencing meat quality and could be important in the development of PSE-like zones in commercial pork (Vautier et al., 2010). Chilling affects pH decline during the first few hours post-mortem and influences meat quality characteristics such as drip loss and colour (Minvielle et al., 2001; Kurt & Klont, 2010). Extremely low chilling temperature early post-mortem, before reaching the ultimate pH, can cause cold shortening of muscles, resulting in less tender meat (Jones et al., 1987; Jeremiah et al., 1992). Previous studies have found that the incidence of PSE-like zones within hams decreases with increased chilling rate. In one study, the frequency of PSE in hams increased more than three-fold due to slow chilling, while drip loss was reduced at fast chilling rates (Vautier et al., 2010). This influence of chilling rate on drip loss may be due to temperature effects on post-mortem energy metabolism (Tomović et al., 2008). The faster chilling rate of a carcass, together with a slow post-mortem pH decline, can reduce the incidence of PSE-like zones (Kurt et al., 2020).

Interaction between high temperature and low pH

Interactions between the rate and extent of post-mortem pH fall and temperature in the muscle influence meat quality attributes such as WHC and colour. High temperature interacts with low pH in PSE meat to cause denaturation and subsequent loss of functionality of the proteins, leading to a reduction in WHC (Adzitey & Nurul, 2011). The myofibrillar components expel fluid into extracellular spaces and cutting such meat results in exudates, reflecting the poor WHC. Light scattering from the surface of affected meat is probably due to differences in the refractive index of the sarcoplasm and myofibrils. Shrinkage of the myofilament lattice increases the amount of light reflected, making PSE meat less red and more yellow. The low pH in PSE also promotes the oxidation of haem pigments from purple or red myoglobin and oxymyoglobin to brown metmyoglobin (Warriss, 2000). The associations between typical pork meat defects (PSE, normal, dark-firm-dry (DFD), etc.) and the rate and extent of pH decline (Matarneh et al.. 2017) and temperature interactions (Honikel, 1999) are shown in Figures 2 and 3, respectively.

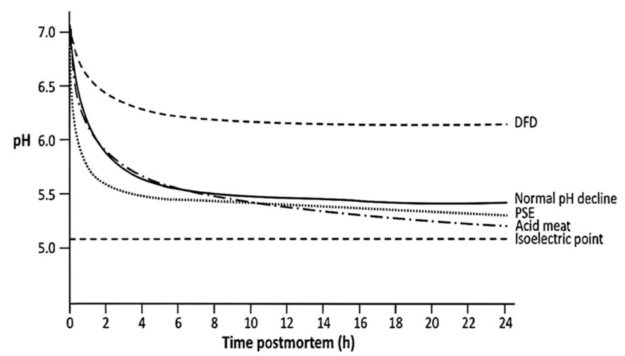

Figure 2. Schematic representation of typical pH changes for different pork defects (source: Matarneh et al., 2017).

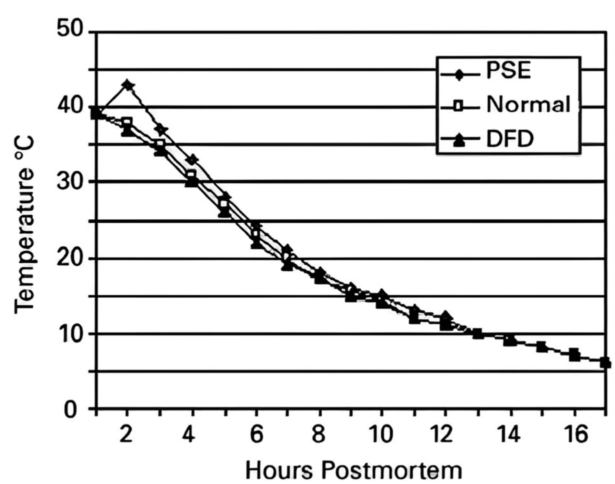

Figure 3. Schematic representation of typical temperature curves for different pork defects (source: Honikel, 1999).

When muscle is converted to meat, pH and WHC change dramatically. All proteins have an electrical charge that changes with the change in pH. A higher pH of meat means a higher net negative charge of proteins and higher WHC, while a pH at which the net electronic charge on proteins is zero (isoelectric pH, pH_i) leads to low WHC because of minimal attraction between proteins and water (Hunt et al., 2011). A recent study found a significant correlation between WHC measured as drip loss and bio-impedance, with reduced bio-impedance response linked to higher drip loss. This indicates that bio-impedance can be a useful marker, in particular for monitoring the structural integrity of meat (Suliga et al., 2022). However, some recent studies have questioned the accuracy with which individual quality parameters can predict PSE-like zones, since relationships between pH and actual presence of this quality defect may be weaker than expected from earlier studies. A recent pilot study found no interaction between ultimate pH and the presence of PSE-like zones (Mashood et al., 2023), contradicting previous findings that ultimate pH is the best predictor of PSE-like zones (Vautier et al., 2008). Similarly, a study by Suliga et al. (2022) found that links between quality parameters, including correlations with bio-impedance parameters (P_y), were typically moderate or weak, which is in line with findings in other studies exploring such correlations (Gjerlaug-Enger et al., 2010; Antosik et al., 2022), suggesting that individual test methods probably convey some unique information related to ham defects and can therefore complement each other.

Temperature has a fundamental effect on the rate of biochemical reactions and to some extent on muscle pH during the post-mortem period (Figure 4). According to the Arrhenius temperature coefficient ($Q_{10} \approx 2$), the rate of metabolic reactions doubles for every 10°C

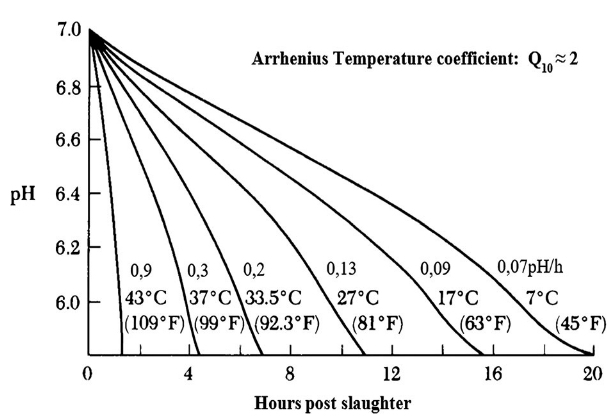

Figure 4. Effect of meat temperature on pH reduction rate (source: modified from Marsh, 1954).

temperature increase, and halves for every 10°C decrease (Chemguide, 2013). Low ultimate pH value appears to be directly correlated with PSE-like defects (Franck et al., 1999). A class prediction curve shows a reduced risk of PSE-like zones with an increasing ultimate value of pH (Figure 5), indicating that it seems to be the best predictor for this defect (Vautier et al., 2008). Genetic evolution in some recent genetic pig lines has resulted in the slope of risk for PSE-like zones increasing with increasing pH at 24 h post-mortem (Schwob et al., 2018).

Effect on glycolysis

Excessively rapid post-mortem glycolysis generates heat, which keeps the carcass warm even with pH values near the ultimate pH level. This was previously regarded as the most common cause of PSE-like defects following normal chilling procedures (Wismer-Pedersen, 1959; Lawrie, 1960). However, it is now generally agreed that abnormal post-mortem glycolysis in PSE-like defects has a multifactor background, i.e. it is caused by many, often interrelated, factors such as Ca^{2+} regulation, muscle ATPase activity, glycogenolytic enzymes, substrate (glycogen) regulation, and muscle fibre type (Bowker et al., 2000). Post-mortem glycolysis rate in pigs increases if the animal is stressed prior to slaughter (Offer, 1991). High post-mortem muscle temperature results in a fast rate of pH decline and the effects on enzyme activity and subsequently on the rate of glycolysis (Newbold & Scopes, 1967). A previous proteomic study found disruption and corrugation of fibres, with significant increases in inter-fibre spacing and accumulation of amorphous extracellular fluid, alongside protein changes due to fast post-mortem glycolysis, resulting in the occurrence of PSE-like zones (Laville et al., 2005). A biochemical study showed that the glycolytic potential of muscles was positively correlated with the presence of PSE-like zones (Minvielle et al., 2001).

Denaturation of proteins

The interaction of high temperature and low pH immediately after slaughter influences meat quality by causing greater protein denaturation and loss of protein functionality (Briskey & Wismer-Pedersen, 1961; Charpentier, 1969; Goutefongea et al., 1971) resulting in reduced WHC, i.e. elevated water loss (Offer, 1991) and altered light scattering characteristics, giving a pale appearance (Goldspink & McLoughlin, 1964). Myosin denaturation results in the shortening of myosin heads and a reduction in inter-fibre space, causing more fluid ejection into extracellular space, resulting in the meat

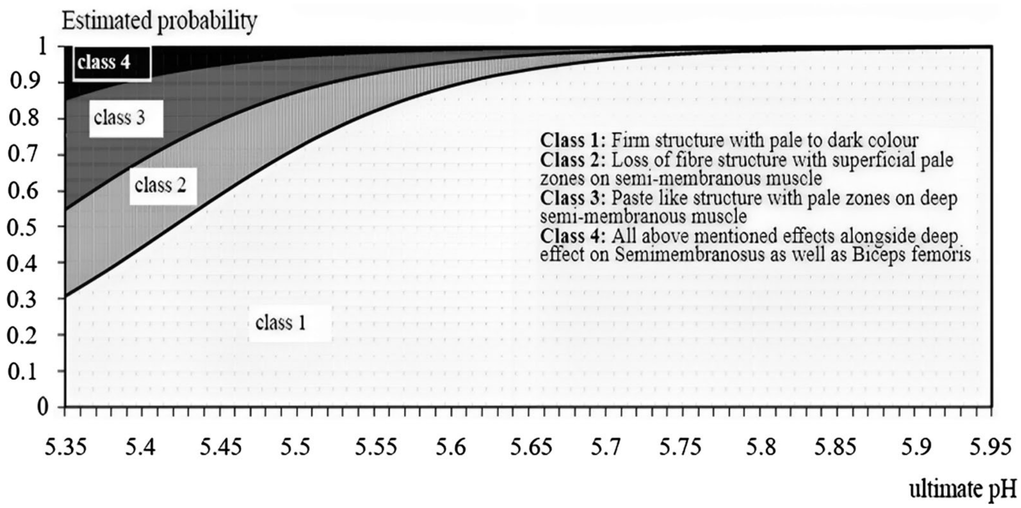

Figure 5. Class prediction curves for PSE-like zones based on ultimate pH (source: Vautier et al., 2008).

becoming pale, soft, and exudative (Offer, 1991; Bertram et al., 2001). Denaturation of sarcoplasmic protein and sarcomere shortening may increase light reflectance from the surface, making it paler in appearance (Swatland, 2004).

The differential intensity of proteins was observed in a study involving label-free quantitation analysis of 10 normal hams and 10 PSE-like hams (Théron et al., 2019). Analysis of samples from the inner and outer parts of *semimembranosus* muscles in each of the PSE-like hams and from the inner part of *semimembranosus* muscles in each of the normal hams revealed that in hams with PSE-like zones, 12 proteins showed higher intensities in outer *semimembranosus* muscle and 20 showed higher intensities in inner *semimembranosus* (Théron et al., 2019). In further proteomics analysis involving structural characterization of 64 proteins in the inner part of *semimembranosus* muscles from PSE-like and normal hams by label-free quantitation, 15 proteins were found to be over-represented in the internal part of hams with PSE-like zones compared with normal hams, while 14 proteins were over-represented in normal hams compared with the internal part of defective hams (Théron et al., 2019). Thirty-five proteins did not show differential expressions between PSE-like and normal hams (Théron et al., 2019). Another proteomics study revealed the presence of 11 proteins with different functional roles that may be linked to structural degradation and are unique to either good-quality or poor-quality hams (Suliga et al., 2022). Cross-comparison of all proteins identified in inner and outer parts of PSE-like zones (Théron et al., 2019) and good-quality and poor-quality meats (Suliga et al., 2022) revealed no similarities except for the presence of Cytochrome C and adenylosuccinate synthetase isozyme 1, where the differences were probably partly due to the different pig breeds used in the two experiments. The studies also differed considerably in other aspects, e.g. in how PSE-like and normal hams were pre-selected (visual ranking vs. multi-parameter, instrument-based identification), general design, and proteomic data analysis.

Spectral fingerprinting of pig plasma using MALDI-TOF mass spectrometry or ATR-FTIR spectroscopy can be employed to obtain protein and chemical function fingerprints. MALDI-TOF mass spectrometry has been found to be better suited to predicting normal hams without the defect, while ATR-FTIR spectroscopy is better in predicting the PSE-like muscle defect (Théron et al., 2020).

Genetic factors

In some pig breeds, including those widely used in Swedish production systems, breeding work has eliminated the recessive *n* allele on the major gene *RYR1* (ryanoid receptor 1), also known as the halothane gene, and reduced the frequency of the dominant RN^{-} allele (R200Q substitution) on the *PRKAG3* gene (protein kinase AMP-activated non-catalytic subunit gamma 3), in efforts to overcome classical PSE (Karlsson et al., 2019). However, in some genetic lines, these alleles in the two major genes still have an impact, with the PSE defect being 3.3-fold more frequent in pigs that are heterozygous (*Nn*) for the *RYR1* gene than in homozygous (*NN*) pigs (Schwob et al., 2018). It is well-known that these two major genes have direct impacts on technological pork quality (Rosenvold & Andersen, 2003). Animals that are homozygous for the mutant *n* allele of the halothane gene (*RYR1*) can develop so-called porcine stress syndrome, also known as malignant hyperthermia or transport myopathy. This syndrome can be triggered by pre-slaughter stress and by several types of anaesthetic, including halothane, giving the gene its popular name, and results in meat being pale and having low WHC. The *PRKAG3* gene has been called the acid meat gene or Hampshire effect, and meat from some animals carrying the *RN* $^{-}$ *200Q* allele has low ultimate meat pH, resulting in low WHC.

Pre-slaughter stress triggers a high rate of post-mortem glycolysis in both homozygous and heterozygous pigs for the *n* allele of the halothane (*RYR1*) gene, but the effect is more severe in homozygous (*nn*) pigs (Mitchell & Heffron, 1982; Lundström et al., 1989). This results in low pH values and high temperature during early post-mortem inducing pale, soft, and exudative meat characterized by high protein denaturation (Bendall & Wismer-Pedersen, 1962). The *RN*$^{-}$ *200Q* allele on the *PRKAG3* gene is associated with high muscle glycogen stores and extended post-mortem pH decline (Estrade et al., 1993). Meat from pigs carrying this *RN*$^{-}$ allele is often called acid meat, due to its low pH value and increased glycogen conversion into lactate (Naveau, 1986), which is again associated with pale meat and low WHC (Roy et al., 2001). Meat from carriers of the *RN*$^{-}$ *200Q* allele shows more denaturation of myosin and sarcoplasmic proteins (Deng et al., 2002).

Oxidative stress and apoptosis

Oxidative stress and apoptosis have been identified as factors involved in the development of PSE-like zones in hams (Théron et al., 2019). Oxidative stability is a very important meat quality attribute and is mainly affected by genotype and feeding regime (Rosenvold & Andersen, 2003). Recent developments in mass spectrometry imaging indicate local heterogeneity between molecular maps of normal hams and inner and outer parts of defective hams that develop PSE-like defects. A study on relative protein abundance, expressed in linear mode at a mass range (m/z) based on four peaks in mass spectrum data, found that the first two (with lower m/z) had significantly higher intensity in the inner part of PSE-like zones compared with the outer part of PSE-like zones and normal hams (Théron et al., 2019). This could be due to oxidation of arginine resulting in a carbonyl product (glutamic semialdehyde), a very well-known alteration in meat products (Estévez, 2011). This agrees with previous findings that proteins from PSE chicken breasts show more susceptibility to oxidative stress due to lower pH and impaired activity of endogenous antioxidant enzymes, i.e. CAT, GSH-Px, SOD, and proteolysis (Estévez, 2015; Carvalho et al., 2017).

Protein–protein interactions network analysis (PPIN) has shown that two specific protein networks are over-represented in the inner part of *semimembranosus* muscle with PSE-like zones, in comparison with the outer part of the same muscles (Théron et al., 2019). Statistical enrichment analysis of the same samples revealed that mitochondria were over-represented with seven corresponding proteins, while the oxidation–reduction process was over-represented with nine proteins, indicating spatial localization of the PSE-like defect within the muscle linked to oxidation–reduction processes (Théron et al., 2019). There are also previous reports of PSE poultry meat showing susceptibility to protein oxidation during chilled storage (Carvalho et al., 2017).

Results obtained in label-free quantitation, which is a mass spectroscopy method for determination of the relative amount of proteins, combined with network analysis suggest a link between PSE-like defect and apoptosis through expressing mitochondrial pro-apoptotic activity in muscle destruction (Théron et al., 2019). Similarly, previous studies using immune blotting and enzyme activity analysis have shown that apoptotic processes occur in *longissimus porcine* muscle, where PSE meat compared with red, firm, and non-exudative meat showed decreased expression of anti-apoptotic factor BC1-2, increased expression of pro-apoptotic factor BAX, increased activity of lysosomal enzyme (Caspase 3) in the apoptotic pathway, and also increased expression of cytochrome C (Guo et al., 2016).

Concluding remarks and suggested future directions

This review of previous studies showed that the occurrence of PSE-like zones, which is a serious meat quality problem for today's pork industry, has a multi-factor background, but the unfavourable status of any of these factors will result in the development of PSE-like zones. The major differences between classical PSE and PSE-like zones lie in their origin, location in the pig carcass, and relationship to pH value. Classical PSE derives from the expression of the *n* allele on the *RYR1* gene (halothane gene; *hal*^{n} allele) and the *RN*$^{-}$ allele on the *PRKAG3* gene (Rendement Napole gene; *RN*$^{-}$ *200Q* allele), is related to early post-mortem pH value and is mostly present in white glycolytic muscles of ham and loin. The origin of PSE-like zones is still unknown, but may mainly be related to ultimate pH value, and the presence of such zones is limited to *adductor* and deep *semimembranosus* muscles. However, it is important to understand the interaction between underlying factors such as increasing slaughter weight over time, chilling regime during processing of carcasses, and high temperature and low pH

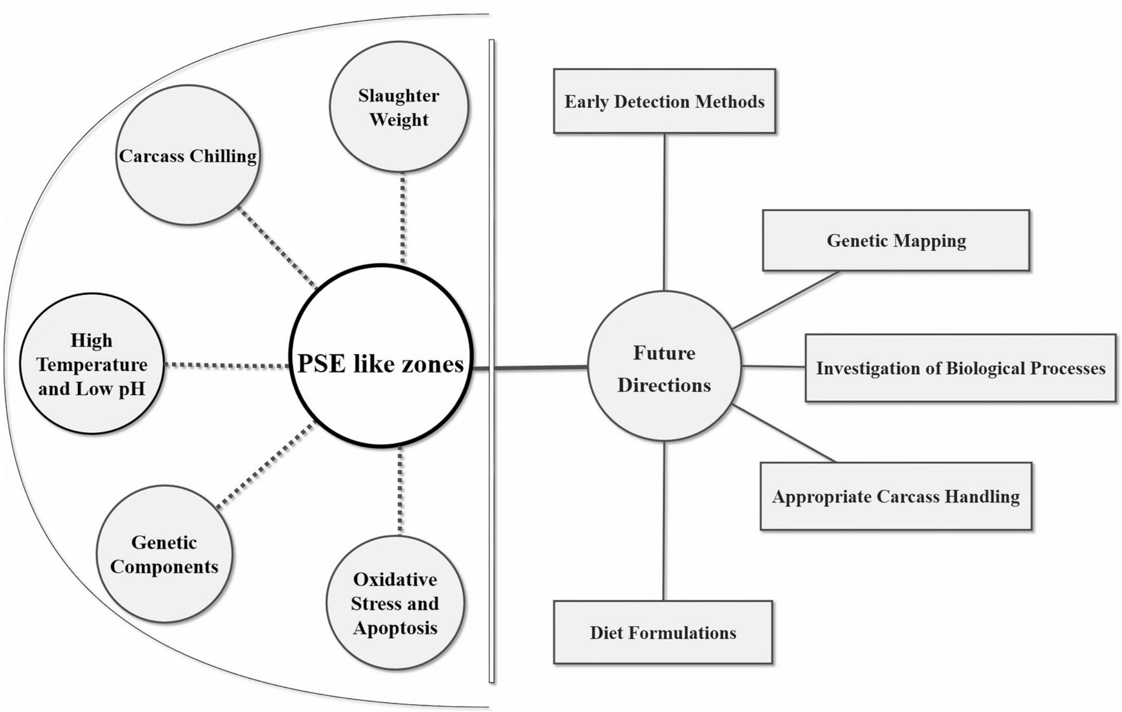

Figure 6. Significant factors in the development of PSE-like zones in pork and suggestions for future research directions.

and the effect on glycogen breakdown in muscles and denaturation of muscle proteins. Our review covered some studies analysing genetic factors contributing to the development of PSE-like zones. There is a research gap as regards why, despite the reduced frequency of the *n* allele on the *RYR1* gene and the RN^{-} *200Q* allele on the *PRKAG3* gene, there are still reports of increasing incidence of PSE-like zones in commercial pig populations, even those that do not show these classical gene mutations. Recent reports indicate the involvement of two major biological processes, oxidative stress and apoptosis, in the initial development of PSE-like zones, but more studies are needed to better understand and confirm the involvement of these processes.

The review also identified other opportunities and research directions to increase understanding of this meat quality defect, as summarized in Figure 6. High post-mortem temperature seems to be a trigger for the development of PSE-like zones. To decrease the incidence of this meat defect, early detection techniques and methods are needed to control changes in ultimate pH and internal temperature of carcasses, in order to reduce pH fall (and increase ultimate pH) and prevent rapid decline in internal muscle temperature and thus in the rate of glycolysis and protein denaturation. Maintaining an average range of carcass weight that can be chilled efficiently could be one future direction. Other interesting aspects to investigate are the effects of gender and season on the occurrence of PSE-like zones and the involvement of biological processes such as oxidative stress and apoptosis and potential biomarkers of these. Analysis of the effect of a diet containing different antioxidants to change the oxidative stability of meat would also be interesting. Finally, defining suitable genetic markers for PSE-like zones would be useful in genetic selection to eliminate this disorder.

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