Session 3 Meat quality

L 1 DETERMINANTS OF ULTIMATE pH OF MEAT

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Introduction

Ultimate pH (pHu) of meat is a major quality determinant. It influences, water-holding capacity, color, tenderness, flavor and shelf life of meat (Pearson and Young, 1989; NPPC, 2000). Variation in meat quality costs the US meat and poultry industry millions of dollars each year (Vimini 1996; Cannon et al. 1996; Kauffman, 1996). If we can control meat pHu, we can reduce variation in meat quality. The current understanding of determinants of meat pHu is limited. Many potential pHu determinants have been identified. None of the factors can explain more than 50% of the variation in pHu. The relationship among the various factors has not been determined. Only once we know which factors determine pHu, can we consistently produce meat with a specific pHu and, thus, consistent meat quality.

Ultimate pH and meat quality

Ultimate pH is a main quality determinant. It influences the water-holding capacity, color, tenderness and shelf-life (Pearson and Young, 1989; NPPC, 2000). In pork color and pHu are related; a higher pHu resulting in a darker color (Warriss and Brown, 1987; Kauffman et al., 1993). A lower pHu is associated with higher drip losses in pork, broiler breast meat and turkey (Warriss and Brown, 1987; Kauffman et al., 1993; Barbut, 1997; van Laack et al. 2000b). In beef, a pHu of 5.5 seems to be a prerequisite for tenderness (Watanabe et al., 1996; Purchas and Yang, 1997; Purchas et al., 1999). At higher or lower pHu the beef is tougher.

Pork from animals carrying the RN (Rendement Napole) gene has a lower pHu than pork from animals without the RN-gene (Monin et al., 1987; Lundström et al. 1996; 1998). RN pork has a lower water-holding capacity and paler color than non-RN pork (Naveau, 1986; LeRoy et al., 1990; Fernandez et al., 1992).

Pale, soft, exudative (PSE) and red, soft, exudative (RSE) pork is undesirable because it has a low water-holding capacity. PSE and RSE quality results from an accelerated post-mortem glycolysis (Greaser, 1986; Pearson and Young, 1989; van Laack et al., 2000a). At pHu higher than 5.7, rate of pH decline does not influence pork quality, and PSE and RSE pork quality problems do not occur (Fernandez et al., 1994). Thus, production of pork with pHu above 5.7 would result in constant quality meat with high water-holding capacity and reddish pink color. In the US, the National Pork Producers Council (NPPC) recommends a pH>5.7 for the production of 'good' quality pork (NPPC, 1998).

Poultry quality problems may be controlled by pHu manipulation. As an example: Pale broiler breast meat has a lower water-holding capacity than normal-colored broiler breast meat. Compared to the normal broiler breast meat, pale meat has 8-10% lower cooking yields (van Laack et al., 2000b). The pale color and reduced water-holding capacity of broiler breast meat, correlate with a lower pHu; pale broiler breast meat has a pHu of 5.70 vs. 5.96 in normal-colored meat (van Laack et al., 2000b). Pale broiler breast meat and the associated reduced yields cost the poultry industry millions of dollars per year (Vimini, 1996). The cause of the lower pHu in pale broiler breast meat is not known. Increasing the pHu of pale meat to that of normal-colored meat results in a product that is comparable to the normal-colored product (Garcia et al., 1999).

Clearly, ultimate pH is an important quality determinant for meat in general. Producing meat of a specific pHu would reduce the variation in meat quality and reduce the occurrence of quality defects such as PSE and RSE pork. To consistently produce meat with a specific pHu, we need to know that factors determine pHu. Without such understanding predicting the impact of new animal and meat production practices on meat quality will be impossible. A better understanding of what determines pHu would help in consistent production of the desired quality.

Possible determinants of ultimate pH

Glycogen concentration, glycolytic potential

Glycogen is the substrate for energy production. Post mortem, glycogen is converted into lactate and energy. The formation of lactate causes the post-mortem pH decline (Greaser, 1986). Thus, pHu would be expected, at least in part, to be a function of muscle glycogen level at death. Measurement of glycogen concentration in the muscle is rather difficult because upon muscle stimulation (=sampling) glycogen is rapidly converted to lactate. Rather than measuring glycogen levels, glycolytic potential (GP) is measured. Glycolytic potential includes all components that can be converted into lactate. Glycolytic potential does not change post mortem (Monin and Sellier, 1985; Maribo et al., 1999). Thus, GP is a consistent and accurate measure of muscle substrate glycogen concentration at the time of death.

Although GP is a determinant of pHu, GP alone does not fully explain pHu variation. Studies by Warriss et al. (1989), Fernandez et al. (1992), Maribo et al. (1999), van Laack and Kauffman (1999) and van Laack et al. (2001), demonstrate that GP variation accounts for a maximum of 40% of the difference in pHu of pork loin. The correlation coefficient between pHu and GP is dependent on the range of pHu included. Since glycolytic potential is a linear and pH a logaritmic characteristic, a linear relationship may seem unlikely. Therefore, we converted pH to hydrogen concentration and recalculated the correlation coefficient. GP accounted for 42% of the variation in hydrogen concentration.

The pHu of horse meat and beef are similar, but glycogen levels in horse meat are higher than those in beef. The GP of pigs from

pigs that carry the RN-gene is more than 25% higher than the GP of pork from pigs without the RN-gene. The difference in pHu of RN and non-RN pork is only about 0.1 units (Monin et al., 1987). Lactate production (=pH decline) seems to stop before all glycogen is consumed (Monin et al., 1987; van Laack and Kauffman, 1999; Immonen and Puolanne, 2000). Immonen and Puolanne (2000) found that the relationship between pH and residual carbohydrate concentration in beef was curvilinear. At pH values <5.8, the residual glycogen concentration varied from 10 to 83 µmol/g. The variation in residual glycogen was independent of ultimate pH. Clearly, other factors in addition to substrate concentration influence pHu.

In the 1950's researchers recognized two forms of glycogen: free and bound (Bloom et al., 1950; Russell and Bloom, 1955). Later these forms were called lyo and desmo glycogen (Charpentier et al., 1966). Meat scientist studied these forms of glycogen as they related to rate of glycolysis but did not determine a possible relationship with ultimate pH (Wismer-Pedersen and Briskey, 1961; Charpentier et al., 1966). More recently the terms macroglycogen and proglycogen have been introduced. The two forms differ in protein content, size and solubility. Proglycogen contains 10% protein and is acid insoluble. It has a MW of 400 kDa. Macroglycogen has a much larger MW (10^7), contains less than 1% protein and is acid soluble (Lomako et al., 1991). Adamo and Graham (1998) suggested that proglycogen is the precursor of macroglycogen. Glycogen stored as proglycogen is readily available for energy production. Increases in glycogen above a certain level result from increases in macroglycogen, the proglycogen level remains relatively constant (Lomako et al., 1991; Adamo et al., 1998). Conversion of macroglycogen to proglycogen seems to occur faster than breakdown of proglycogen to glucose. Currently, we can only speculate about the importance of the two forms of glycogen in pork. Possibly, the residual glycogen in RN pork is present as the 'unavailable' macroglycogen. We did not find a relationship between proglycogen concentration and pHu (van Laack unpublished data). How post-mortem conditions influence this conversion of macroglycogen to proglycogen needs to be evaluated.

Creatine phosphate

Scopes (1974) evaluated factors that may influence pHu. Using a reconstituted muscle system, he found that creatine phosphate influenced pHu. Higher creatine phosphate levels were associated with higher pHu. Creatine phosphate reacts with ADP to form ATP (=energy). Creatine phosphate is readily available for regeneration of ATP (and thus for energy production) and is broken down immediately after slaughter, before glycogen or glucose. When an animal is stressed, creatine phosphate levels will decrease rapidly. Stress shortly before slaughter will result in lower creatine phosphate levels immediately after slaughter. Possibly, variation in pHu results from differences in creatine phosphate levels at slaughter. Yang (2000) reported that creatine phosphate concentration and pHu are not related. In his study, samples were taken soon after slaughter. At that time creatine phosphate may already have been broken down. To get an accurate measure of creatine phosphate levels, samples need to be taken at death. To determine a possible relationship between creatine phosphate and pH, measurement of the concentration of this compound, lactate and creatine at several times post mortem is required.

Glycogen phosphorylase and AMP deaminase

Using a model system consisting of all glycolytic enzymes in a solution, Scopes (1974) determined that, if there is enough glycogen to produce lactate, pHu was determined by the activity of two enzymes: glycogen phosphorylase and AMP deaminase.

Glycogen phosphorylase a, the active form of phosphorylase, influences the conversion of glycogen into glucose-1-phosphate and, thus, the substrate availability. Scopes (1974) reported that higher levels of glycogen phosphorylase resulted in a lower pHu of the system. Van Laack et al. (2001) found similar results in pork muscle. Glycogen phosphorylase activity explained 28% of the different in pHu; a higher activity was associated with a lower pHu.

Glycolysis requires glucose, ADP and phosphate to proceed (Greaser, 1986). Glycolysis stops if either glucose or ADP runs out. AMP-deaminase converts AMP to IMP. Thus, adenine nucleotides are irreversibly converted to IMP, ADP is no longer available for resphosphorylation, and glycolysis stops. Scopes (1974) reported that higher amounts of AMP-deaminase resulted in higher pHu. Van Laack et al. (2001) studied the relationship between AMP-deaminase and pHu of pork. Variation in AMP-deaminase explained only 10% of the variation in pHu. AMP-deaminase activity was measured under 'optimal' in vitro conditions. We cannot exclude that the activity in the muscle (*in vivo*) was different.

Recently, Milan et al. (2000) identified the mutation associated with excess glycogen content in RN carrier pigs as AMPK-kinase. AMPK-kinase is activated by an increase in the ratio of AMP to ATP. Activated kinase stimulates ATP-producing pathways and inhibits ATP-consuming pathways. Milan et al. (2000) found that AMPK-kinase activity was higher in non-RN carrier pigs than in RN-carrier pigs. How and if AMPK kinase affects glycogen breakdown, glycolysis, and possibly pHu, has not been determined.

Buffering capacity and titratable acidity

The pH of a system is not only determined by the presence of acids and bases, but also by the presence of strong ions (Stewart, 1981). In chicken (van Laack et al., 2000b) and pork (van Laack and Kauffman, 1999) muscles with similar lactate levels may have a different pHu. Differences in buffering capacity may explain these differences in pHu.

Buffering capacity is the ability of weak acids to resist a change in pH when acid or alkali is added. Muscle fibers have the characteristics of weak acids. The compounds that affect the buffering capacity in the pH range of meat are: phosphate compounds, histidylimidazole residues of proteins and dipeptides (Kivikari, 1996). Olsman and Slump (1981) reported that differences in buffering capacity of different types of muscles are due to differences in histidine content. Puolanne and Kivikari (2000) explained differences in buffering capacity by differences in the amounts of the dipeptides carnosine and anserine. They claim that differences in buffering capacity are too small to give a solid basis for expecting differences in pHu. In pork longissimus muscle (n=60) pHu and buffering capacity were correlated (r=-0.43) (van Laack et al., 2001).

If the differences in pHu at same lactate concentration cannot be explained by differences in buffering capacity, other acids must contribute. Titratable acidity is a measure of the quantity of acid in meat. The change in free amino acids or carboxyl groups will result in an alteration of titratable acidity (Madovi, 1980). Titratable acidity of a muscle is influenced by processes such as cooking. If and how ante- and post-mortem biochemical factors influence titratable acidity needs to be determined.

ATP-ase activity

Selection for a leaner muscle leads to selection of animals with a larger percentage of type IIb or white muscle (Solomon et al., 1998). White or type IIb fibers are characterized by a larger diameter, less fat, a glycolytic metabolism and faster contraction, or higher ATP-ase activity. Type Ia or red fibers contain more fat, are smaller and are mostly oxidative in metabolism (Pearson and Young, 1989). The pHu of white muscles is lower than pHu of red muscles which contain more type Ia fibers. The lower pHu of white fibers can be explained by the fact that these muscle fibers are predominantly glycolytic; they contain more glycogen and their metabolic enzymes allow for a rapid conversion of glycogen into lactate.

ATP-ase converts ATP into ADP, Pi and energy. Rigor onset occurs when there is no ATP left for contraction and relaxation (Greaser, 1986; Pearson and Young, 1989). As long ADP and glycogen are present, ATP can be produced and thus glycolysis proceeds. Rigor onset will occur if either glycogen or ADP is depleted. Consequently, if at pHu some glycogen remains, glycolysis must have stopped because of ADP depletion.

A higher ATP-ase activity (as in the white muscles) will result in a faster depletion of ATP and a faster onset of rigor. Some researchers have suggested that a higher ATP-ase activity results in a lower pHu and vice versa. White fibers have a lower pHu and higher ATP-ase activity but is this a causal relationship? In a model system, ATP-ase levels did not affect the pHu (Scopes, 1974). The ATP-ase used in the model system by Scopes (1974) was potato ATP-ase.

Possibly, the relationship between ATP-ase activity and pHu is an indirect relationship; a more glycolytic muscle (higher levels of glycogen) has higher ATP-ase activity and a lower pHu. The lower pHu results from increased glycogen and glycolysis, and not from increased ATP-ase activity.

Glycolysis will stop if there is no ADP to convert to ATP. This implies that glycolysis could stop even if there is remaining ATP in the muscle. As long as ATP is not converted to ADP and Pi, glycolysis will not occur. Theoretically, if ATP-ase activity is zero and all ADP has been converted to either ATP or to AMP, IMP etc, glycolysis will cease; no lactate will be produced. Thus, it may be suggested that inactivation of ATP-ase determines pHu. When there is no ATP-ase activity left, no ADP will be produced, the ADP will be depleted and glycolysis ceases. During the post-mortem, pre-rigor phase, ATP-ase activity decreases as a result of denaturation (Offer and Knight, 1988). At rigor, some ATP-ase activity remains. The enzyme is not completely denatured (Warner, 1994). Furthermore, if ATP-ase inactivation would cause the glycolysis to stop and thus determine pHu, PSE pork (in which glycolysis is faster and denaturation is more extensive than in normal pork) would have a higher pHu than normal pork.

The question remains if and how ATP-ase activity might be related to pHu. As mentioned above, meat with a higher ATP-ase activity tends to produce a lower pHu. Pale broiler breast meat, PSE turkey and PSE pork have a faster post mortem glycolysis then their normal counterparts. In many cases the pHu of this pale meat is also lower. That this lower pHu is not purely related to glycogen concentration (related to fibre type) is evidenced by the observations that rapid chilling of meat results in a higher ultimate pH.

The lower pHu in fast glycolyzing conditions and the higher pHu under rapid chilling (slower glycolysis) suggest that the ADP depletion is influenced by rate of glycolysis. Possibly, we need to look at the balance between ADP production and ADP depletion. At high ATP-ase activity ADP production is rapid. Some of the ADP will be lost via AMP deaminase, and some will be reconverted to ATP via glycolysis. The ratio of what will be converted to ATP and what will be converted to AMP and then to IMP will depend on the activity of the various enzymes involved. We hypothesize that when ATP-ase activity is lower, the depletion of ADP via AMP, IMP route will be faster than the regeneration of ATP. In other words, at slower ATP-ase activity adenosine depletion is relatively faster and, thus, ultimate pH will be higher. Factors that influence adenosine depletion need to be evaluated.

Summary

We have some understanding of possible determinants of meat pHu.. Substrate concentration (glycogen level) explains 40-50% of the variation in pHu. We do not know the importance of the availability of glycogen. How do macroglycogen, proglycogen and the conversion between those two forms influence substrate availability and, thus, post-mortem glycolysis?

We do not know the importance of other pHu determinants such as enzyme activities, level, buffering capacity and titratable acidity. The relationship between these possible pHu determinants needs to be determined. A detailed analysis of various metabolites of glycolysis (glucose-1-phosphate, glucose-6-phosphate etc) and ATP, ADP, IMP and other products will give information about additional factors that influence meat pHu Before we can relate enzyme activities to pHu, we should measure enzyme activities under the conditions they experience in the muscle. Since ADP depletion determines when glycolysis stops, a detailed analysis of factors that influence this depletion seems warranted.

Ultimate pH of meat is a main quality determinant. A better understanding of the determinants of meat pHu will allow us to better predict and control meat quality. Once we know which mechanisms are involved in controlling ultimate pH, we may be able to more effectively select animals that consistently produce meat with the desired pHu.

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