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Dose- and type-dependent effects of long-chain fatty acids on adipogenesis and lipogenesis of bovine adipocytes

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ABSTRACT

Differentiation and lipid metabolism of adipocytes have a great influence on milk performance, health, and feed efficiency of dairy cows. The effects of dietary long-chain fatty acids (FA) on adipogenesis and lipogenesis of dairy cows are often confounded by other nutritional and physiological factors in vivo. Therefore, this study used an in vitro approach to study the effect of dose and type of long-chain FA on adipogenesis and lipogenesis of bovine adipocytes. Stromal vascular cells were isolated from adipose tissue of dairy cows and induced into mature adipocytes in the presence of various long-chain FA including myristic, palmitic, stearic, oleic, or linoleic acid. When concentrations of myristic, palmitic, and oleic acids in adipogenic mediums were 150 and 200 μM, the induced mature adipocytes had greater lipid content compared with other concentrations of FA. In addition, mature adipocytes induced at 100 μM stearic acid and 300 μM linoleic acid had the greatest content of lipid than at other concentrations. High concentrations of saturated FA were more toxic for cells than the same concentration of unsaturated FA during the induction. When commitment stage was solely treated with FA, the number of differentiated mature adipocytes was greater for oleic and linoleic acids than other FA. When the maturation stage was treated with FA, the number of mature adipocytes was not affected, but the lipid content in adipocytes was affected and ranked oleic > linoleic > myristic > stearic > palmitic. In summary, this study showed that adipogenesis and lipogenesis of bovine adipocytes were differentially affected by long-chain FA, with unsaturated FA more effective than saturated FA.
Key words: fatty acid, adipogenesis, lipogenesis, stromal vascular cell, dairy cow

INTRODUCTION

Adipose tissue is a heterogeneous cellular depot that stores and releases fatty acids (**FA**) to maintain energy homeostasis of animals. The compartment is composed of adipocytes and stromal vascular cells (**SVC**). The SVC include endothelial cells, immune and nerve cells, mesenchymal stem cells (**MSC**), and preadipocytes (Ouchi et al., 2011). Mesenchymal stem cells are multipotent stem cells and able to differentiate into adipocytes, myocytes, osteoblasts, and chondrocytes depending on niche cues (Gesta et al., 2007). The function of MSC and preadipocytes is to renew and replace senesced mature adipocytes in adipose tissue.

Adipogenesis from MSC to mature adipocytes is practically categorized into 2 phases (Lowe et al., 2011). The first phase, known as the commitment stage, is the determining point when the adipogenic lineage of MSC become preadipocytes. Morphologically, the preadipocyte is difficult to distinguish from the MSC, but has lost the capacity to differentiate into other cell types (Du et al., 2015). The number of adipocytes can be affected by factors that are able to influence the adipogenic lineage in this stage (Jo et al., 2009). In the second phase, known as the maturation stage, committed preadipocytes obtain the characteristics of mature adipocytes, such as the formation of lipid droplets, insulin sensitivity, and adipokine secretions. The adipocyte size is determined in this stage (Jo et al., 2009). Each stage is controlled by well-organized, relatively independent, and complicated signal cascades (Rosen and MacDougald, 2006).

Adipogenesis presents in all life stages of mammals, but the ability to form new adipocytes declines as the animal ages (Tang et al., 2008; Du et al., 2013, 2015). In dairy cows, physiological changes in adipose tissue are dramatic during the lactation period (McNamara and Baldwin, 2000). In the first 60 d after calving, approximately 11 kg of triglycerides is mobilized from adipose tissue, and around 35 kg of triglycerides is re-deposited in the following 60 d (McNamara and

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Baldwin, 2000). Besides the mass change, the adipocyte number is also shifted during the lactation period (Smith and McNamara, 1990). Because adipose tissue is critical for energy balance, feed efficiency, health, and milk performance of dairy cows, it is essential to understand the environmental factors affecting adipogenesis and lipogenesis of bovine adipocytes (McNamara and Baldwin, 2000; McNamara et al., 2016).

Long-chain FA are building blocks for lipid droplets in adipocytes and can be actively involved in the regulation of adipogenesis and lipogenesis. For example, the peroxisome proliferator activated receptor gamma (***PPARg***) is a well-known master regulator of adipogenesis and lipogenesis in adipocytes, and can control the expression of other adipogenic genes (Tontonoz et al., 1994b). Smith et al. (2009) observed the metabolic health of transition cows was greatly improved through attenuation of body fat mobilization when cows were infused intrajugularly with thiazolidinediones, an agonist of *PPARg*. Fatty acids are natural ligands that activate the expression of PPARg (Rosen et al., 2000), and different FA have been observed to possess various potencies in activation of *PPARg* in bovine mammary gland epithelial cells and kidney cells (Kadegowda et al., 2009a; Thering et al., 2009a). However, effects of FA on adipogenesis and lipogenesis in bovine adipocytes are not well defined.

In dairy cows, myristic, palmitic, stearic, oleic, and linoleic acids are the most abundant FA in the digestive tract and blood; also, each FA can differentially affect the metabolism of body tissues and organs (Boerman et al., 2015). Rumen fermentation can be negatively affected by biohydrogenation of oleic and linoleic acids, and the intermediate products of biohydrogenation, such as C18:1 *trans*-10 and C18:2 *trans*-10 *cis*-12, are also identified as strong precursors that inhibit milk fat synthesis (Chilliard et al., 2007). The mammary gland prefers palmitic acid for milk fat synthesis, whereas adipose tissue prefers stearic acid for lipogenesis (Loften et al., 2014; Rico et al., 2014). Obviously, each FA not only serves as an energy source, but also has some special functions in regulating physiological metabolism. Improving our understanding of the roles of these FA on adipogenesis and lipid accumulation in the adipocyte could be beneficial for fully understanding lactation and health of dairy cows as regulated by FA.

The objective of this study was to understand the roles of major long-chain FA in adipogenesis and lipogenesis of bovine adipocytes and help to develop nutritional strategies to optimize adipocyte development and lipid metabolism of dairy cows. Our hypothesis was that long-chain FA would have different effects on adipogenesis and lipogenesis of bovine stromal vascular cells isolated from dairy cows dependent on the dose and specific FA. In the first study, the dose-dependent effects of FA on adipogenesis were investigated. In the second study, selected concentrations of each FA were used to study their effects on adipogenic differentiation and maturation, respectively.

MATERIALS AND METHODS

All experimental procedures involving animals were conducted with the guidelines of the Washington State University Animal Care and Use Committee.

Isolation of SVC and Adipogenic Induction

Five Holstein dairy cows (BW, 691 ± 18.8 kg; DIM, 61 ± 5.9; milk yield, 54.2 ± 3.36 kg/d) were used as adipose tissue donors. Adipose tissue was taken from alternate sides of the tail head as described by Smith and McNamara (1989). After the biopsy, fresh tissue was kept on ice and immediately transported to the laboratory for processing. Tissue was washed with PBS and minced into small pieces, and then digested in a medium containing 0.75 unit/mL of collagenase D (no. 11088874103, Roche, Pleasanton, CA) and 1.0 unit/mL of Dispase type II (no. 4942078001, Roche) for 30 min in an Eppendorf AG shaking incubator (New Brunswick, Germany) at 90 rpm at 37°C. The lysate was filtered with 100-μm nylon mesh (Thermo Fisher Scientific, Asheville, NC) and centrifuged at 500 × *g* for 5 min at 4°C. The precipitated pellet was resuspended and seeded in Dulbecco's modified Eagle medium/F-12 (**DMEM**/F-12, no. 12500–096, Thermo Fisher, Waltham, MA) with 10% fetal bovine serum (**FBS**; no. SH30401, HyClone, South Logan, UT) and 1% antibiotics (no. 15070063, Thermo Fisher). The cell culture was maintained in a 37°C and 5% CO_2 incubator (Eppendorf AG). Culture medium was renewed every 48 h.

The SVC reached about 80 to 90% confluence after 5 to 7 d of culture, subculture (less than 2 passages) was used to get sufficient SVC for studies. The SVC were washed with PBS buffer and digested in trypsin-EDTA solution (no. SLBN6048V, Sigma) in an incubator for ~10 min until cells were detached from the inside surface of the plates. When cells were detached, fresh DMEM/F-12 containing FBS and antibiotics was added to the medium to cease the activity of trypsin. Collected cells from 5 donor animals were mixed and used for experiments. Cell treatments were initiated after SVC reached 100% confluence.

Adipogenic induction was initiated using a standard adipogenic cocktail (Yang et al., 2013). The first 4 d was considered as the commitment stage when cellular morphology was spindle-like and lipid droplets were not

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