ABSTRACT Reducing fat has been a major goal for the broiler industry. To gain insight into the molecular mechanisms underlying the regulation of fat deposition in chickens, a 2-dimensional electrophoresis-based proteomic approach was used to analyze the differentially expressed proteins in abdominal adipose tissues of Northeast Agricultural University broiler lines divergently selected for abdominal fat content (NEAUHLF). A total of 20 differentially expressed protein spots were found in abdominal adipose tissue between fat and lean broilers at 7 wk of age. Among them, 12 protein spots were upregulated and 8 protein spots were downregulated in fat birds compared with those in lean birds. These 20 protein spots were then identified by matrix-assisted laser desorption-ionization time-of-flight mass spectrometry and matched to 15 proteins by searching against the NCBI nr and SWISS-PROT databases, including adipocyte fatty acid-binding protein, apolipoprotein A-I, long-chain acyl-coenzyme A dehydrogenase, heat shock protein β 1, glutathione S-transferase theta 1, glutathione S-transferase class α, guanine nucleotide-binding protein β polypeptide 1, syntaxin 2, vimentin, coflin 2, otokeratin, telomerase catalytic subunit, and 3 hypothetical proteins. These proteins are mainly related to lipid metabolism, chaperone, redox, signal transduction, transport, and cytoskeleton. The results, from the point of view of protein expression, establish the groundwork for further studies of the basic genetic control of growth and development of broiler adipose tissue.

Key words: broiler, adipose tissue, differentially expressed protein, two-dimensional electrophoresis

INTRODUCTION

During the past decades, intensive selection has made significant success in growth velocity and meat production capacity of broilers. However, selection for rapid growth has also been accompanied by increased fat deposition in these broilers (Nones et al., 2006). Fat is considered as a by-product because of the low commercial value, and much body fat deposition can degrade chicken production performance. Reduction of fat mass has been a major goal for the broiler industry, and several studies have been performed to elucidate the mechanisms underlying the fat deposition by traditional genetic methods, but not much progress has been made because fatness is a complicated trait involving multifactorial regulation.

Functional genomics provides hope for dissecting the fatness trait. Several studies have used gene array technology to compare the gene expression profiles between fat and lean chickens, and these studies have provided clues to understand the mechanisms of obesity at the transcriptome level (Bourneuf et al., 2006; Wang et al., 2007). However, proteins are the executants of physiologic functions and almost all biological processes, and there are poor correlations between the mRNA expression level and the protein expression level. Therefore, characterizing and comparing the proteomes of adipose tissues between fat and lean chickens is pivotal for elucidating the molecular mechanisms underlying the fatness trait.

Proteomic analysis has been extensively used to investigate protein expression profiles of adipose tissues from obesity and normal-weight individuals in human and rodents, and many proteins associated with lipid metabolism, energy metabolism, and endoplasmic reticulum stress are found to be involved in obesity occurrence (Schmid et al., 2004; Von Eyben et al., 2004; Boden et al., 2008). Recently, a few proteomic research studies on the mechanisms of fat deposition were carried out in livestock species, including pigs and cattle. Zhang et al. (2007) used cDNA microarray and 2-dimensional electrophoresis (2DE) to construct the differential gene expression profiles of pig adipose tissues.
treated with or without clenbuterol and found that the apolipoprotein R increased at both the mRNA and protein expression levels with clenbuterol treatment. Ikegami et al. (2008) performed a large-scale proteome analysis of bovine white adipose tissue and found that in the high carcass weight group, 95 protein spots were upregulated and 2 protein spots were downregulated compared with those in the low carcass weight group. These 97 differentially expressed proteins were associated with energy metabolism, cell structure, cell defense, transport, and signal transduction. There have been few studies about the protein expression profiles of adipose tissue in chickens. The objectives of the present study were to construct the protein expression profiles of abdominal adipose tissues of fat and lean broilers by 2DE and to identify differentially expressed proteins in adipose tissues between fat and lean birds.

**MATERIALS AND METHODS**

**Experimental Populations and Management**

Broilers derived from the Northeast Agricultural University broiler lines divergently selected for abdominal fat content (NEAUHLF) were used in the present study. All birds were kept in similar environmental conditions and had free access to feed and water. Commercial corn-soybean-based diets, which met all NRC requirements (NRC, 1994), were provided to the birds.

**Sample Preparation for 2DE**

Our sample size was determined according to the literature (Molloy et al., 2003; Horgan, 2007). Six male birds of generation 11, three from the fat line and 3 from the lean line, respectively, were used in the present study (Table 1). The birds were slaughtered at 7 wk of age, abdominal adipose tissues were collected, frozen immediately in liquid nitrogen, and stored at −80°C. Total proteins were extracted from abdominal adipose tissues using Trizol reagent (Invitrogen, Carlsbad, CA) according to the protocol of the manufacturer with minor modifications. The samples were dissolved in lysis buffer containing 8 M urea, 2 M thiourea, 4% (wt/vol) 3-[(3-cholamidopropyl)dimethylammonio]-1-propanesulfonate, 50 mM DTT, and 0.5% carrier ampholytes, pH 3 to 10. All gels were run in duplicate. First-dimension electrophoresis was conducted with the IPGphor3 isoelectric focusing system (GE Healthcare) using the dry IPG strips (24 cm pH 3 to 10 nonlinear and 24 cm pH 4 to 7, GE Healthcare) via rehydration for 12 h at 50 V. Proteins were then focused under the following conditions: 100 V for 1.5 h, 300 V for 1.5 h, 500 V for 1.5 h, 1,000 V for 0.5 h, and 10,000 V for 8.5 h. When completing the first-dimension electrophoresis, the IPG strips were equilibrated first with equilibration buffer containing 50 mM Tris-HCl, pH 8.8, 6 M urea, 30% glycerol, 2% SDS, 1% DTT, and a trace of bromophenol blue for 15 min, followed by a second equilibration with 2.5% iodoacetamide replacing the 1% DTT for 15 min. The strips were rinsed with deionized water and blotted to remove excess equilibration buffer, then embedded in low melting temperature agarose and transferred onto 12.5% acrylamide gels (26 × 20 cm²). The second-dimension electrophoresis was conducted with the Ettan Daltix Electrophoresis System (GE Healthcare). Gels were run at constant power first with 2 W/strip for 45 min and then 15 W/strip until the bromophenol blue reached the bottoms of the gels and then were stained with the blue silver method (Candiano et al., 2004). The stained gels were scanned using an Imagescanner III with Labscan 6.0 software (GE Healthcare). Protein spot detection, volume calculation, matching, and the patterns were analyzed using ImageMaster 2D Platinum 6.0 Software (GE Healthcare) according to the instructions of the manufacturer, and routine statistical analysis software available within this software package was used to identify spots up- or downregulated under specified conditions.

**Protein Identification**

After image analysis, the differentially expressed protein spots were selected and excised from the gels, sub-

<table>
<thead>
<tr>
<th>Trait</th>
<th>Lean 1</th>
<th>Lean 2</th>
<th>Lean 3</th>
<th>Fat 1</th>
<th>Fat 2</th>
<th>Fat 3</th>
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<tbody>
<tr>
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<td>2.290</td>
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<td>59.92</td>
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<tr>
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<td>0.54</td>
<td>0.68</td>
<td>3.52</td>
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<td>2.64</td>
</tr>
</tbody>
</table>

Table 1. Body weight, abdominal fat weight (AFW), and abdominal fat percentage (AFP) of broiler chickens used in the study.
RESULTS AND DISCUSSION

Characterization of the Lean and Fat Broiler Lines Used in the Present Study

The NEAUHLF had been divergently selected over 11 generations using abdominal fat percentage (AFP) and plasma very low density lipoprotein concentration as selection criteria. The 2 divergent broiler lines (NEAUHLF) originated from the same ancestor and had common genetic background. They had no difference in BW but had a striking difference in AFP (Figure 1). In generation 11, the AFP of the fat line was 3.7 times that of the lean line. Six male birds, 3 from the fat line and 3 from the lean line, respectively, were used in the present study (Table 1). The average AFP of the 3 fat birds used in the present study was 5.29 times greater than that of the 3 lean birds (Table 1). Obviously, NEAUHLF are unique experimental models to study obesity.

Proteomic Analysis of Adipose Tissue Between Fat and Lean Broilers

Two-dimensional electrophoresis mass spectrometry is a powerful tool to screen differentially expressed proteins from organism between different physiological conditions. In the present study, the protein lysates were separated by 24-cm dry IPG strips (pH 3 to 10 nonlinear) using 2DE and detected with the blue silver staining method (Figure 2A). The number of protein spots identified on 6 gels ranged from 953 to 1,126, and most of the protein spots were matched among gels. Eighteen protein spots showing >1.5-fold relative differences (P < 0.05) between the 2 lines were found. Because most of the protein spots on the gels were displayed at pH 4 to 7, to improve the resolution of 2DE maps at this pH area, the narrow pH gradient dry strips (pH 4 to 7) were also used to screen the differentially expressed proteins (Figure 2B), and 2 more differentially expressed protein spots were found. A total of 20 differentially expressed protein spots between fat and lean birds were found. These protein spots were excised from the gels, digested subsequently with trypsin, and then identified by MALDI-TOF-MS. The 20 protein spots were matched to 15 proteins including 3 hypothetical proteins by searching against the NCBInr and SWISS-PROT databases. Figure 3 shows the protein expression profiles of these 15 identified proteins in adipose tissue of fat and lean birds (3 from the fat line and 3 the from lean line). Table 2 lists these 15 proteins and provides their protein expression fold changes between fat and lean birds, their corresponding P-value, CV, percentage of coverage, Mascot score, accession number, subcellular location, and function. These 15 proteins can be classified into at least 6 categories, including lipid metabolism, chaperone, redox, signal transduction, transport, and cytoskeleton.

Three proteins, adipocyte fatty acid-binding protein (AFABP), apolipoprotein A-I (APOA-I), and long-chain acyl-coenzyme A dehydrogenase (ACADL), which are important in lipid metabolism, were identified as changed by selection. Fatty acid-binding proteins belong to a superfamily of lipid-binding proteins and are involved in the development of fatness traits (McArthur et al., 1999). Adipocyte fatty acid-binding protein is one member of the fatty acid-binding proteins and is mainly involved in fatty acid transport. It transports fatty acids to the positions of fatty acid oxidation and triglyceride composition and effectually promotes esterification reaction (Haunerland and Spener, 2004). It is upregulated during adipogenesis (Lynch et al., 1993; DeLany et al., 2005). Our previous study showed that a single nucleotide polymorphism of the AFABP gene located in exon 1 was associated with abdominal fat weight and percentage of abdominal fat (Wang et al., 2006b). Long-chain acyl-coenzyme A dehydrogenase is the key enzyme in fatty acid β oxidation (Gregersen, 1985) and participates in the fatty acid metabolism pathway. Ji and Friedman (2007) reported that the ACADL expression level was increased in rats fed with the high-fat diet compared with that in rats fed with the low-fat diet. Consistent with the literature, the present results showed that both AFABP and ACADL were upregulated in adipose tissues of the fat birds compared with those of the lean birds. Apolipoprotein A-I is a lipid-binding protein that participates in the reverse transport of cholesterol from tissues to the liver for excretion by promoting cholesterol efflux.
from tissues and by acting as a cofactor for the lecithin cholesterol acyltransferase (Mukhamedova et al., 2008). It is a major component of high-density lipoprotein and plays an important role in cholesterol dynamic balance (Bhattacharyya et al., 1993). Genetic deficiency in APOA-I is associated with excessive intracellular cholesterol accumulation in humans and poultry (Breslow, 1989; Kiss et al., 2001; Wang et al., 2006a). In our previous study, we found a single nucleotide polymorphism upstream of the ATG initiation codon of the APOA-I gene, which was associated with abdominal fat weight and percentage of abdominal fat (Wang et al., 2005). In the present study, we found that APOA-I was downregulated in adipose tissues of the fat birds compared with that of the lean birds. This may be partially responsible for different abdominal fat deposition between the 2 lines.

Heat shock proteins serve as chaperones preventing protein damage and proteolysis and are related with the occurrence of obesity and diabetes (Cherian and Abraham, 1995; Ozcan et al., 2004). Previous study reported that heat shock protein 27 (HSP27) interacted with the insulin-like growth factor receptor 1 and its signal transducer Akt (the serine-threonine kinase protein), which together modulated adipocyte metabolism in mammals (Rane et al., 2003). Induction of HSP27 may blunt the adverse effect of fat overexposure on insulin function in mammals (McCarty, 2006). Heat shock protein β 1 (homologous to HSP27 in mammals) was downregulated in the fat birds compared with that of the lean birds. This may be partially responsible for different abdominal fat deposition between the 2 lines.

**Figure 2.** Two-dimensional (2-D) protein profiles of abdominal adipose tissues of fat and lean broiler lines. A) The 2-D protein profiles with pH 3 to 10 nonlinear IPG strips (GE Healthcare, Uppsala, Sweden). B) The 2-D protein profiles with pH 4 to 7 IPG strips (GE Healthcare). Color version available in the online PDF.
in the lean birds in the present study. This may imply that the action mechanism of this protein in chicken is similar to that in mammals.

Glutathione S-transferases are a multigene family of broad-specificity detoxification enzymes and play an important role in cytoprotective function through detoxification of lipid peroxides in adipocytes (Jowsey et al., 2003). Glutathione S-transferase class α and glutathione S-transferase theta 1 are also involved in diverse signaling pathways related to adipocyte differentiation in mammals. For example, they facilitate the formation of 15-deoxy-Δ12, 14-prostaglandin J2, which serves as an activating ligand for the transcription factor peroxisome proliferator-activated receptor γ (Jowsey et al., 2003; Cortón et al., 2008). In the present study, glutathione S-transferase class α and glutathione S-transferase theta 1 were upregulated in adipose tissues of the fat birds compared with those of the lean birds. This may imply that these 2 proteins are also involved in signaling pathways related to adipocyte proliferation and differentiation in chicken.

Guanine nucleotide-binding proteins (G proteins, GNB) are important signal transducer proteins, which participate in the signal transducer of many hormones and neurotransmitters (Robertson et al., 1991). It is the molecular switch of signal transducer in cells. Previous study has reported that G proteins-GNB were associated with insulin synthesis and secretion in humans (Robertson et al., 1991). Polymorphisms of the gene encoding the G protein were found to be associated with obesity in humans (Chen et al., 2003; Danoviz et al., 2006). In the present study, the upregulation of GNB1 in the fat birds may imply that it is associated with obesity in chicken.

Syntaxins are a family of receptors for intracellular transport vesicles, and they are involved in neuronal exocytosis, endoplasmic reticulum-Golgi transport and Golgi-endosome transport (Bennett et al., 1993). To

<table>
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<tr>
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<th>Lean line 1-2</th>
<th>Lean line 1-5</th>
<th>Fat line 2-1</th>
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<td>APOA-I</td>
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<td>AFABP</td>
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<tr>
<td>GSTα</td>
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</table>

Figure 3. Protein features showing different expression levels in adipose tissues between fat and lean broiler lines. GNB1 = guanine nucleotide-binding protein β polypeptide 1; ACADL = long-chain acyl-coenzyme A dehydrogenase; APOA-I = apolipoprotein A-I; AFABP = adipocyte fatty acid-binding protein 4; GSTα = glutathione S-transferase class α; GSTT1 = glutathione S-transferase theta 1; HSPβ1 = heat shock protein β 1.
some extent, syntaxin 2 has been implicated in insulin-induced solute carrier family 2 (facilitated glucose transporter), member 4 translocation in adipocytes (Tamori et al., 1998; Lee et al., 2006). Insulin has been demonstrated to advance the uptake of glucose in adipose tissue, mainly due to the regulation of intracellular trafficking of the solute carrier family 2 (facilitated glucose transporter), member 4 glucose transporter isoform (Olson et al., 1997; Tamori et al., 1998).

The present study also found that 3 members of the cytoskeleton protein family, coflin 2, vimentin, and otokeratin, were differentially expressed between fat and lean birds in abdominal adipose tissue, suggesting that the volume and cell structure of adipocytes between fat and lean birds were different. Recent study reported that the number of adipocytes remained constant in adulthood in both lean and obese individuals and that the volume of adipocytes was the crucial factor for obesity in adults (Spalding et al., 2008). Cofilin 2, a specific cytoskeleton protein, controls the mechanical tension of cell by regulating actin polymerization (DeLany et al., 2005). Vimentin intermediate filaments are reorganized to form cage-like structures around the nascent lipid droplets and play the supporting role to lipid droplet formation (Lieber and Evans, 1996). They are also found differentially expressed during adipogenesis in the mammalian preadipocyte model (Welsh et al., 2004; DeLany et al., 2005). The different expression levels of coflin 2 and vimentin indicated that the adipocyte structure between lean and fat birds was different. Otokeratin was first detected in the tegumentum vasculosum, a richly vascular epithelium in the inner ear of the chicken. It is suggested that otokeratin contributes to mechanical stability by the expression of the molecule in the endothelial cell layer of chicken cardiac ventricles, which is exposed to constant mechanical stress by deformation and pressure changes (Heller et al., 1998). The function of otokeratin in chicken adipose tissue is not very clear, and it may play a role similar to that in chicken cardiac ventricles.

Interestingly, the current study found that telomerase catalytic subunit was downregulated in adipose tissue of the fat birds. Telomeres are the repeated series of DNA sequences of chromosome ends that cap and protect the ends of linear chromosomes (Effros, 2009). Telomeres become shorter after cell division or under oxidative stress, which is one of the mechanisms of gradual aging. Some studies have reported that telomere length was associated with an obesity phenotype in humans (Nordfjäll et al., 2008), and obese adults had shorter telomeres than their normal-weight counterparts (Zannolli et al., 2008). Telomere shortening is believed to occur on account of the decrease in telomerase activity (Liu et al., 2002). The downregulation of telomerase catalytic subunit in adipose tissue of the fat birds implies that fat birds may have shorter telomeres than lean birds.

Besides the above-identified proteins, there were 3 hypothetical proteins being found differentially expressed between the fat and lean birds. One hypothetical protein (hypothetical protein 1) contains a conserved domain of 56 kDa selenium-binding protein (SBP56), one (hypothetical protein 2) contains a conserved domain of 5C = cytoplasm; M = membrane; N = nucleus; NR = not reported; S = secreted.

### Table 2. Features of differentially expressed protein identified by matrix-assisted laser desorption-ionization time-of-flight mass spectrometry

<table>
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<th>Spot no.</th>
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<th>CV (L)</th>
<th>CV (F)</th>
<th>Sequence coverage (%)</th>
<th>Mascot score</th>
<th>Accession number</th>
<th>Subcellular location</th>
<th>Function</th>
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1. GNB1 = guanine nucleotide-binding protein β polypeptide 1; ACADL = long-chain acyl-coenzyme A dehydrogenase; APOA-I = apolipoprotein A-I; AFBP = adipocyte fatty acid-binding protein 4; GSTα = glutathione S-transferase class α; GSTT1 = glutathione S-transferase theta 1; HSP31 = heat shock protein β 1.
2. Fold change = average relative volume ratio (fat broilers vs. lean broilers).
3. CV (L) = the CV of the 3 lean birds.
4. CV (F) = the CV of the 3 fat birds.
5. Location: C = cytoplasm; M = membrane; N = nucleus; NR = not reported; S = secreted.
of inorganic pyrophosphatase (PPi), and another (hypothetical protein 3) harbors a conserved domain of the putative PEP-CTERM system TPR-repeat lipoprotein (PEP-TPR_lipo). A lot of proteins with the conserved domains (SBP56, PPi, and PEP-TPR_lipo) were associated with obesity in mammals and poultry (Takahashi et al., 2004; Zhao et al., 2007). In chickens, a lot of proteins have unknown function, and many proteins have low sequence homology to mammalian proteins. The functions of these identified hypothetical proteins here remain to be investigated.

In conclusion, the current study characterized the proteomic profiles of adipose tissues in the 7-wk-old fat and lean broiler chickens and identified differentially expressed proteins by MALDI-TOF-MS. These identified proteins are mainly involved in lipid metabolism, cytoskeleton, and redox. These findings establish the ground for further research on the regulation of growth and development of chicken adipose tissue.

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