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Selenoprotein W gene expression in the gastrointestinal tract of chicken is affected by dietary selenium

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Abstract Selenoprotein W (SelW) and selenium (Se) plays important roles in gastrointestinal function and that SelW expression in the gastrointestinal system of mammals is sensitive to Se levels. However, little is known about the pattern of SelW expression in the bird gastrointestinal tract. To investigate the distribution of SelW and effects of dietary Se levels on the SelW mRNA expression in the gastrointestinal tract tissues of birds, 1-day-old male chickens were fed either a commercial diet or a Se-supplemented diet containing 1.0, 2.0, 3.0 or 5.0 mg/kg sodium selenite for 90 days. The gastrointestinal tract tissues (tongue, esophagus, crop, proventriculus, gizzard, duodenum, small intestine, cecum and rectum) were collected and examined for Se content and mRNA levels of SelW. The mRNA expression of SelW was detected in all tissues. The greatest increase in SelW mRNA levels was observed in the gizzard, whereas Se content was highest in the duodenum and small intestine. A significant increase in SelW mRNA levels was observed in the gastrointestinal tract tissues of chickens fed the diets containing 1–3 mg/kg sodium selenite while decreased SelW mRNA levels were observed in the esophagus, crop, proventriculus, gizzard, duodenum and cecum in chickens fed the diet containing 5 mg/kg sodium selenite. These data indicate that SelW is widely expressed in the gastrointestinal tract tissues of birds and the transcription of the SelW gene is very sensitive to dietary Se.

Keywords Chicken · Selenoprotein W · Selenium · mRNA expression · Gastrointestinal tract tissues

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Introduction

Selenium (Se) is an essential nutritional trace element that is critical to the normal physiology of a wide range of species, including birds. Previous data suggest that Se plays important roles in chemoprevention (Combs et al. 2001; Li et al. 2010), neurobiology (Schweizer et al. 2004), aging (Martin-Romero et al. 2001), immune functions (i.e. immune responses, and

anti-inflammatory and antiviral activity) (Rayman 2000; Hoffmann and Berry 2008), muscle metabolism (Chariot and Bignani 2003), reproduction (Kaur and Bansal 2005), redox reactions (Rayman 2000), and in many other aspects of health (Brown and Arthur 2001; Mahmoud and Edens 2005). The activity of Se within animal systems is mainly elicited via selenoproteins (Stadtman 2000), a group of proteins that contain the amino acid selenocysteine (Sec) as an integral part of their polypeptide chain. These proteins have been found in the three domain of life but not in all species of bacteria, archaea and eukaryotes. Much of selenoproteins beneficial on health is attributed to its presence with at least 30 selenoprotein families (Kryukov et al. 2003; Kryukov and Gladyshev 2004; Castellano et al. 2005; Zhang et al. 2005; Papp et al. 2007). In recent years, 25 families of human selenoprotein genes have been identified, 24 of which are also present in rodents (Kryukov et al. 2003). However, the selenoproteome in birds remains unclear. Most members of the selenoprotein families exhibit diverse tissue distribution patterns, ranging from ubiquitous to tissue-specific expression. The subcellular localization of selenoproteins also varies, as some selenoproteins are exclusively expressed in specific organelles or as transmembrane proteins, while others are expressed in the extracellular spaces or plasma (Reeves and Hoffmann 2009). These and other properties have provided important information about the physiological roles of selenoproteins.

Selenoproteins are involved in cellular defense against oxidative damage, metabolic and developmental pathways and in the responses to environmental challenges (Lu and Holmgren 2009). There is increasing evidence that the biological functions of Se are mediated by selenoproteins; thus, it is important to identify, characterize and determine the functions of all selenoproteins. In particular, the roles of selenoprotein W (SelW) have yet to be fully determined. SelW is highly conserved among mammalian species (83% homology) with the Sec residue present in the N-terminal region as part of the—CXXU—redox motif (Beilstein et al. 1996; Gu et al. 1999; Aachmann et al. 2007). We have cloned the avian SelW gene (GenBank accession no. GQ919055), and observed that the structure of chicken SelW is similar to that of mammals. This selenoprotein can bind reduced glutathione (GSH) (Beilstein et al. 1996), suggesting that its expression may be an important component of the cellular defense system against oxidative stress (Beilstein et al. 1996; Wang et al. 2010). SelW is ubiquitously expressed in tissues, and its expression is regulated by Se status and intake. Se deficiency was shown to reduce the expression of SelW in skeletal muscles, heart, intestine, prostate, esophagus and skin, but not its expression in the brain, in rodents (Whanger 2000). Although the biological characteristics of SelW, including its amino acid sequence, distribution and the regulatory effect of Se on its expression, are already known in rodents, the characteristics of avian SelW remain unknown, except for its amino acid sequence.

The digestive tract of any animal, including chickens, is important in converting the food they eat into the nutrients their body needs for maintenance, growth and production (such as eggs). The digestive tract is also referred to as the gastrointestinal tract. The gastrointestinal tract of a chicken is much stronger than that of a human being due to the chicken's lack of teeth. SelW was expressed in the tongue, esophagus, stomach, small intestine and colon in Se-supplemented rats, but was not expressed in these tissues in Se-deficient rats (Sun et al. 1998; Whanger 2000; Pagmantidis et al. 2005). Provision of adequate Se elicited a significant increase in SelW mRNA levels in human intestinal Caco-2 cells. Additionally, Se supplementation could prevent colorectal cancer (Combs 2005). These data indicate that SelW expression in the gastrointestinal system of mammals is sensitive to Se levels and that Se and SelW play important roles in gastrointestinal function and during gastrointestinal diseases. By contrast, the pattern of SelW expression in the avian gastrointestinal tract remains unknown. Therefore, the aims of the present study were to (1) investigate the distribution of SelW and Se in the gastrointestinal tract tissues of chickens and (2) evaluate the dose-dependent effect of dietary supplementation containing a range of Se levels on the regulation of SelW mRNA expression in these tissues.

Materials and methods

Birds and diets

All procedures used in this experiment were approved by the Institutional Animal Care and Use Committee

of Northeast Agricultural University. Fifty male chickens (1-day-old; Weiwei Co. Ltd., Harbin, China) were divided into five groups (10 chickens/group) and fed either the commercial granulated diet or the Se-supplemented granulated diet containing 1.0, 2.0, 3.0 or 5.0 mg/kg sodium selenite for 90 days. The basal commercial granulated diet was shown by analysis to contain 0.145 mg/kg Se. On the 90th day of the experiment, all of the chickens were fasted overnight. Following euthanasia with sodium pentobarbital, the gastrointestinal tract tissues of the chickens were quickly removed, blotted and then rinsed with ice-cold sterile deionized water, frozen immediately in liquid nitrogen and stored at −80°C until required. Se content and mRNA levels of SelW were measured in these tissues.

Determination of Se concentration in tissues

Se content in the tissues and whole blood was estimated by the method described by Hasunuma et al. (1982). The assay is based on the principle that Se contained in samples is converted to selenous acid in response to acid digestion. The reaction between selenous acid and aromatic-*o*-diamines, such as 2,3-diamino-naphthalene (DAN), leads to the formation of 4,5-benzopiazselenol, which displays a brilliant lime-green fluorescence when excited at 366 nm in cyclohexane. The fluorescence emission in extracted cyclohexane was measured by a fluorescence spectrophotometer with an excitation and emission wavelengths of 366 and 520 nm, respectively. The Se content was calculated by reference to a standard curve.

Determination of the SelW mRNA level by quantitative RT-PCR

Total RNA was isolated from the tissue samples (50 mg tissue; $n = 3$/diet group) using TRIzol reagent according to the manufacturer's instructions (Invitrogen, China). The dried RNA pellets were resuspended in 50 μl of diethyl-pyrocarbonate-treated water. The concentration and purity of the total RNA were determined spectrophotometrically at 260/280 nm. First-strand cDNA was synthesized from 5 μg of total RNA using oligo dT primers and Superscript II reverse transcriptase according to the manufacturer's instructions (Invitrogen, China). Synthesized cDNA was diluted five times with sterile water and stored at −80°C before use.

Primer Premier Software (PREMIER Biosoft International, USA) was used to design specific primers for SelW and GADPH based on known chicken sequences (Table 1).

General PCRs were first performed to confirm the specificity of the primers. The PCR products were electrophoresed on 2% agarose gels, extracted, cloned into the pMD18-T vector (TaKaRa, China) and sequenced. Quantitative real-time PCR was performed on an ABI PRISM 7500 Detection System (Applied Biosystems, USA). Reactions were performed in a 20-μl reaction mixture containing 10 μl of 2× SYBR Green I PCR Master Mix (TaKaRa, China), 2 μl of either diluted cDNA, 0.4 μl of each primer (10 μM), 0.4 μl of 50× ROX reference Dye II and 6.8 μl of PCR-grade water. The PCR procedure for SelW and GADPH consisted of 95°C for 30 s followed by 40 cycles of 95°C for 15 s, 60°C for 30 s and 60°C for 30 s. The melting curve analysis showed only one peak for each PCR product. Electrophoresis was performed with the PCR products to verify primer specificity and product purity. A dissociation curve was run for each plate to confirm the production of a single product. The amplification efficiency for each gene was determined using the DART-PCR program (Peirson et al. 2003). The mRNA relative abundance was calculated according to the method of Pfaffl (2001), accounting for gene-specific efficiencies and

Table 1 Primers used for quantitative real-time PCR

Target gene	GenBank accession no	Primer	Sequence (5′–3′)	PCR fragment length (bp)
Chicken SelW	GQ919055	Forward	5′-CTCCGCGTCACCGTGCTC-3′	150
		Reverse	5′-CACCGTCACCTCGAACCATCCC-3′	
GADPH	K01458	Forward	5′-AGAACATCATCCCAGCGT-3′	182
		Reverse	5′-AGCCTTCACTACCCTCTTG-3′	

was normalized to the mean expression of GADPH, and expressed as the ratio of Se dietary content.

Statistical analysis

Statistical analysis of Se concentration and mRNA level was performed using SPSS statistical software for Windows (version 13; SPSS Inc., Chicago, IL, USA). When a significant value ($P < 0.05$) was obtained by one-way analysis of variance, further analysis was done. All data showed a normal distribution and passed equal variance testing. Differences between means were assessed by Tukey's honestly significant difference test for post hoc multiple comparisons. The relationship between Se concentrations in whole blood or tissues and the abundance of SelW mRNA were assessed using Pearson's correlation coefficient. Data are expressed as mean ± standard deviation. Differences were considered to be significant at $P < 0.05$.

Results

Se content in whole blood and tissues

The effects of the different concentrations of dietary Se on Se content in whole blood and tissues are shown in Fig. 1. Chickens fed the basal diet had significantly lower ($P < 0.05$) Se content in whole blood and in the gastrointestinal tract tissues compared with those of chickens fed Se-supplemented diets (Fig. 1a). A significant increase in the whole blood Se concentration was observed for chicken fed diets containing 1–5 mg/kg sodium selenite for 90 days. When chickens were fed the diets containing 1–3 mg/kg sodium selenite, the Se content in the gastrointestinal tract tissues dose dependently increased with increasing dietary Se content (Fig. 1b). In contrast, although the Se content in the gastrointestinal tract tissues of chickens fed diets containing 3–5 mg/kg sodium

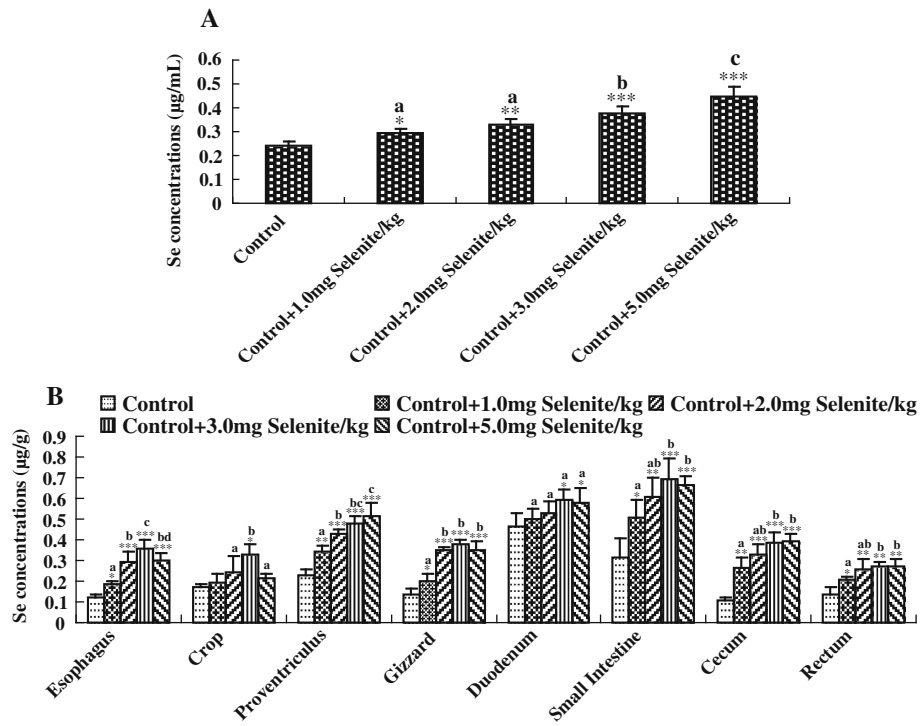

Fig. 1 Whole blood (**a**; μg/ml) and gastrointestinal tract tissue (**b**; μg/g, wet wt of tissue) Se content in chickens fed diets containing various concentrations of Se. *Bars* represent mean ± standard deviation ($n = 3$/group). *Bars with asterisk* "*" are statistically significantly different from control by one-way analysis of variance followed by Tukey's multiple comparison test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Within the groups treated with various levels of Se, *bars* sharing a common letter are not significantly different ($P > 0.05$)

selenite increased with increasing dietary Se concentrations, gastrointestinal tract Se content reached a plateau in the proventriculus, gizzard, duodenum, small intestine, cecum and rectum ($P > 0.05$). Furthermore, there was a significant decrease in the Se content in the esophagus and crop in the chickens fed diets containing 5 mg/kg sodium selenite, as compared with 3 mg/kg ($P < 0.05$).

Effect of Se supplementation on SelW mRNA abundance

The SelW mRNA abundance measured by quantitative RT-PCR is shown in Figs. 2 and 3. The basal SelW expression level of the gastrointestinal tract tissues of chicken in control group from high to low is as follows: gizzard, duodenum, crop, small intestine, esophagus, rectum, cecum, tongue, proventriculus (Fig. 2). When chickens fed diets containing 3 mg/kg sodium selenite, the SelW mRNA abundance from high to low is as follows: gizzard, proventriculus, duodenum, small intestine, crop, rectum, esophagus, cecum, tongue (Fig. 2). Of note, the SelW mRNA abundance in the gizzard was the highest in the gastrointestinal tract tissues of chicken fed diets containing 0–5 mg/kg sodium selenite (all, $P < 0.05$).

When compared with the control group, a significant increase in the SelW mRNA levels was observed in all of the gastrointestinal tract tissues, except for the cecum, in chickens fed diets containing 1–5 mg/kg sodium selenite (Fig. 3). The greatest increases in SelW mRNA expression were observed in the gastrointestinal tract tissues, except for the tongue, small intestine and rectum, in chickens fed the diet containing 3 mg/kg sodium selenite ($P < 0.001$). Of note, the mRNA expression of SelW in the gizzard increased by about 27.28-fold with 3 mg/kg diet Se, as compared with the control group. When the chickens were fed the diet containing 5 mg/kg sodium selenite, the greatest levels of SelW mRNA were found in the tongue, small intestine and rectum. However, after reaching the maximal level, further increases in Se dose actually led to a reduction in SelW mRNA in the esophagus, crop, proventriculus, gizzard, duodenum and cecum (Fig. 3).

Correlation between Se concentrations and SelW mRNA abundance

The Pearson correlation coefficient between Se concentrations in whole blood or tissues and the SelW mRNA abundance in the gastrointestinal tract tissues of chicken are reported in Table 2. Tissue Se content was significantly correlated with the abundance of SelW mRNA in the esophagus, proventriculus, gizzard, small intestine and rectum (all, $P < 0.01$) and crop ($P < 0.05$), but not in the duodenum or cecum ($P > 0.05$). The whole blood Se concentration was directly correlated with the abundance of SelW mRNA in the small intestine and rectum (both, $P < 0.01$), and the proventriculus and

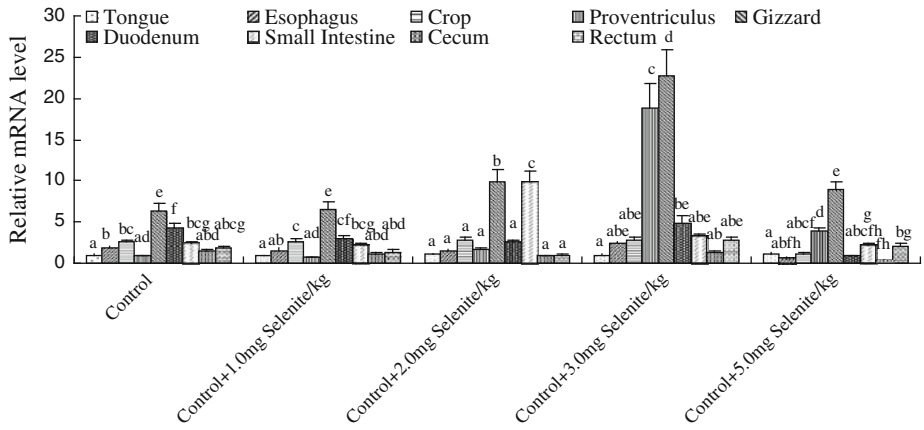

Fig. 2 Comparisons of the same concentrations of Se on the abundance of SelW mRNA in the different parts of the gastrointestinal tract tissues of chicken, such as tongue, esophagus, crop, proventriculus, gizzard, duodenum, small intestine, cecum and rectum. Within the gastrointestinal tract tissues of chicken, *bars* sharing a common letter are not significantly different ($P > 0.05$)

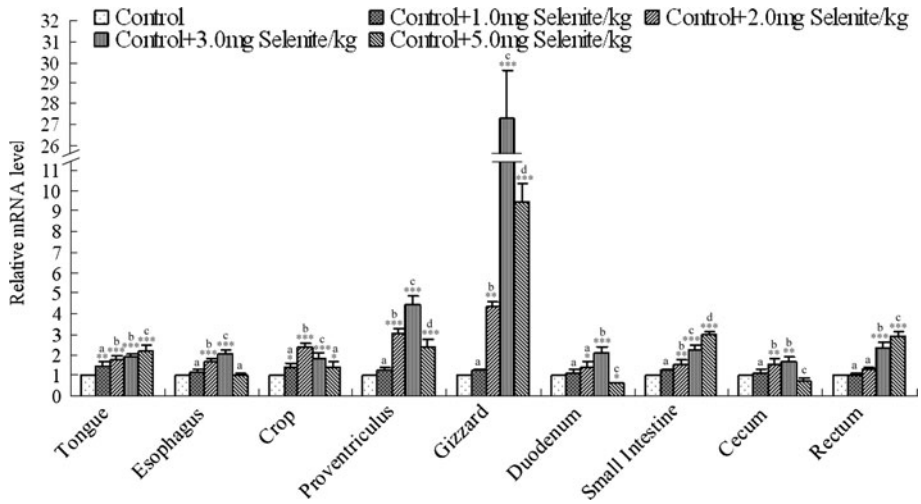

Fig. 3 Effects of different concentrations of Se on the abundance of SelW mRNA in the gastrointestinal tract tissues of chicken. *Bars* represent mean ± standard deviation ($n = 3$/group). *Bars with asterisk* "*" are statistically significantly different from control by one-way analysis of variance followed by Tukey's multiple comparison test (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Within the groups treated with various levels of Se, *bars* sharing a common letter are not significantly different ($P > 0.05$)

Table 2 Pearson correlation coefficients between whole blood Se, tissue Se and the abundance of SelW mRNA in the gastrointestinal tract tissues of chickens fed diets containing different concentrations of Se

Parameter	Esophagus	Crop	Proventriculus	Gizzard	Duodenum	Small intestine	Cecum	Rectum
SelW								
Whole blood Se	0.184	0.275	0.514*	0.529*	0.013	0.936**	–0.157	0.899**
Tissue Se	0.706**	0.619*	0.807**	0.760**	0.459	0.681**	0.430	0.664**

* $P < 0.05$; ** $P < 0.01$

gizzard (both, $P < 0.05$), but not in the esophagus, crop, cecum or duodenum ($P > 0.05$).

Discussion

In our previous study, we determined the cDNA sequence for SelW from chicken cerebral tissue and found that SelW is expressed widely in chicken tissues, with predominant expression in the nervous tissue, muscle tissue, gizzard, blood vessel, and cartilaginous tissue, and weak expression in the pancreas, testis, ovary, kidney and veins (unpublished data). In this study, we observed the mRNA expression of SelW in the gastrointestinal tract tissues of 90-day-old male chickens. The SelW mRNA levels in rodents (Vendeland et al. 1995; Yeh et al. 1995, 1997b, 1998; Sun et al. 1998), primates (Gu et al. 1999, 2000; Bellingham et al. 2003), pigs (Terry et al. 2009; Zhou et al. 2009) and sheep (Yeh et al. 1997a; Sun et al. 1999) are generally sensitive to Se status. The results of the present work confirm that SelW gene expression in the gastrointestinal tract of avian is also sensitive to dietary Se content, consistent with these earlier studies.

The tissue distribution of SelW differs among animals. In previous studies, it was reported that SelW was expressed in the gastrointestinal system including tongue, esophagus, stomach, intestine and colon in rodents, primates and sheep, and in a gastrointestinal cell line (Caco-2) (Yeh et al. 1997a, 1998; Sun et al. 1998; Gu et al. 2000; Pagmantidis et al. 2005). However, the distribution of SelW in the avian gastrointestinal tract tissues was unknown until now. We observed that the SelW gene was more widely expressed in the gastrointestinal tract tissues

of male chickens fed the basal commercial diets and Se-supplemented diets than we originally thought. Thus, these data suggest that the tissue distribution of SelW in the digestive system of birds may be similar to that of mammals.

Numerous studies have shown that SelW levels increase in response to Se dietary supplementation. SelW mRNA and protein expression in muscles, hearts, testis and spleen in rats and sheep are very sensitive to Se (Sun et al. 1998; Yeh et al. 1995, 1997a, b, 1998). However, there was a significant difference in terms of the changes in gastrointestinal SelW expression between rats and sheep in response to dietary supplementation with Se. When animals were fed Se-supplemented diets, higher levels of SelW were found in the tongue (rats and sheep) and colon (rats), whereas an indistinct increase in the levels of SelW was observed in the esophagus, stomach and small intestine of rats (Yeh et al. 1997a; Sun et al. 1998; Pagmantidis et al. 2005). In the present study, chickens fed diets containing 1–3 mg/kg sodium selenite showed increased expression of SelW mRNA in the gastrointestinal tract tissues. However, increasing the dietary content of sodium selenite to >3 mg/kg diet, SelW mRNA levels decreased in the esophagus, crop, proventriculus, gizzard, duodenum and cecum (Fig. 2). Thus, these data suggest that the transcription of the SelW gene in the gastrointestinal tract tissues of birds are more sensitive to Se than that in mammals. SelW appears to bind to glutathione (Beilstein et al. 1996) and acts as an antioxidant in vivo (Jeong et al. 2002) and in vitro (Wang et al. 2010). Therefore, we hypothesized that Se and SelW may play an important role in the function of the gastrointestinal tract in birds and during digestive system diseases. It was consistent with the previous study about rats (Pagmantidis et al. 2005).

Previous studies have reported no correlations between the relative tissue distributions of Se and SelW (Gu et al. 2000; Yeh et al. 1997a). The results of present study support these finding. The greatest increase in SelW mRNA abundance was observed in the gizzard (Fig. 2), whereas Se content was highest in the duodenum and small intestine (Fig. 1b). Nevertheless, there was a significant direct relationship between tissue Se content and the SelW mRNA abundance in the esophagus, proventriculus, gizzard, small intestine and rectum of chickens fed Se-supplemented diets (Table 2).

The question arises as to the mechanism by which Se regulates SelW expression. Se is present in selenoproteins as the amino acid Sec, and is incorporated during protein synthesis. This incorporation requires the recoding of a UGA codon that involves the formation of a complex between an RNA stem-loop structure (SECIS) located in the 3′-untranslated region of selenoprotein mRNAs and various trans-acting proteins (Berry 2005). Thus, selenoprotein expression can depend on dietary Se intake and genetic factors. Gu et al. (2002) reported that Se stabilizes SelW mRNA but has no effect on its transcription in cultured L8 rat skeletal muscle cells. However, Pagmantidis et al. (2005) reported that SelW expression in the colonic mucosa from rats and human intestinal Caco-2 cells is highly sensitive to Se depletion. Under circumstances of low Se, mRNA is degraded through nonsense-mediated decay (Moriarty et al. 1998). The levels of SelW mRNA are highly dependent on adequate dietary Se intake and on the levels of selenoprotein P (Pagmantidis et al. 2005; Sunde et al. 2009; Hoffmann et al. 2007). Thus, differences in SelW mRNA levels may be due to multiple factors acting individually or in combination. However, the detailed mechanisms involved by which Se regulates SelW transcription in the gastrointestinal tract tissues of chickens remain unclear.

In summary, SelW gene expression was found in the gastrointestinal tract tissues of chickens. The transcription of the SelW gene in the gastrointestinal tract tissues of chickens is very sensitive to dietary Se. SelW is an antioxidant protein and we believe that it plays an important role in cellular defense against oxidative damage and Se metabolic pathways in the digestive system of birds. Further studies are needed to determine the mechanism by which Se regulates SelW gene expression in birds.

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References

Aachmann FL, Fomenko DE, Soragni A, Gladyshev VN, Dikiy A (2007) Solution structure of selenoprotein W and NMR analysis of its interaction with 14-3-3 proteins. J Biol Chem 282(51):37036–37044

Beilstein MA, Vendeland SC, Barofsky E, Jensen ON, Whanger PD (1996) Selenoprotein W of rat muscle binds glutathione and an unknown small molecular weight moiety. J Inorg Biochem 61(2):117–124

Bellingham J, Gregory-Evans K, Fox MF, Gregory-Evans CY (2003) Gene structure and tissue expression of human selenoprotein W, SEPW1, and identification of a retro-processed pseudogene, SEPW1P. Biochim Biophys Acta 1627(2–3):140–146

Berry MJ (2005) Insights into the hierarchy of selenium incorporation. Nat Genet 37(11):1162–1163

Brown KM, Arthur JR (2001) Selenium, selenoproteins and human health: a review. Public Health Nutr 4(2B): 593–599

Castellano S, Lobanov AV, Chapple C, Novoselov SV, Albrecht M, Hua D et al (2005) Diversity and functional plasticity of eukaryotic selenoproteins: identification and characterization of the SelJ family. Proc Natl Acad Sci USA 102(45):16188–16193

Chariot P, Bignani O (2003) Skeletal muscle disorders associated with selenium deficiency in humans. Muscle Nerve 27(6):662–668

Combs GF Jr (2005) Current evidence and research needs to support a health claim for selenium and cancer prevention. J Nutr 135(2):343–347

Combs GF Jr, Clark LC, Turnbull BW (2001) An analysis of cancer prevention by selenium. Biofactors 14(1–4):153–159

Gu QP, Beilstein MA, Barofsky E, Ream W, Whanger PD (1999) Purification, characterization, and glutathione binding to selenoprotein W from monkey muscle. Arch Biochem Biophys 361(1):25–33

Gu QP, Sun Y, Ream LW, Whanger PD (2000) Selenoprotein W accumulates primarily in primate skeletal muscle, heart, brain and tongue. Mol Cell Biochem 204(1–2):49–56

Gu QP, Ream W, Whanger PD (2002) Selenoprotein W gene regulation by selenium in L8 cells. Biometals 15(4):411–420

Hasunuma R, Ogawa T, Kawanishi Y (1982) Fluorometric determination of selenium in nanogram amounts in biological materials using 2,3-diaminonaphthalene. Anal Biochem 126(2):242–245

Hoffmann PR, Berry MJ (2008) The influence of selenium on immune responses. Mol Nutr Food Res 52(11):1273–1280

Hoffmann PR, Hoge SC, Li PA, Hoffmann FW, Hashimoto AC, Berry MJ (2007) The selenoproteome exhibits widely varying, tissue-specific dependence on selenoprotein P for selenium supply. Nucleic Acids Res 35(12):3963–3973

Jeong D, Kim TS, Chung YW, Lee BJ, Kim IY (2002) Selenoprotein W is a glutathione-dependent antioxidant in vivo. FEBS Lett 517(1–3):225–228

Kaur P, Bansal MP (2005) Effect of selenium-induced oxidative stress on the cell kinetics in testis and reproductive ability of male mice. Nutrition 21(3):351–357

Kryukov GV, Gladyshev VN (2004) The prokaryotic selenoproteome. EMBO Rep 5(5):538–543

Kryukov GV, Castellano S, Novoselov SV, Lobanov AV, Zehtab O, Guigo R et al (2003) Characterization of mammalian selenoproteomes. Science 300(5624):1439–1443

Li JL, Gao R, Li S, Wang JT, Tang ZX, Xu SW (2010) Testicular toxicity induced by dietary cadmium in cocks and ameliorative effect by selenium. Biometals 23(4):695–705

Lu J, Holmgren A (2009) Selenoproteins. J Biol Chem 284(2): 723–727

Mahmoud KZ, Edens FW (2005) Influence of organic selenium on hsp70 response of heat-stressed and enteropathogenic *Escherichia coli*-challenged broiler chickens (*Gallus gallus*). Comp Biochem Physiol C 141(1):69–75

Martin-Romero FJ, Kryukov GV, Lobanov AV, Carlson BA, Lee BJ, Gladyshev VN et al (2001) Selenium metabolism in Drosophila: selenoproteins, selenoprotein mRNA expression, fertility, and mortality. J Biol Chem 276(32): 29798–29804

Moriarty PM, Reddy CC, Maquat LE (1998) Selenium deficiency reduces the abundance of mRNA for Se-dependent glutathione peroxidase 1 by a UGA-dependent mechanism likely to be nonsense codon-mediated decay of cytoplasmic mRNA. Mol Cell Biol 18(5):2932–2939

Pagmantidis V, Bermano G, Villette S, Broom I, Arthur J, Hesketh J (2005) Effects of Se-depletion on glutathione peroxidase and selenoprotein W gene expression in the colon. FEBS Lett 579(3):792–796

Papp LV, Lu J, Holmgren A, Khanna KK (2007) From selenium to selenoproteins: synthesis, identity, and their role in human health. Antioxid Redox Signal 9(7):775–806

Peirson SN, Butler JN, Foster RG (2003) Experimental validation of novel and conventional approaches to quantitative real-time PCR data analysis. Nucleic Acids Res 31(14):e73

Pfaffl MW (2001) A new mathematical model for relative quantification in real-time RT-PCR. Nucleic Acids Res 29(9):e45

Rayman MP (2000) The importance of selenium to human health. Lancet 356(9225):233–241

Reeves MA, Hoffmann PR (2009) The human selenoproteome: recent insights into functions and regulation. Cell Mol Life Sci 66(15):2457–2478

Schweizer U, Schomburg L, Savaskan NE (2004) The neurobiology of selenium: lessons from transgenic mice. J Nutr 134(4):707–710

Stadtman TC (2000) Selenium biochemistry. Mammalian selenoenzymes. Ann N Y Acad Sci 899:399–402

Sun Y, Ha PC, Butler JA, Qu BR, Yeh JY, Whanger PD (1998) Effect of dietary selenium on selenoprotein W and glutathione peroxidase in 28 tissues of the rat. J Nutr Biochem 9:23–27

Sun Y, Butler J, Forsberg N, Whanger PD (1999) Selenoprotein W, selenium and glutathione peroxidase in rat and sheep brains and in brain cell cultures. Nutr Neurosci 2: 227–237

Sunde RA, Raines AM, Barnes KM, Evenson JK (2009) Selenium status highly regulates selenoprotein mRNA levels for only a subset of the selenoproteins in the selenoproteome. Biosci Rep 29(5):329–338

Terry EN, Michal JJ, Hostetler CE, Kincaid RL, Johnson KA (2009) Levels of mRNA for three selenoproteins in skeletal muscle of fetal and newborn pigs. Livest Sci 124: 21–25

Vendeland SC, Beilstein MA, Yeh JY, Ream W, Whanger PD (1995) Rat skeletal muscle selenoprotein W: cDNA clone and mRNA modulation by dietary selenium. Proc Natl Acad Sci USA 92(19):8749–8753

Wang XL, Yang CP, Xu K, Qin OJ (2010) Selenoprotein W depletion in vitro might indicate that its main function is not as an antioxidative enzyme. Biochemistry 75(2):201–207

Whanger PD (2000) Selenoprotein W: a review. Cell Mol Life Sci 57(13–14):1846–1852

Yeh JY, Beilstein MA, Andrews JS, Whanger PD (1995) Tissue distribution and influence of selenium status on levels of selenoprotein W. FASEB J 9(5):392–396

Yeh JY, Gu QP, Beilstein MA, Forsberg NE, Whanger PD (1997a) Selenium influences tissue levels of selenoprotein W in sheep. J Nutr 127(3):394–402

Yeh JY, Vendeland SC, Gu Q, Butler JA, Ou BR, Whanger PD (1997b) Dietary selenium increases selenoprotein W levels in rat tissues. J Nutr 127(11):2165–2172

Yeh JY, Ou BR, Gu QP, Whanger PD (1998) Influence of gender on selenoprotein W, glutathione peroxidase and selenium in tissues of rats. Comp Biochem Physiol B 119(1):151–155

Zhang Y, Fomenko DE, Gladyshev VN (2005) The microbial selenoproteome of the Sargasso Sea. Genome Biol 6(4):R37

Zhou JC, Zhao H, Li JG, Xia XJ, Wang KN, Zhang YJ et al (2009) Selenoprotein gene expression in thyroid and pituitary of young pigs is not affected by dietary selenium deficiency or excess. J Nutr 139(6):1061–1066