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Selenium in Food Chain and Animal Nutrition: Lessons from Nature -Review-

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ABSTRACT : Selenium is considered to be one of the most controversial trace elements. On the one hand, it is toxic at high doses and there is a great body of information related to environmental issues of Se contamination. On the other hand, Se deficiency is a global problem related to an increased susceptibility to various diseases of animals and humans and decreased productive and reproductive performance of farm animals. Optimisation of Se nutrition of poultry and farm animals will result in increased efficiency of egg, meat and milk production and even more important, will improve quality. From the data presented in the review it is clear that the main lesson which we have to learn from nature is how to use organic selenium in animal and human diets. Selenium-enriched yeast (Sel-Plex) is the result of such a lesson and it is just a matter of time before animal nutrition moves completely from using ineffective sodium selenite to organic selenium. Other lessons from nature will follow. Recent advances in genomics and proteomics, in association with descriptions of new selenoproteins, will be a driving force in reconsidering old approaches related to Se nutrition. Probably 90% of all Se research has been conducted with sodium selenite and we now understand that the natural form of selenium is different. The main advances in Se status assessment and Se requirements were established based on the activity of glutathione peroxidase (GSH-Px), an enzyme which for many years was considered to be the main selenoprotein. Recently it was discovered that it is only one of at least 25 various selenoproteins. Se research and practical applications are developing quickly and they are very exciting and promising. (**Key Words :** Selenium, Selenomethionine, Se-yeast, Nutrition, Poultry, Farm Animals)

INTRODUCTION

Selenium is considered to be one of the most controversial trace elements. On the one hand, it is toxic at high doses and there is a great body of information related to environmental issues of Se contamination. On the other hand, Se deficiency is a global problem related to an increased susceptibility to various diseases of animals and humans and decreased productive and reproductive performance of farm animals.

The selenium cycle in the food chain of land animals and humans starts from the soil and includes plant and animal sources ultimately dependent on its assimilation from the soil. Indeed, soils are the major source of Se for plants and therefore for animals eating those plants and humans consuming plant and animal-derived foods. Considering food and feed sources of Se it is necessary to mention that Se levels vary greatly in different foods as well as in the same foods grown in different areas. In fact it seems likely that low Se availability from various soils is a result of agricultural practises. Firstly, usage of inorganic fertilizers containing sulphur decreases Se availability. Secondly, soil acidification also substantially decreases Se availability. Furthermore, decreased soil aeration also decreases Se availability. There have been several attempts to solve this problem by using Se fertilization. In particular, such a technique has been widely used in Finland for the last 20 years. However, there are several relevant questions to answer before the technique can be widely used in other countries. For example, it is not known how Se fertilization could affect the microbial population of the soil.

There is an inconsistency in the common practise of selenium supplementation of animal diets. On the one hand, naturally occurring organic selenium is represented by a mixture of selenoamino acids with selenomethionine (SeMet) comprising more than 50% of the total selenium in many feed ingredients, including grains and forages, etc. In

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fact SeMet fulfils the criteria of an essential amino acid (Schrauzer, 2003; 2006). On the other hand, until recently the supplemental form of selenium for farm animals and poultry has been inorganic, either selenite or selenate. It seems likely that changes in the feed formulation for poultry, pigs and dairy related to usage of the most effective organic selenium in the diets could be a solution for the global Se deficiency. Recent approval by the US Food and Drug Administration of organic selenium in the form of selenized yeast (Sel-Plex®, Alltech Inc.) for poultry, pigs, cows and pets will resolve the discrepancy between natural and supplemental selenium sources. Indeed, it has been proven that usage of this form of dietary Se supplementation in animal diets substantially improved their Se status, increased productive and reproductive performances and provided an opportunity to produce Se-enriched eggs, meat and milk and in this way to improve the Se status of the general population (Surai, 2006).

SELENIUM IN SOILS AND PLANTS

Selenium (Se) is a chemical element with atomic number 34 and atomic weight 78.96 belonging to group VI of the periodic table of elements. This group also includes such non-metals as sulphur and oxygen. In nature Se exists in two chemical forms, organic and inorganic. In particular, inorganic Se can be found in different minerals in the form of selenite, selenate and selenide as well as in the metallic (Se^0) form. In contrast, selenium in feed ingredients (forages, grains, oilseed meals, etc.) is an integral part of various organic compounds including amino acids selenomethionine (SeMet) and selenocysteine (SeCys) and exists in the Se^{-2} oxidation state. As a result, in nature animals receive Se mainly in the form of SeMet which is considered to be a most effective nutritional form of selenium for animals and human.

The selenium cycle in the food chain of land animals and humans starts from soils and includes plant and animal sources ultimately dependent on its assimilation from the soil. Selenium concentration in soils varies significantly. The Se content of most soils ranges between 0.1 and 2 ppm; and soil Se exists in various forms, including selenides, elemental Se, selenites, selenates and organic Se compounds (Selenium in Nutrition, 1983). High concentrations of Se are found mainly in sedimentary rocks and shales formed during the cretaceous period, while lower concentrations of Se are characteristic for igneous (volcanic) rock, sandstone, granite and limestone (Van Metre and Callan, 2001). Investigations conducted in China indicated that soils developed under tropic and subtropic conditions (laterite, yellow soil and red soil) are characterised by comparatively high Se levels (>0.3 ppm)(Tan et al., 2002). In contrast, the soils developed under the temperate (warm) steppe and desert conditions (chernozem, chestnut soil, calcic brown soil, desert soil and solonchak) have moderate Se concentrations (0.14-0.30 ppm). Finally, such soils as brown earth, drab soil, dark brown soil, loessial soils, purple soil, red drab soil, developed under the temperate (warm) humid/sub-humid conditions are quite poor in Se.

Furthermore, Se availability to plants depends on many factors including soil pH, the oxidation-reduction potential and mineral composition of the soil, rate of artificial fertilization and rainfall. In fact, the bioavailability of Se in soils for plants depends more on its form than on its total concentration:

- In the case of acidic soils or poor soil aeration, Se can form insoluble complexes with iron hydroxide and become poorly available. For example, at pH 6, only 47% of labelled Se was transferred from soil to ryegrass leaves. Increasing pH to 7 increased Se assimilation to 70% (Haygarth et al., 1995). Indeed, Se in alkaline soils occurs in the selenate form, where it is soluble and easily available to plants.
- Since sulfate competes with selenate for uptake by the sulfate transporter, high soil sulfate decreases Se uptake by plants (Terry et al., 2000). It seems likely that phosphate also competes with Se uptake (Sors et al., 2005). This explains low Se availability from soils following application of certain types of fertilizers.
- Selenium can also be leached from the topsoil in areas of high rainfall. Therefore areas with higher rainfall have lower forage selenium content.
- Solubility is the critical determinant of Se bioavailability to plants and the amount of water-soluble Se in soils varies substantially and does not correlate with total soil Se (Combs and Combs, 1986).
- Selenite is strongly adsorbed by soils while selenate is only weakly absorbed and leaches easily.
- Selenide and elemental Se are usually found in reducing environments and are unavailable to plants and animals.
- Selenite is present in mildly oxidizing, neutral pH environments and typically humid regions, while selenate is the predominant form under ordinary alkaline and oxidized conditions (Goh and Lim, 2004). The authors also showed that the adsorption of selenite and selenate by soils appeared to be influenced by the variable pH-dependent charges on the soil particle surfaces. In particular, phosphate had more profound effects than sulfate on Se adsorption in the soil.
- Application of gypsum (calcium sulfate) to soils decreased Se availability for plants (Selenium in Nutrition, 1983)
- Leaching during the soil development process and

irrigation water decreased Se level in plants (Selenium in Nutrition, 1983)

- Forage Se is reported to be low on sandy soils and lower on mineral upland soils than on organic moorland soils in the British Isles (MacPherson, 2000).
- The main chemical changes under long-term waterlogged conditions are depletion of molecular oxygen, decrease of redox potential, and reduction of Fe (III) to Fe (II) and SeO_3^{-2} to Se^0. This leads to low availability of Se in soils, and subsequently low Se content (29 μg/kg) in brown rice grain produced in this region of China (Cao et al., 2001). Indeed, selenite binds tightly to iron and aluminium oxides and thus is quite insoluble in soils (Jonnalagadda and Rao, 1993).
- Selenium is transported via the xylem to chloroplasts in leaves where it is processed by the sulphur assimilation pathway into organic compounds. The selenate form is transported more easily from root to shoot than selenite or organic Se (Terry et al., 2000).

After absorption, the distribution of Se in various parts of the plant depends on species, phase of development and physiological conditions. For example, Se distribution was studied in *Astragalus bisulcatus*, an accumulator species capable of accumulating up to 0.65% of its shoot dry biomass as Se (Pickering et al., 2000). It was shown that plants exposed to 5 μM selenate for 28 days contained predominantly selenate in the mature leaf tissue, whereas the young leaves and the roots contained exclusively organic Se. From this work it is clear that the fate of selenate differs with plant tissues and stage of growth. Therefore chemical reduction of selenate to organic Se in plants is tissue-specific, inducible and developmentally dependent. It is likely that selenate reduction is rate-limiting in the conversion of Se to organic forms (Pickering et al., 2000).

PLANTS AS MAJOR SOURCES OF SELENIUM FOR ANIMALS AND HUMAN

The plant absorbs Se from the soil in the form of selenite or selenate and synthesises selenoamino acids with SeMet representing more than 50% of the Se in cereal grains (Olson and Palmer, 1976) and with Se-methyl-selenomethionine, selenocysteine and Se-methyl-selenocysteine being the other seleno-compounds found in plants (Brody, 1994). In general, plants can also take up from the soil organic forms of selenium such as SeMet. At present, Se in any form has not been scientifically demonstrated to be an essential nutrient for higher plants. Regardless, SeMet is the major selenocompound in cereal grains, grassland legumes and soybeans (Whanger, 2002). For example, in corn, rice, wheat and soybeans, SeMet comprises 45.5-82%, 54.9-86.5%, 50.4-81.4% and 62.9-71.8% of total Se, respectively (Yang et al., 1997). Even in wheat grown on seleniferous soils (up to 31 ppm Se), almost half occurred in the form of SeMet (Olson et al., 1970). Similarly, in seleniferous corn and soybeans, SeMet represented more than 80% of total Se. The majority of the Se is present as SeMet in both rice and corn (Beilstein et al., 1991). Wheat is considered to be the most efficient accumulator of Se within the common cereal crops: wheat>rice>maize>barley>oats (Lyons et al., 2003; Broadley et al., 2006). It was shown that SeMet is stored mainly in the grain and the root, while lower concentrations of this amino acid are found in the stems and leaves (Schrauzer, 2003). SeMet was the main Se-containing amino acid identified in most of the extracts of Indian mustard (*Brassicaj uncea*), sunflower (*Helianthus annus*), and white lupine (*Lupinus albusl*) (Ximenez-Embun et al., 2004). The variability in results of Se specification investigations of plant material reflects analytical difficulties. For example, by using a SeMet determination based on its reaction with CNBr, it has been shown that wheat samples, though having a 30-fold range in total Se content, all have about 45% of their total Se values in the form of SeMet (Wolf and Goldschmidt, 2004). However, the authors suggested that additional experiments were needed to verify that all selenomethionine in the wheat samples had been accounted for.

It is interesting to note that the richest source of Se for human consumption, Brazil nuts, also contains SeMet as the most abundant selenoamino acid (Vooonderheide et al., 2002). However, organic Se compounds can differ substantially, depending on the plant material analysed and a range of selenocompounds have been detected. Analytical speciation studies showed that the bulk of the Se in Se-garlic and Se-yeast is in the form of gamma-glutamyl-Se-methylselenocysteine (73%) and SeMet (85%), respectively (Ip et al., 2000). Se-methylselenocysteine is the major selenocompound in Se-enriched plants such as garlic, onions, broccoli florets and sprouts, and wild leeks (Whanger, 2002).

SELENIUM ABSORPTION AND METABOLISM

Recent advances in Se biochemistry have provided a deeper understanding of the principal differences in metabolism of the two forms of Se, namely inorganic Se (sodium selenite or selenate) and organic Se (mainly SeMet). Results of various *in vitro* and *in vivo* experiments with a variety of animal species and model systems have demonstrated that SeMet is readily absorbed through the gut. For example, in dogs this process was two times faster than SeCys and four times faster than selenite absorption (Reasbeck et al., 1981). Indeed, SeMet is better absorbed

than selenite (Daniels, 1996). However, absorption is not a limiting factor to bioavailability.

A number of factors influence the bioavailability and distribution of selenium in the body (Thomson, 1998) including:

- chemical form of Se
- other dietary components
- selenium status
- physiological status
- species

Selenite is taken up by red blood cells within several minutes, reduced to selenide by glutathione, and then transported to the plasma, bound selectively to albumin and transferred to the liver (Suzuki and Ogra, 2002). Contrary to selenite, intact selenate is either taken up directly by the liver or excreted into the urine. About 3% of total plasma Se of healthy adults was bound to lipoproteins, mainly to the LDL fraction (Ducros et al., 2000). After solvent fractionation of LDL and HDL, the major part of the Se was recovered in the protein extract, suggesting that it may be incorporated in apolipoproteins. The exact form of Se is not yet clearly established, but considering the different Se compounds found in proteins, it was postulated to be SeMet. The distribution of Se in plasma fractions was investigated in guinea pigs fed various levels (basal, 0.5, 1.0, 2.0, 4.0, 6.0 and 8.0 mg Se/kg) of dietary SeMet (Gu et al., 1998). There was a corresponding increase of Se concentration in liver, kidney, brain, testis, spleen, heart and muscle with each increase of dietary Se, but glutathione peroxidase (GSH-Px) activity did not change in liver, brain, testis, heart or muscle in pigs fed any of the Se levels as compared to controls fed a basal commercial diet. There was a redistribution of Se between various fractions in the blood. For example, on a percentage distribution basis, the Se in selenoprotein P decreased, and that in the albumin fraction increased with increased dietary intakes of Se as SeMet. Similarly, the greatest percentage of Se was in the albumin fraction of Chinese people living in the high Se areas, whereas the greatest amount was in the selenoprotein P fraction in subjects living in Se-deficient areas of China (Gu et al., 1998). Increases in the ratios of Se:albumin in either the plasma or the albumin fraction also occurred with increases of Se intake of these subjects.

The majority of the Se was in the hemoglobin (Hb) fraction in women taking supplemental SeMet, but was about equally distributed between GSH-Px and Hb in women taking selenate (Butler et al., 1991). Therefore, the percentage of Se associated with GSH-Px was found to be greater in erythrocytes and plasma of women taking selenate than of those taking SeMet. About 68% of erythrocyte Se was associated with GSH-Px in monkeys given selenite whereas only 34% was associated with GSH-Px in those administered SeMet (Butler et al., 1990). Selenium in breast milk occurs as GSH-Px (4-32% total Se) >selenocystamine>selenocystine>selenomethionine (Dorea, 2002). The results of recent study (Okuno et al., 2001) indicated that in mouse liver SeMet was directly metabolized to CH_3SeH by an alpha, gamma-elimination enzyme analogous to bacterial L-methionine gamma-lyase, in addition to the generally accepted pathway via selenocysteine. It has been suggested that L-selenohomocysteine generated from SeMet metabolism can be efficiently recycled to SeMet in mammals (Zhou et al., 2000).

The number of published studies in animals and man suggested that the metabolic fate and physiological function of dietary selenite may differ from that of SeMet or of food Se. It has been postulated that there are two distinct metabolic pools of Se in the body (Daniels, 1996). The main exchangeable metabolic pool includes all forms of Se derived from inorganic selenite/selenide, including endogenously synthesized selenoproteins (e.g. GSH-Px, selenoprotein P, etc.), excretory Se metabolites (trimethylselenium ion) and various other intermediary products of selenite metabolism. This is an active Se pool providing for synthesis of the primary functionally important selenocompounds (Daniels, 1996). The second Se pool consists of SeMet-containing proteins and potentially can contribute to the first pool via participation in selenoprotein synthesis. In fact, Burk et al. (2001) demonstrated that Se from SeMet, but not that from selenate or selenocysteine, can be incorporated into albumin, presumably as SeMet in the methionine pool. In another study, albumin was purified from plasma of a human before and after 28 days of supplementation with 400 μg Se/day as SeMet. It was shown that the albumin contained 1 Se atom, presumably as SeMet, per 8,000 methionine residues before supplementation and 1 per 2,800 after supplementation (Hondal et al., 1999). These findings support the view that SeMet is a non-specific form of Se that is metabolized as a constituent of the methionine pool, where it is randomly distributed, and it is unaffected by specific Se metabolic processes. Therefore SeMet can be considered as a storage form of Se in animals and humans and it is metabolized as a constituent of the methionine pool. In contrast, no evidence was obtained for non-specific incorporation of Se into plasma proteins when it was administered as selenate or as selenocysteine. These forms of the element appear to be metabolized by specific Se metabolic processes (Burk et al., 2001).

The chemical species-specific metabolic pathway for Se was explained by the metabolic regulation through selenide as the assumed common intermediate for the inorganic and organic Se sources and as the checkpoint metabolite between utilization for selenoprotein synthesis and methylation for the excretion of Se (Suzuki and Ogra, 2002).

In particular, organic Se, which can be found in grains, forages and other feed ingredients, is primarily in the form of SeMet and is metabolised in the same way as methionine. It is actively transported through intestinal membranes during absorption and actively accumulated in such tissues as liver and muscle. It is well known that methionine is not synthesised by animals or humans and therefore it is an essential amino acid. The same is true for SeMet, which is not synthesised in animals or humans, and must be derived from feed sources.

The skeletal muscles are the major Se-storage organ, accounting for about 46.9% of the total Se in the human body, while kidney contains only 4% of Se reserves. In humans, whole body Se depends on the geographic location of the person and varies from 3-6 mg up to 13-20 mg. GSH-Px activity and deposition of Se were examined in tissues of rats given dietary Se for 7 weeks as either selenite or SeMet with a ^{75}Se radiotracer of the same chemical form (Beilstein and Whanger, 1988). The authors showed that the proportion of ^{75}Se as SeMet was higher in tissues of rats fed SeMet (highest in muscle and hemoglobin, 70%, and lowest in testes, 16%). In contrast, selenocysteine was the predominant form of Se present in tissues of rats given selenite. As mentioned above SeMet is considered to be a storage form of Se in the body. Indeed, when organic Se is used in the diet, the Se reserve is built in muscles in the form of SeMet. These reserves can be used in stress conditions, when the Se requirement increases but feed consumption decreases. In stress conditions, protein catabolism by proteasomes can release SeMet, which could serve as a source of Se for newly synthesized selenoproteins, such as GSH-Px, thioredoxin reductase and methionine sulphoxide reductase. Those enzymes can deal with overproduction of free radicals and prevent a decrease in productive and reproductive performance of farm animals. It was proven that Se from both selenite and SeMet are readily available for synthesis of the selenoenzyme GSH peroxidase in rat tissues (Pierce and Tappel, 1977).

There are several lines of evidence confirming the idea that Se accumulates in tissues in the form of SeMet and is available for selenoprotein synthesis.

- First, studies in our laboratory (Surai, 2000; Surai, 2002) indicated that chicks hatched from eggs enriched with Se by means of using Se yeast (Sel-Plex®) had higher liver GSH-Px activity not only at hatching, but more importantly, even at 5 days posthatch. More recent observations, with quail and chickens, indicate that when organic Se in the form of Sel-Plex was included in the maternal diet, Se concentration in the liver of the progeny was elevated up to 3 weeks posthatch (Pappas et al., 2005; Surai et al., 2006). This could be explained by usage of SeMet accumulated in tissues as a result of Se transfer from the egg during embryogenesis.
- Secondly, the bioavailability of the Se pool in maintaining liver GSH-Px activity during a period of Se deprivation, following excess selenite or SeMet loading was assessed in rats (Ip and Hayes, 1989). In this study, half-life of decay of the enzyme was calculated to be 4.2 and 9.1 days, respectively, in rats that had already been exposed to 3 ppm Se as either selenite or SeMet.
- Thirdly, in a human study Persson-Maschos et al. (1998) showed that in individuals who had been supplemented with organic Se, the decline in the level of selenoprotein P following a period of supplementation was slower than in individuals who had been supplemented with selenite.
- Fourthly, when wheat and selenate were used as Se sources in a supplementation study in Finnish men it was shown that once the supplements were withdrawn, platelet GSH-Px activity declined less in the group given wheat Se (Levander et al., 1983).
- Fifthly, after several weeks of supplementation with high-Se bread, plasma Se of New Zealand subjects increased from 50-70 ng/ml to 120-175 ng/ml (Robinson et al., 1985) and remained elevated for some time when supplementation ceased.
- Finally, six adults received a single oral 200 μg dose of ^{74}Se as L-SeMet. Average turnover time of the plasma Se compounds varied from 0.01 to 1.1 days and the turnover time in the liver-pancreas subsystem ranged from 1.6 to 3.1 days. On the other hand, turnover time ranged from 61 to 86 days in peripheral tissues with the slowest turnover (Swanson et al., 1991). The whole body residence time was approximately 5-fold greater than the turnover time of the tissue pool with the slowest turnover, reflecting substantial reutilization of labelled material.
- In addition, in SeMet or Se-yeast supplemented mice, liver GSH-Px activities declined more slowly during Se depletion than in mice given selenite (Spallholz and Rafferty, 1987 cited by Schrauzer, 2003).
- Furthermore, in children the relative bioavailability of Se-yeast versus selenite measured as GSH-Px activity was similar in plasma, red blood cells, and platelets, however, Se-yeast provided a longer lasting body pool of Se (Alfthan et al., 2000).

These data are in agreement with the suggestion that SeMet is the major selenocompound initially found in animals given this selenoamino acid, but it is converted with time to selenocysteine when incorporated into functional selenoproteins (Whanger, 2002).

Weanling male rats were fed a basal Se-deficient diet or this diet plus 2 ppm Se as either selenite, SeCys or SeMet for nine weeks (Deagen et al., 1987). Except for the kidney,

the tissue Se concentrations were similar in rats fed selenite or SeCys, but the Se content in testis, muscle, pancreas, heart, spleen, whole blood, erythrocytes and plasma was significantly higher in rats fed SeMet than in those fed either selenite or SeCys. The greatest increase, due to SeMet compared with the selenite and SeCys treatments, was about 10-fold in the muscle compared with 1.3- to 3.6-fold for the other tissues (Deagen et al., 1987). In general SeMet has a slower, whole body turnover in comparison to sodium selenite and there is greater efficiency in the re-utilization of Se from SeMet (Swanson et al., 1991). Indeed, the average whole body half-lives of SeMet and selenite in humans were shown to be 252 and 102 days, respectively, confirming re-utilization of SeMet in the body (Patterson et al., 1989). It should be noted that only a small proportion of the methionine pool can be replaced by SeMet, since only part of methionine could be replaced by SeMet in the diet. Furthermore, protein turnover prevents accumulation of SeMet to toxic levels in the organism (Schrauzer, 2003).

In fact, rapid turnover of various selenoproteins and dependence of this process on Se status were described. For example, the half-life of GSH-Px is approximately 3 days (Sunde et al., 1989), and 2-iodothyronine deiodinase has a half-life of only 30-45 minutes (Curcio et al., 2001; Botero et al., 2002; Kim et al., 2003), while that of selenoprotein P in plasma is 3-4 h (Burk and Hill, 1994). In growth medium there was an increase in TR mRNA levels of 2-5-fold at 1 microM Se and an increase in the stability of TR mRNA with a half-life for degradation of 21 h compared to 10 hrs in the absence of Se (Gallegos et al., 1997). Similarly, the selenoprotein W mRNA half-life in myoblasts is about 57 hrs for cells grown in a low Se medium while Se treatment increased half-life by 2-fold (Gu et al., 2002). Therefore, it is clear that Se reserve development could be an important regulatory mechanism for maintaining an effective antioxidant defence during periods of increased demand. Therefore, from a nutritional viewpoint, SeMet is superior to selenite, especially with respect to maintenance of GSH-Px during periods of Se inadequacy (Ip and Hayes, 1989) or during increased demands for selenoproteins to deal with oxidative stresses.

At physiological levels of Se intake, urine is the most important route of excretion and regulates Se homeostasis (Daniels, 1996). For example, recently a study has been conducted to evaluate the bioavailability of Se from pork in humans (Bugel, 2004). Twelve male volunteers (age 21-30 years) participated in a study with a diet containing 170 g pig meat per day and 106 +/- 13 μg Se/day for three weeks. Complete faecal and urinary collections were made during the last week of each period. The apparent absorption of Se was very high (94+/-2%). Faecal and urinary excretions were 7+/-1 μg/day and 39+/-21 μg/day, respectively, resulting in a retention of 61+/-24 μg/day (Bugel, 2004). At generous intakes, faecal Se represents mainly unabsorbed dietary Se. Various Se metabolites were found in urine, but only trimethylselenium was well characterised. There is a large body of evidence indicating that urinary Se is lower when organic Se is used in comparison to selenite.

Recently, metabolic pathways of Se in human have been re-evaluated and it has been shown that selenosugar 1 is the major urinary metabolite after increased selenium intake, and it is suggested that previously accepted pathways for human metabolism of selenium involving trimethylselenonium ion as the excretory end product may need to be re-evaluated (Kuehnelt et al., 2005). In the study selenium speciation analysis by HPLC/ICPMS was used on samples of human urine from one volunteer over a 48-hour period after ingestion of selenium (1.0 mg) as sodium selenite, L-selenomethionine, or DL-selenomethionine. The major species in background urine were two selenosugars, namely methyl-2-acetamido-2-deoxy-1-seleno-beta-D-galactopyranoside (selenosugar 1) and its deacylated analog methyl-2-amino-2-deoxy-1-seleno-beta-D-galactopyranoside (selenosugar 3). Indeed, in all experiments, the major metabolite was selenosugar 1, constituting approximately 80% of the total selenium excreted over the first 24 h after ingestion of selenite or L-selenomethionine or approximately 65% after ingestion of DL-selenomethionine. Selenite was not present at significant levels (<1 μg Se/L) in any of the samples; selenomethionine was present in only trace amounts (approximately 1 μg/L) following ingestion of L-selenomethionine, but it constituted about 20% of the excreted selenium in the first 24 h after ingestion of DL-selenomethionine. Trimethylselenonium ion, a commonly reported urine metabolite, could not be detected (<1 μg/L) in the urine samples after ingestion of selenite or selenomethionine (Kuehnelt et al., 2005).

The amount of volatile dimethylselenide (DMSe) in breath has been monitored after ingestion of sub-toxic amounts of selenium (300 μg ^{77}Se, as selenite) by a healthy male volunteer (Kremer et al., 2005). Dimethylselenide was the only selenium species detected in breath samples before and after the ingestion of ^{77}Se-enriched selenite. It was also shown that the high Se dose led to a significant increase of DMSe and renal excretion of background selenium. These data confirmed the idea that selenium ingested as selenite is homeostatically controlled by excretion. Overall excretion as DMSe was calculated to be 11.2% from the ingested selenite within the first 10 days whereas urinary excretion accounts for nearly 18.5% (Kremer et al., 2005).

SELENIUM-YEAST AS AN EFFECTIVE SUPPLEMENTAL SOURCE OF SELENIUM

Since Se levels in soils vary and Se availability to plants also depends on many factors, the general agricultural

practice in the world includes Se supplementation of diets fed to farm animals and poultry. The FDA first approved Se supplements for poultry and swine in 1974 in the form of selenite or selenate. While the Se form was not rigorously considered in the initial research into Se nutrition, for the last 30 years information has accumulated indicating that the natural form of Se in plant-based feed ingredients consists of various selenoanimo acids with SeMet being major form of Se in grains, oil seeds and other important feed ingredients. Therefore, organic Se is the natural form of the element to include in feed formulations. However, sodium selenite remains in use in many animal feeds. The limitations of using inorganic Se are now well known and include toxicity, interactions with other minerals and vitamins, low efficiency of transfer to milk, meat and eggs and an inability to build and maintain Se reserves in the body (Kim and Mahan, 2003). As a result, a high proportion of the element consumed in the inorganic form is simply excreted. Further, a pro-oxidant effect of the selenite ion (Spallholz, 1997) is a great disadvantage, particularly when the shelf life of food animal products is considered.

It is well known that the chemical and physical properties of Se and sulphur are very similar, reflecting similar outer-valence-shell electronic configurations and atomic sizes (Combs and Combs, 1984). Therefore plants cannot distinguish between these two elements when synthesising amino acids. As a result they can synthesize SeMet when Se is available. This biological feature was the basis for the development of the commercial technology of organic Se production from yeast (Sel-Plex, Alltech Inc., USA). Selenium composition in this product closely match that found in most grains with more than 50% of total Se being in the form of SeMet.

Analysis of the protein fraction of Se yeast has shown that Se is present in all the major soluble proteins. SeMet was identified as the major Se-containing compound in the protein fraction as well as in the whole cell (Korhola et al., 1986). Yeast cells can take up Se in the form of selenite or selenate from media and synthesise selenoamino acids. In particular certain strains of yeast are capable of accumulating as much as 3,000 ppm Se in the organic form when the sulphur in the growth medium is replaced by selenium compounds and proper growth conditions are provided (Demirci et al., 1999; Gassner et al., 1999). Definitive, mass spectrometry based evidence has now been provided for the non-specific incorporation of selenomethionine in the yeast proteome involving the replacement of about 30% of all methionine with selenomethionine (McSheehy et al., 2005). The influence of various Se concentrations from organic (SeMet) and inorganic (sodium selenite) Se compounds on growth pattern and cell viability and the alterations in the antioxidant enzyme system of yeast have been evaluated (Bansal and Kaur, 2002). A continuous decrease in cell and colony-forming units counts was observed with increasing concentrations of Se from either source. Increasing Se status of yeast cells was observed with increasing concentrations of Se with both forms, with a much greater uptake for organic Se at maximum Se concentrations. However, high concentrations of sodium selenite in the culture medium have a strong inhibitory effect on the growth of yeast (Suhajda et al., 2000). Sodium selenite exhibited stronger inhibition on yeast growth than sodium selenate and the ratio of selenium to protein was higher with sodium selenate than with sodium selenite. Recently it has been shown that the synthesis of SeMet in yeast actively takes place in the growth phase (Ponce de Leon et al., 2002).

As mentioned above, SeMet is the major selenocompound in Se-enriched yeast. For example, SeMet in yeast and nuts comprised respectively 65% and 75% of total Se (Wrobel et al., 2003). Similarly, a proteolytic enzyme extract of Se yeast was found to contain Se as SeMet (74.8%), selenocystine (9.9%), selenite (5.1%) and as at least three unknown Se compounds (10.2%, Yoshida et al., 2002). SeMet comprised 79.0% of the extracted selenium and 63.9% of the total selenium present in the yeast (McSheehy et al., 2005a). Similarly, the concentration of SeMet measured in the yeast was equivalent to 66.43+/-0.24% of total Se and 30.31+/-0.11% of total Met is in the form of SeMet (Yang et al., 2004). SeMet comprised about 85% of total Se compounds found in selenized yeast used for human trials (Ip et al., 2000). Similarly selenized yeasts, which were used as a source of Se in the trial called PRECISE and other trials, contained SeMet at 54-60% of the total selenium (Larsen et al., 2004). A commercial source of Se-enriched yeast tablets containing 210 μg Se/g was found to contain 73% of the total Se as SeMet (Wolf et al., 2001). It has recently been demonstrated that more than 80% of selenium in the selenized yeast is present in the form of selenomethionine and it has been suggested that many results reported elsewhere for the concentration of this vital amino acid in selenized yeast may be negatively biased (Polatajko et al., 2005).

It seems likely that the selenoamino acid composition of the yeast depends on various factors, including yeast species, growth conditions as well as the analytical techniques used. For example, recently three different commercial yeast products were analysed. Results showed that the proportion of water-soluble Se varied from 11.5% up to 28.0% and the water insoluble polysaccharide bound Se proportion varied from 15.5% up to 72% (Encinar et al., 2003). This suggests that not all yeast products are the same and results obtained in studies with one product cannot be generalized to all yeasts. The technologies used for Se-yeast production could substantially vary and therefore, final product composition and quality could also be quite

different. For example, in a recent publication from China results of the analysis of a tablet obtained from a local drugstore were presented indicating the presence of SeCys (25 μg/g), Selenite (1.3 μg/g) and SeMet (3.2 μg/g) (Liang et al., 2006). Therefore, that particular so called Se-Yeast supplement contained mainly SeCys and probably was not a Se-yeast product. Furthermore, analytical difficulties of SeMet analysis could substantially affect final results of the analysis. For example, recently it has been shown that by employing various techniques of sample digestion, SeMet recovery was in a range of only 49-76% (Hinojosa Reyes et al., 2006). Both acidic and enzymatic hydrolysis, has been widely used for the extraction of protein-bound selenoamino acids in selenized yeast. In particular, the *in vitro* gastrointestinal digestion of selenized yeast allows the Se recovery of 89±3% of the total Se present, but only 41±2% of it is free SeMet (Reyes et al., 2006). In general, Se extraction with such treatments is quite effective allowing recoveries as high as 85-95% (Larsen et al., 2001; Polatajko et al., 2005) and the main Se-species, as observed by HPLC-ICP-MS and ESI MS/MS, was again SeMet accounting for up to 70-76% of the total Se (Larsen et al., 2001).

When selecting a Se supplement, another important consideration is composition of organic Se compounds in the supplement. While SeMet represents the dominant Se form in Se-enriched yeast, each yeast has a unique combination of organic Se compounds which must be considered when beneficial effects from organic Se are expected. This means that SeMet alone could sometimes be less effective than Se-enriched yeast. For example, in mice high-Se yeast caused the largest increase of GSH-Px activity followed by sodium selenite and SeMet (Bergman and Slanina, 1986). Furthermore, SeMet in purified form is unstable and easily oxidised. For example, recently it has been shown that in freeze-dried samples of oyster the total Se and the Se species evaluated were stable for at least 12 months, under all the conditions tested. However, after purification of Se species, including SeMet, in the enzymatic extracts they were only stable for 10 days if stored at 4°C in Pyrex containers (Moreno et al., 2002). In contrast, SeMet is quite stable in the yeast. Indeed, analysis of high-Se yeast stored at room temperature for more than 10 years showed SeMet as the major Se product (Block et al., 2004). Furthermore, the shelf life of Se yeast at 25°C, predicted from the Arrhenius plot, exceeded 1,126 days (Szulc et al., 2003).

Se-Yeasts have been characterised by comparatively high Se availability. For example, the bioavailability of Se in Se yeast, as assessed by slope-ratio analysis using selenite as a reference Se in rats, was 135% to 165% in the tissue Se content and 105% to 197% in the GSH-Px activities (Yoshida et al., 1999). Indeed, Se in Se yeast is more bioavailable than selenite Se, and therefore is the preferred form for supplementation. Similarly, it was shown that the bioavailability of Se in the form of yeast is higher than that of other Se compounds used for preterm infants (Bogye et al., 1998). Utilization (absorption, retention and appearance in milk and blood) of two different chemical forms of Se (selenite and SeMet) in lactating, non-lactating and never pregnant women, using stable isotope tracers was studied. It was shown that significantly more Se from SeMet than from selenite was absorbed and appeared in the plasma in all groups. Milk contained more Se most likely from absorbed SeMet than from selenite. All groups retained significantly more Se from SeMet than from selenite (Moser-Veillon et al., 1992). It has been shown that SeMet-Se was more effective than selenite in raising plasma and erythrocyte Se in men (Luo et al., 1985).

The most common dietary supplement form of Se for humans is Se-enriched yeast. The development and commercial application of Sel-Plex with a guaranteed composition and evidence from research and commercial trials opens a new era in animal nutrition providing opportunities not only for the improvement of animal health and productivity but also for production of Se-enriched meat, milk, eggs and other foods considered to be important steps in improvement of human diets. Indeed, a comparison between Sel-Plex and selenite, based on published data (Surai, 2006), clearly showed advantages of the natural form of Se in comparison to selenite (Table 1). Indeed sodium selenite has a range of properties, which are not shared by other forms of selenium. Therefore, it seems appropriate that selenite be considered as a drug and should be used accordingly. For example, when Se deficiency is diagnosed based on clinical signs, selenite would be the preparation of the choice. Using it via feed, water or injection will solve the short-term or acute problem and this has been demonstrated under various experimental conditions with chickens, pigs and cattle. However, when the goal is to meet the physiological requirements of the animals in order to maintain a high productive and reproductive performance, optimum food animal product quality and immunocompetence, a Se supplement such as Se-yeast supplies the needs of the tissue reserves.

A fascinating part of Se-related research comes from understanding the principal difference between various Se sources in the diet. The digestive system of animals, including birds, adapted to metabolise organic Se from plant-based feedstuffs during evolution. Therefore, inclusion of selenite or selenate in the diet is not the 'natural' situation and the differences in assimilation, distribution and accumulation of Se in tissues depend on the source of Se. Furthermore, SeMet itself possesses antioxidant properties, which could be beneficial during digestion. In contrast, selenite is a prooxidant and in

Table 1. Major differences between organic selenium (Se-yeast) and selenite (Adapted from Surai, 2006)

	Organic selenium	Selenite
Absorption	Similar to Methionine with active transport in the gut	Similar to other minerals with passive transport in the gut
Accumulation	Building Se reserves by non-specific incorporation of SeMet into the proteins	Not accumulated in the body
Toxicity	At least 3 times less toxic than selenite	Highly toxic, can penetrate via skin causing problems
Bioavailability	Higher bioavailability in comparison to selenite to animals and humans	Very low availability for ruminants due to reduction by rumen microbes
Antioxidant activity	SeMet possess antioxidant properties per se and could scavenge NO and other radicals	Possesses pro-oxidant properties and could stimulate free radical production when reacting with GSH
Effect on DNA	SeMet stimulate DNA-repair enzymes	Selenite can cause DNA damage
Transfer to eggs, milk and meat	Transferred to eggs, milk and meat giving a possibility to produce designer/ functional foods	Poorly transferred to eggs, milk and meat
Transfer via placenta	Better transferred via placenta than selenite	Poorly transferred via placenta
Reactions with other elements	Neutral, ascorbic acid promotes SeMet assimilation from the diet	Highly reactive, reduced to metallic, unavailable selenium by ascorbic acid
Protective effect in stress conditions	Provides additional protection due to Se reserves in the body	Cannot provide additional protection due to absence of Se reserves in the body
Effect on drip loss	Did not affect drip loss	Increases drip loss
Environmental issues	Better retention in tissues, less released with faeces and urine	Low retention in tissues and high release with faeces and urine
Stability during storage and feed processing	Stable	Stable
Classification based on the mode of action	Feed additive	Drug

(Surai, 2006)

combination with iron and zinc could potentially stimulate lipid peroxidation and cause damage to enterocytes and as a result decrease absorption efficiency of various nutrients, including antioxidants. In addition, the natural form of Se, selenomethionine, contributes to Se tissue reserves thereby providing a better chance for animals to respond to stress conditions by synthesizing additional selenoproteins. However, most of the Se-related research in food animals was until recently conducted using inorganic Se. Therefore much of the data related to effects of Se on various physiological processes and on the productive and reproductive performance of animals needs to be re-evaluated using natural sources of Se. Indeed, more research should be carried out with organic sources of Se in order to better understand and exploit its physiological role and to solve Se deficiencies as a cause of numerous pathological conditions in human and animals.

SELENIUM FOR POULTRY

It is quite clear that the roles of Se in avian nutrition and reproduction need new consideration in light of our current and better understanding of molecular mechanisms of Se action at the cellular and sub-cellular levels. In particular, discovery and characterisation of a range of new selenoproteins, better understanding of relationships between different antioxidants as important parts of integrated antioxidant system with possibilities for antioxidant recycling *in vivo* have yielded new insights in this matter.

The data accumulated over the past few years indicate that organic selenium is a choice for diets designed to maintain a high productive and reproductive performance of poultry (Table 2). In particular, replacement of sodium selenite by organic selenium in the form of Se-Yeast (Sel-Plex) in the breeder diet is related to an improvement of fertility, hatchability and viability of chicks in early postnatal development. Indeed, organic selenium is more effectively transferred from the diet to the egg and further to the developing embryo. This improves antioxidant defences and helps chickens overcome the oxidative stress of hatching, leading to improvement of hatchability. Data are accumulating showing similar positive effects of organic Se on goose, turkey and guinea fowl reproduction (Surai, 2006). It is well known that when chickens are hatched many physiological systems, including the immune system, are not mature and continue to develop at least 2 weeks posthatch. Therefore this is the most vulnerable period of ontogenesis of the chicks. Data indicate that Se transferred from the egg to the embryo as a result of organic Se

Table 2. Advances of organic selenium for poultry

Parameter	Effect of organic vs. inorganic selenium	References
Chicken sperm morphology	Improved	Edens, 2002; Edens and Sefton, 2003
Duration of fertility	Improved	Agate et al., 2000
Fertility	Improved	Edens, 2002
Hatchability	Improved	Edens, 2002; Edens and Sefton, 2003
Egg production of breeders	Increased	Renema, 2004
Chicken early mortality	Decreased	Lanning et al., 2000
Se transfer to the egg	Improved	Paton et al., 2002; Cantor et al., 2003
Chicken feathering	Improved	Edens, 1996; 1997; 2001; 2002
FCR in broilers	Improved	Naylor et al., 2000; Edens, 2001; Edens and Gowdy, 2004
Chicken growth	Improved	Vlahovic et al., 1998; Edens, 2001; Stolic et al., 2002; Anciuti et al., 2004; Edens and Gowdy, 2004; Srimongkol et al., 2004
Eviscerated weight and breast yield in broilers	Improved	Naylor, 2000
Drip loss	Decreased	Edens, 1996; Naylor et al., 2000
Lipid peroxidation in chicken meat	Decreased	Surai and Dvorska, 2002; 2002a
Chicken growth in stress conditions	Improved	Edens, 2001
Negative effects of heat stress for chicken	Decreased	Mahmoud and Edens, 2003
Ascites	Decreased	Roch et al., 2000
Performance of laying hens	Improved	Pan and Rutz, 2003
Egg freshness during storage	Improved	Wakebe, 1999; Pan and Rutz, 2003
Egg shell quality	Improved	Klecker et al., 1997, 2001; Paton and Cantor, 2000; Rutz et al., 2003
Chicks/hen housed	Increased	Edens and Sefton, 2003; Rutz et al., 2003; Sefton and Edens, 2004c
Se-enriched egg and chicken production	Effective	Yaroshenko et al., 2003; 2003a; 2004
Se-enriched turkey meat production	Effective	Sims et al., 2003
Toxicity	Less toxic at high doses	Gowdy et al., 2003 (Surai, 2006)

supplementation of the maternal diet had positive effect on the Se status of the developing chicks up to 4 weeks posthatch (Pappas et al., 2005; Surai et al., 2006).

Advantages of organic selenium for commercial laying hens are related to better shell quality and improvement of egg production. Data on Se content in the shell and possibility of its manipulation by inclusion of organic Se in the laying hen diet are a background for further research (Surai et al., 2006). Indeed, it is well recognised that eggshell consists of about 95% of minerals and 5% organic matrix. Recent evidence indicates that the organic matrix is responsible for regulation of crystal formation in the developing shell. This means that 5% of the organic matrix determines shell quality. Since organic Se is an integral part of the organic matrix it was suggested that it could affect shell quality and information is accumulating to substantiate this claim. The second advantage of organic selenium for laying hens is related to egg production maintenance at the peak of production. The problem is that even low stresses in a commercial egg production facility could affect peak egg production. Once egg production is decreased it is almost impossible to return it to the original level. Since Se provides additional antioxidant protection, this could help to overcome those small stresses and maintain high egg production at the peak. An additional benefit of organic Se for commercial layers is related to egg freshness during storage. Indeed organic selenium transferred from the diet to the egg, stimulates GSH-Px in the egg yolk, in the white and probably in the perivitelline membrane, leading to decreased lipid and protein oxidation and helping to maintain Hough units at a high level during egg storage.

Advantages of organic Se for broilers include improvement of growth rate, feed conversion ratio (FCR), decreased mortality and decreased drip loss during meat storage (Choct and Naylor, 2004). This could be related to antioxidant Se action, activation of thyroid hormones, as well as an improvement in immunity. Indeed, it is very expensive to maintain an activated immune system. Many nutrients are distributed from growth and development to the immune system. Therefore the immunomodulating properties of Se (Song et al., 2006; Surai, 2006) could help the broiler use the nutrients properly and avoid losing them due to an unnecessary stimulated immune system.

SELENIUM FOR PIGS

The main problem of newly born piglets is low efficiency of antioxidant defences. Indeed, the placenta

restricts antioxidant (e.g. vitamin E and selenium) transfers from the sow to the piglet. Therefore, increased Se transfer via placenta, colostrum and milk would improve the antioxidant defences of the piglets and would be beneficial for the piglet's general health. It is well established that a low-Se maternal diet is a risk factor for the sow and the developing pig embryo.

In the experiments conducted by Mahan (2000) six dietary treatments were used in a 2×2 factorial arrangement with two additional treatments. Inorganic (sodium selenite) or organic (Sel-Plex) Se sources were added to the diet at 0.15 or 0.30 ppm Se. A non-Se-fortified corn-soybean meal basal diet served as a negative control, and a sixth group was fed 0.15 ppm Se from both inorganic and organic Se sources. A total of 43 sows were fed their treatment diets at 2.2 kg/day from 6 day pre-partum to parturition and at full feed through a 14 day lactation period. The major results can be summarised as follows:

- Firstly, it was concluded that Se dietary supplementation is an important means to maintain the antioxidant defences of sows. For example, when the basal diet was fed, sow serum GSH-Px activity declined from 6 day prepartum and remained low throughout lactation (Mahan, 2000). Therefore, inclusion of selenium into the sow's diet caused an increase in sow serum Se concentration and serum GSH-Px activity at both 7 and 14 days postpartum.
- Secondly, it was confirmed that colostrum is an important source of selenium for newly born piglets. However, selenium transfer to the colostrum was minimal if it was added to the sow's diet in the form of sodium selenite. Indeed, the short-term feeding of selenite at 0.15 or 0.30 ppm Se did not affect colostrum Se content (Mahan, 2000). In contrast, inclusion of Sel-Plex into sow's diet significantly increased the Se content of colostrum.
- Thirdly, a positive effect of organic selenium was observed in relation to Se concentration in the milk. For example, milk Se at 7 and 14 d postpartum was 2.5 to 3 times higher when the organic Se source was provided.
- Fourthly, low efficiency of selenite transfer to colostrum and milk was confirmed by using a combination of inorganic and organic Se at 0.15 ppm Se. Indeed, colostrum and milk Se contents were similar to those of sows fed 0.15 ppm Se from the organic Se source (Mahan, 2000). It seems likely that Se in the colostrum and milk is present in an organic form and selenomethionine represents a substantial proportion of those forms. Since SeMet is not synthesised in the animal's body, only when organic selenium was included in the sow's diet was Se concentration in colostrum and milk substantially increased.
- Furthermore, organic selenium in the maternal diet was also effective in increasing the Se concentration in the serum of piglets at 7 and 14 days of age.

When sodium selenite or Sel-Plex at doses 0.1 and 0.3 ppm were fed to first-parity gilts, starting approximately 60 days before breeding until weaning at 21 days, it was shown that organic selenium had the following advantages in comparison to selenite (Mahan and Kim, 1996):

- more effectively transferred via placenta resulting in higher Se content in loin and liver in the neonate piglet;
- more efficiently transferred to the milk;
- more efficiently maintained Se status of the developing piglet until weaning resulting in higher Se concentration in weaning pig loin.
- In general, it was shown that an increased Se supplementation from 0.1 to 0.3 ppm with both Se sources was related to increased Se concentration in neonatal loin, milk and weaning pig loin, with organic selenium being more efficient. As parities progressed, sow milk Se concentration decreased when the diet was supplemented with sodium selenite (Mahan, 1991; 1994; Mahan and Peters, 2004).

Recently, maternal effects of selenium on piglets was characterized in great detail (Mahan and Peters, 2004). Indeed, Se from organic sources (Sel-Plex) was more effectively transferred to colostrum, milk and sow hair, and a combination of organic and inorganic selenium was not effective in increasing the Se content of colostrum and milk. At 0.3 ppm dietary supplementation, Se levels in the liver, loin and pancreas of the sows were substantially higher when organic selenium was used in the diet. Similarly, in neonate pig liver and loin, Se concentration was twice as high as in piglets from sows supplemented with selenite. Furthermore, the total Se content in neonate piglets was doubled when selenized yeast in the form of Sel-Plex was used in sow's diet (Mahan and Peters, 2004). It is interesting to note that sodium selenite fed to sows had some detrimental effects on piglets. The percentage of piglets with spray legs and stillborn piglets was increased by selenite supplementation of the maternal diet. In contrast, under the same conditions, organic selenium had protective effects (Mahan and Peters, 2004). It could well be that the prooxidant properties of selenite are responsible for these detrimental changes in the sow's progeny.

Recently published data of experiments conducted under commercial conditions in Iowa (USA) confirmed the positive effect of organic selenium in the form of Sel-Plex on sows and piglets. Substitution of inorganic selenium in diets fed commercial sows with Sel-Plex (0.3 ppm added

Table 3. Advances of organic selenium for pigs (Adapted from Surai, 2006)

Parameter	Effect of organic vs. inorganic selenium	References
Serum, liver, colostrum and milk selenium	Increased	Kim and Mahan, 2001, Mahan, 2000, Mahan and Peters, 2004
Toxicity	Less toxic	Kim and Mahan, 2001a; 2001b
Tissue Se concentration	Increased	Mahan et al., 1999
Drip loss	Decreased	Mahan et al., 1999
Meat colour	Improved	Mahan et al., 1999
Liver Se	Increased	Ortman and Pehrson, 1998
Blood Se	Increased	Ortman and Pehrson, 1998
Weanling pig loin Se	Increased	Mahan and Kim, 1996
Placental Se transfer	Increased	Mahan and Kim, 1996
Se transfer to the fetus and status at birth	Improved	Mahan and Kim, 1996 Mahan and Jacques, 1998
Total Se in neonate	Increased	Mahan and Peters, 2004
Gilt tissue Se level	Increased	Mahan and Kim, 1996
Muscle Se level	Increased	Mahan and Parrett, 1996
Se excretion	Decreased	Mahan and Parrett, 1996
Backfat depths	Decreased	Wolter et al., 1999
Loin-eye area	Increased	Miller et al., 1997; Wolter et al., 1999
Se bioavailability in sow milk to the nursing pig	Increased	Mahan, 1996
Piglet weight at birth and weaning and daily gain pre-weaning	Increased	Janyk et al., 1998; Janyk, 2001; Pineda et al., 2004
Total piglet born and piglet born alive	Increased	Pineda et al., 2004
Pre-weaning mortality	Reduced	Janyk et al., 1998, Janyk, 2001; Close, 2003; Lampe et al., 2005
Piglet survivability in the nursery	Increased	Lampe et al., 2005a
Number of stillbirths	Decreased	Mahan and Peters, 2004
Splay legs and stillborn	Decreased	Mahan and Peters, 2004
Growth rate	Increased	Janyk et al., 1998, Janyk, 2001; Bobcek et al., 2004
FCR	Improved	Bobcek et al., 2004 (Surai, 2006)

Se) resulted in more piglets weaned and with a lower pre-weaning mortality (9.76 vs. 11.3%; Gourley et al., 2005). Furthermore, culls were reduced in nursery pigs weaned from sows given organic selenium. Therefore, the authors concluded that in commercial production, prewean piglet survivability and piglet survivability in the nursery can be enhanced when Sel-Plex replaces sodium selenite as a dietary selenium source in the sow.

Therefore, there is no need for sodium selenite to be a part of the premixes for pigs and sows and replacement of sodium selenite by organic selenium in the form of Se-yeast was shown to be highly beneficial (Table 3).

SELENIUM FOR RUMINANTS

Selenium nutrition of ruminants has some important features, which create specific problems in the dairy and beef industries. In particular, in many places in the world the Se levels in feed ingredients are not adequate to meet the high Se demand of growing, reproducing and lactating animals. The common practise of dietary Se supplementation in an inorganic form has proved to be of low efficiency. Thus in many cases veterinarians are trying to correct problems of inadequate nutrition and Se injections are still a common practise in the dairy industry. Indeed, part of the selenite consumed is reduced to metallic Se or selenide by rumen bacteria and both of these compounds are not available for further metabolism. The second part of selenite is incorporated into proteins synthesised by the rumen bacteria and it seems likely that Se is also of low availability for animals (Surai, 2006). The replacement of sodium selenite by organic Se sources, in particular, by selenized yeast in the form of Sel-Plex, has been proven to be an effective means of solving Se problems in the dairy, beef and sheep industries. The data accumulated over the past 10 years clearly indicate advantages of such replacement (Table 4). This includes increased Se concentration in blood and GSH-Px activity, approximately doubled Se concentration in colostrum and milk, higher Se transfer via placenta. As a result, cows' health is improved with lower somatic cell counts, decreased mastitis and retained placenta and improved conception rates. The

Table 4. Advances of organic selenium for ruminants

Parameter	Effect of organic vs. inorganic selenium	References
Drip loss of beef	Decreased	Simek et al., 2002
Se in cow plasma	Increased	Pehrson et al., 1999; Hemken et al., 1998
Se in cow milk	Increased	Conrad and Moxon, 1979; Malbe et al., 1995; Ortman and Pehrson, 1997; Knowles et al., 1999; Ortman and Pehrson, 1999; Pehrson et al., 1999
Se in cow colostrum	Increased	Harrison et al., 2005
Se in whole blood of calves	Increased	Pehrson et al., 1999
Se in plasma of calves	Increased	Pehrson et al., 1999
Se in whole blood of calves	Increased	Gunter et al., 2003
GSH-Px in erythrocytes of calves	Increased	Pehrson et al., 1999
Se in cow whole blood	Increased	Fisher et al., 1995; Malbe et al., 1995; Awadeh et al., 1998a ; Hemken et al., 1998; Knowles et al., 1999; Gunter et al., 2003;
Se in whole blood of calves at birth	Increased	Gunter et al., 2003
Se in cow blood, liver and milk	Increased	Valle et al., 2003; Harrison et al., 2005a
Se in cow serum	Increased	Fisher et al., 1995
Se in calve liver	Increased	Valle, 2001
GSH-Px in erythrocytes of yearling heifers and cows	Increased	Pehrson et al., 1989
GSH-Px in whole blood of cows	Increased	Malbe et al., 1995
GSH-Px in erythrocytes of calves at birth	Increased	Gunter et al., 2003
Se in goat milk, plasma and whole blood	Increased	Khaled and Illek, 1999
GSH-Px in whole blood of goats	Increased	Khaled and Illek, 1999
Casein selenium	Increased	Knowles et al., 1999
Triiodothyronine (T3) in plasma of calves at birth	Increased	Awadeh et al., 1998
IgM in cow serum	Increased	Awadeh et al., 1998
Proportion of Se in serum albumin fraction	Decreased	Awadeh et al., 1998a
Se in skeletal muscles of lambs	Increased	Ehlig et al., 1967
Se in skeletal muscles of cows and calves	Increased	Ortman and Pehrson, 1997; Pavlata et al., 2001
Urinary Se excretion in lambs	Decreased	Ehlig et al., 1967
Urinary Se excretion in goats	Decreased	Aspila, 1991
Se in bull muscles	Increased	Ekholm et al., 1991
Daily gains in calves	Increased	Valle, 2001
Somatic cell counts	Decreased	McIntosh and Royle, 2002; Diaz et al., 2004; Foltys et al., 2004; Eliott et al., 2005; Harrison et al., 2005b
Retained placenta	Reduced	Erokhin and Nikonov, 2001; Huang Zhi Jian et al., 2002; Eliott et al., 2005
Postpartum endometritis morbidity	Decreased	Erokhin and Nikonov, 2001; Eliott et al., 2005
Services per conception	Decreased	Erokhin and Nikonov, 2001; Huang Zhi Jian et al., 2002; Eliott et al., 2005
Nutritional muscular degeneration in nursing calves	Decreased	Pehrson, 2004 (Surai, 2006)

benefit to the newly born calves is coming from improvements in their antioxidant defences and thermoregulation leading to better immunity, viability and lower mortality during first months of the postnatal development. Similar to monogastric animals, when organic selenium is used ruminants can also build Se reserves in their tissues, in particular in muscles, and these reserves can be effectively used by animals in stress conditions, when Se requirement is increasing, while feed consumption is declining.

SELENIUM-ENRICHED EGGS, MEAT AND MILK

Since the selenium content in plant-based food depends on its availability from soil, the level of this element in human (or food animal) foods varies among regions. In general eggs and meat are considered to be good sources of Se in the human diet. When considering ways to improve human selenium intake, there are several potential options. These include:

• direct supplementation

Table 5. Some examples of Se-enriched eggs produced in various countries

Trade name	Countries
Columbus	UK, Belgium, Netherlands, France, Spain, USA, Japan, South Africa, India, Israel, Korea, Australia
Origin	Northern Ireland
Mega-eggs	Ireland
Vita-eggs	UK
NutriPlus	Malaysia
LTK omega plus	Malaysia
Selenium plus	Malaysia
TPC egg with organic selenium	Malaysia
Selen egg	Thailand
Doctor hen egg	Thailand
Bounty eggs	Philippines
Organic selenium egg	Singapore
Bon egg	Columbia
Mr egg	Mexico
Heart beat eggs	New Zealand
Tavas yumurta	Turkey
Seker yumurta	Turkey
Selenyum eggs	Turkey
SelPlex eggs	Switzerland
NutriPlus	Portugal
Omega pluss	Hungary
Vi omega-3	Greece
Splepacich vajec eggs	Slovakia
Bag of life (Koshik zhitja)	Ukraine
Spring of life (Dzherelo zhitja)	Ukraine
Rejuvenating (Molodiljnije)	Russia
Aksais' sun (Aksaiskoye solnishko)	Russia
Spring of cheerfulness (Rodnik bodrosti)	Russia
Universal (vSELENskoye)	Russia
Cossack village egg (Stanichnije)	Russia
Mettlesome eggs (Molodetskoye)	Belarus (Surai, 2006; 2006a)

- soil fertilisation
- supplementation of food staples such as flour
- production of Se-enriched functional foods.

• It seems likely that a fourth strategy, production of 'functional foods' enriched with selenium, deserves more attention (Surai, 2000; 2002; 2006; 2006a). Indeed, analysis of the current literature indicates that an enrichment of eggs, meat and milk with Se is a valuable option to improve the Se status of the general population. Such eggs are currently being produced in more than 25 countries worldwide, delivering approximately 50% RDA in Se with a single egg (Table 5). There are also various other combinations of egg enrichment, including omega-3 polyunsaturated fatty acids (PUFAs), vitamin E, carotenoids, iodine, etc. An example of a very successful production and marketing effort of Se, vitamin E and omega-3 enriched eggs is Columbus eggs which are sold in many countries worldwide. Commercial technologies of the production of Se-meat and Se-milk are under the development in various countries (Surai, 2006).

It has been suggested that for the past 150 years our diet has changed substantially, while our genes have not been changed. In particular, animal-derived food composition has been dramatically changed as a result of using inexpensive feed ingredients in animal diets. The meat from animals in the wild and chicken eggs produced under completely natural conditions contains higher amounts of omega-3 fatty acids compared to cultivated ones. Indeed, decreased Se levels in feeds and foods, in many cases, reflect consequences of our agricultural practices. Therefore, eggs or meat produced by free-range poultry/animals fed on natural feed sources, grown on well-balanced soils 100-200 years ago, would contain a much higher Se concentration than we currently have in many European and Asian countries. Again, by supplementing the animal's diet with natural organic sources of Se we are returning back to nature. Recent data on the Se profile of eggs from various avian species in the wild has confirmed this idea. The Se concentration in eggs collected from the wild, in many cases contained much higher levels than what is observed in commercial poultry production (Pappas et al., 2006). The Se level in the chicken eggs, even after organic Se supplementation (Surai, 2000), only raised the yolk Se level into the lower end of the range achieved by avian species in the wild, suggesting there may be scope for much higher levels of supplementation for poultry. It seems likely that Se levels which are considered to be the norm for commercial eggs will be too low to be meet physiological requirements and this should be studied in more detail in the future.

Therefore Se-enrichment of eggs, meat and milk is simply the production of naturally-designed food ingredients. Indeed, production and commercialisation of such organic Se sources such as selenized yeast (for example Sel-Plex) opened a new era in Se supplementation of animals and has provided an opportunity for producers to meet the growing requirements of the consumer. Plus, production of these kinds of animal-derived foodstuffs is a natural way to health promotion.

It is indeed possible to provide consumers with a range of animal-derived products with nutritionally modified composition in such a way that they can deliver substantial amounts of health-promoting nutrients, such as selenium, to improve the general diet and to help maintain good health. Therefore, without the changing habits and traditions of various populations, it is possible to solve problems related to the deficiency of various nutrients, in particular selenium. The consumer will go to the same supermarket to buy the same animal-derived products (egg, milk and meat), cook and consume them as usual. The only difference will be in

the amount of specific nutrients delivered with such products.

CONCLUSIONS

The analysis of the literature presented above, reinforces the importance of Se in animal and human nutrition and health. Indeed, the global Se inadequacy is responsible for an increased susceptibility to various diseases, including major modern killers such as cancer and cardio-vascular diseases. Optimisation of Se nutrition of poultry and farm animals will result in increased efficiency of egg, meat and milk production and even more important, will improve quality. From the data presented above it is clear that the main lesson which we have to learn from nature is how to use organic selenium in animal and human diets. Sel-Plex is the result of such a lesson and it is just a matter of time before animal nutrition moves completely from using ineffective sodium selenite to organic selenium. Other lessons from nature will follow. Recent advances in genomics and proteomics, in association with descriptions of new selenoproteins, will be a driving force in reconsidering old approaches related to Se nutrition. Probably 90% of all Se research has been conducted with sodium selenite and we now understand that the natural form of selenium is different. The main advances in Se status assessment and Se requirements were established based on the activity of GSH-Px, an enzyme which for many years was considered to be the main selenoproteins. Recently, it was discovered that it is only one of at least 25 various selenoproteins. Se research and practical applications are developing quickly and they are very exciting and promising.

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