Reevaluation of the Metabolic Essentiality of the Vitamins[a] - Review -

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ABSTRACT : In recent years a great deal of information has accumulated for livestock on vitamin function, metabolism and supplemental needs. The role of the antioxidant "vitamins" (carotenoids, vitamin E and vitamin C) in immunity and health of livestock has been a fruitful area of research. These nutrients play important roles in animal health by inactivating harmful free radicals produced through normal cellular activity and from various stressors. Both *in vitro* and *in vivo* studies showed that these antioxidant vitamins generally enhance different aspects of cellular and noncellular immunity. A compromised immune system will result in reduced animal production efficiency through increased susceptibility to diseases, thereby leading to increased animal morbidity and mortality. Vitamin E has been shown to increase performance of feedlot cattle and to increase immune response for ruminant health, including being beneficial for mastitis control. Vitamin E given to finishing cattle at higher than National Research Council (NRC) requirements dramatically maintained the red color (oxymyoglobin) compared with the oxidized metmyoglobin of beef. Under commercial livestock and poultry production conditions, vitamin allowances higher than NRC requirements may be needed to allow optimum performance. Generally, the optimum vitamin supplementation level is the quantity that achieves the best growth rate, feed utilization, health (including immune competency), and provides adequate body reserves. (*Asian-Aus. J. Anim. Sci. 2000. Vol. 13, No. 1 : 115-125*)

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INTRODUCTION

Vitamins are defined as a group of complex organic compounds present in minute amounts in natural foodstuffs that are essential to normal metabolism and lack of which in the diet causes deficiency diseases. The term vitamin(e) was first used in 1911 by the Polish biochemist Casimir Funk. Since that time, 15 vitamins (table 1) have been established and classified as either fat or water soluble. The number of compounds justifiably classified as vitamins is controversial. The term vitamin has been applied to many substances that do not meet the definition or criteria for a vitamin. Of the 15 vitamins listed, choline is only tentatively classified as one of the B-complex vitamins. Unlike other B vitamins, choline can be synthesized in the body, is required in larger amounts, and apparently functions as a structural constituent rather than as a coenzyme. Likewise, carnitine is a tentative vitamin but apparently for only a few species under special circumstances.

Some vitamins deviate from the preceding definition in that they do not always need to be constituents of food. Certain substances that are considered to be vitamins are synthesized by intestinal tract bacteria in quantities that are often adequate for body needs. However, a clear distinction is made

Table 1. Fat- and water-soluble vitamins with synonym names

Vitamin	Synonym
Fat soluble	
Vitamin A_1	Retinol, retinal, retinoic acid
Vitamin A_2	Dehydroretinol
Vitamin D_2	Ergocalciferol
Vitamin D_3	Cholecalciferol
Vitamin E	Tocopherol, tocotrienols
Vitamin K_1	Phylloquinone
Vitamin K_2	Menaquinone
Vitamin K_3[a]	Menadione
Water soluble	
Thiamin	Vitamin B_1
Riboflavin	Vitamin B_2
Niacin	Vitamin pp, Vitamin B_3
Vitamin B_6	Pyridoxol, pyridoxal, pyridoxamine
Pantothenic acid	Vitamin B_5
Biotin	Vitamin H
Folic acid	Folacin, folate, Vitamin M, Vitamin B_c
Vitamin B_{12}	Cobalamin
Choline	Gossypine
Vitamin C	Ascorbic acid
Carnitine	

[a] The synthetic form is water-soluble.

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between vitamins and substances that are synthesized in tissues of the body. Ascorbic acid for example, can be synthesized by most species of animals, except when they are young or under stress conditions. Likewise, in most species, niacin can be synthesized from the amino acid tryptophan and vitamin D from action of ultraviolet light on precursor compounds in the skin. Thus, under certain conditions and for specific species, vitamin C, niacin, and vitamin D would not always fit the classic definition of a vitamin.

During the past 10-15 years, a great deal of new information on vitamins has accumulated (McDowell, 2000). For many years the major functions of the B-vitamins were known. Now there is a clearer picture of the metabolism and functions of vitamins A, D, E, K, and C. As an example, vitamins A and D both have hormone functions and functions of vitamins K and D are not just limited to blood clotting and bone formation, respectively. Vitamin C, which is normally synthesized by most species, still can provide benefits when provided to animals under stress. Animals with a functional rumen were thought to synthesize B-vitamins and vitamin K with no need for supplementation. However, under special conditions deficiencies have occurred and hence supplementation has proven beneficial for thiamin, niacin, vitamin B_{12}, choline, biotin and vitamin K. Supplemental carnitine has been shown to be beneficial for several species.

Classical deficiency signs and non specific parameters (e.g., lowered production and reproduction rates) are associated with vitamin deficiencies or excesses. Vitamin nutrition should no longer be considered important only for preventing deficiency signs but also for optimizing animal health productivity and product quality. Due to the enormity of this subject, this report will emphasize the role of vitamins, particularly antioxidant vitamins, in enhancing the immune system and optimizing animal product quality. Also the concept of optimum vitamin allowances and supplemental vitamins most needed by livestock will be noted.

ANTIOXIDANT AND IMMUNITY ROLE

Free radicals can be extremely damaging to biological systems (Padh, 1991). Free radicals, including hydroxy, hypochlorite, peroxy, alkoxy, superoxide, hydrogen peroxide, and singlet oxygen are generated by autoxidation, radiation, or from activities of some oxidases, dehydrogenases, and peroxidases. Also, phagocytic granulocytes undergo respiratory burst to produce oxygen radicals to destroy intracellular pathogens. However, these oxidative products can, in turn, damage healthy cells if they are not eliminated. Antioxidants serve to stabilize these highly reactive free radicals, thereby maintaining the structural and functional integrity of cells (Chew, 1995). Therefore, antioxidants are very important to immune defense and health of humans and animals.

Tissue defense mechanisms against free-radical damage generally includes vitamin C, vitamin E, and β-carotene as the major vitamin antioxidant sources. In addition, several metalloenzymes which include glutathione peroxidase (selenium), catalase (iron), and superoxide dismutase (copper, zinc, and manganese) are also critical in protecting the internal cellular constituents from oxidative damage. The dietary and tissue balance of all these nutrients are important in protecting tissues against free-radical damage. Both *in vitro* and *in vivo* studies show that the antioxidant vitamins generally enhance different aspects of cellular and non-cellular immunity. The antioxidant function of these vitamins could, at least in part, enhance immunity by maintaining the functional and structural integrity of important immune cells. A compromised immune system will result in reduced animal production efficiency through increased susceptibility to diseases, thereby leading to increased animal morbidity and mortality.

One of the protective effects of vitamin C may partly be mediated through its ability to reduce circulating glucocorticoids (Degkwitz, 1987). The suppressive effect of corticoids on neutrophil function in cattle was alleviated with vitamin C supplementation (Roth and Kaeberle, 1985). In addition, ascorbate can regenerate the reduced form of α-tocopherol, perhaps accounting for observed sparing effect of these vitamins (Jacob, 1995). In the process of sparing fatty acid oxidation, tocopherol is oxidized to the tocopheryl free radical. Ascorbic acid can donate an electron to the tocopheryl free radical, regenerating the reduced antioxidant form of tocopherol.

Vitamin C is the most important antioxidant in extracellular fluids and can protect biomembranes against lipid peroxidation damage by eliminating peroxyl radicals in the aqueous phase before the latter can initiate peroxidation (Frei et al., 1989). Vitamin C and E supplementation resulted in a 78% decrease in the susceptibility of lipoproteins to mononuclear cell-mediated oxidation (Rifici and Khachadurian, 1993).

In guinea pigs, vitamin C was shown to be important in maintaining normal primary and secondary antibody responses and was important for neutrophil function (Anderson and Lukey, 1987). Ascorbic acid is reported to have a stimulating effect on phagocytic activity of leukocytes, on function of the reticulo-endothelial system, and on formation of antibodies. Vitamin C can stimulate the production of interferons, the proteins that protect cells against viral attack (Siegel, 1974). Ascorbic acid is very high in

phagocytic cells with these cells using free radicals and other highly reactive oxygen containing molecules to help kill pathogens that invade the body. In the process, however, cells and tissues may be damaged by these reactive species. Ascorbic acid helps to protect these cells from oxidative damage.

Considerable attention is presently being directed to the role vitamin E and selenium play in protecting leukocytes and macrophages during phagocytosis, the mechanism whereby animals immunologically kill invading bacteria. Both vitamin E and selenium may help these cells to survive the toxic products that are produced in order to effectively kill ingested bacteria (Badwey and Karnovsky, 1980). Macrophages and neutrophils from vitamin E-deficient animals have decreased phagocytic activity. Large doses of vitamin E protected chicks and poults against *Escherichia coli* with increased phagocytosis and antibody production (Tengerdy and Brown, 1977). Vitamin E supplementation of the feed at levels of 150 to 300 IU per kg decreased chick mortality due to *E. coli* challenge from 40% in the birds not supplemented with vitamin E to 5% in supplemented birds (Tengerdy and Nockels, 1975).

Since vitamin E acts as a tissue antioxidant and aids in quenching free-radicals produced in the body, any infection or other stress factors may exacerbate depletion of the limited vitamin E stores from various tissues. With respect to immunocompetency, dietary requirements may be adequate for normal growth and production; however, higher levels have been shown to positively influence both cellular and humoral immune status of ruminant species. The former two responses are generally used as criteria for determining the requirement of a nutrient. During stress and disease, there is an increase in production of glucocorticoids, epinephrine, eicosanoids, and phagocytic activity. Eicosanoid and corticoid synthesis and phagocytic respiratory bursts are prominent producers of free radicals which challenge the animal antioxidant systems. Vitamin E has been implicated in stimulation of serum antibody synthesis, particularly IgG antibodies (Tengerdy, 1980). The protective effects of vitamin E on animal health may be involved with its role in reduction of glucocorticoids, which are known to be immunosuppressive. Vitamin E also most likely has an immune enhancing effect by virtue of altering arachidonic acid metabolism and subsequent synthesis of prostaglandin, thromboxanes and leukotrienes. Under stress conditions, increased levels of these compounds by endogenous synthesis or exogenous entry may adversely affect immune cell function (Hadden, 1987).

The effects of vitamin E and selenium supplementation on protection against infection by several types of pathogenic organisms, as well as antibody titers and phagocytosis of the pathogens have been reported for calves (Cipriano et al., 1989; Reddy et al., 1987a) and lambs (Reffett et al., 1988; Finch and Turner, 1989; Turner and Finch, 1990). As an example, calves receiving 125 IU of vitamin E daily were able to maximize their immune responses compared to calves receiving low dietary vitamin E (Ready et al., 1987b). Antioxidants, including vitamin E, play a role in resistance to viral infection. Vitamin E deficiency allows a normally benign virus to cause disease (Beck et al., 1994). In mice, enhanced virulence of a virus resulted in myocardial injury that was prevented with vitamin E adequacy. A selenium or vitamin E deficiency leads to a change in viral phenotype, such that an avirulent strain of a virus becomes virulent and a virulent strain becomes more virulent (Beck, 1997).

Carotenoids have been shown to have biological actions independent of vitamin A (Chew, 1995; Burton, 1989; Olson, 1989). Recent animal studies indicate that certain carotenoids with antioxidant capacities, but without vitamin A activity, can enhance many aspects of immune functions, can act directly as antimutagens and anticarcinogens, can protect against radiation damage, and can block the damaging effects of photosensitizers. In animal models, β-carotene and canthaxanthin have protected against UV-induced skin cancer as well as some chemically induced tumors. In some of these models, an enhancement of tumor immunity has been suggested as a possible mechanism of action of these carotenoids (Bendich, 1989). β-carotene can function as a chain-breaking antioxidant, it deactivates reactive chemical species such as singlet oxygen, triplet photochemical sensitizers and free radicals which would otherwise induce potentially harmful processes (e.g., lipid peroxidation).

Vitamin A and β-carotene have important roles in protecting animals against numerous infections including mastitis. Potential pathogens are regularly present in the teat orifice, and under suitable circumstances can invade and initiate clinical mastitis. Any unhealthy state of the epithelium would increase susceptibility of a mammary gland to invasion by pathogens. There are reports of improved mammary health in dairy cows supplemented with β-carotene and vitamin A during the dry (Dahlquist and Chew, 1985) and lactating (Chew and Johnston, 1985) periods.

Polymorphonuclear neutrophils (PMN) are the major line of defense against bacteria in the mammary gland. β-carotene supplementation seems to exert a stabilizing effect on PMN and lymphocyte function during the period around dry off (Tjoelker et al., 1990). Daniel et al. (199la, b) reported that β-carotene enhanced the bactericidal activity of blood and milk PMN, against *S. auereus* but did not affect phagocytosis. Vitamin A either had no effect or

suppressed bactericidal activity and phagocytosis. Control of free radicals is important for bactericidal activity but not for phagocytosis. The antioxidant activity of vitamin A is not important; it does not quench or remove free radicals. β-carotene, on the other hand, does have significant antioxidant properties and effectively quenches singlet oxygen free radicals (Mascio et al., 1991; Zamora et al., 1991).

Supplemental levels of vitamin E higher than recommended by the dairy cattle NRC (1989a) have been beneficial in the control of mastitis. Smith and Conrad (1987) reported that intramammary infection was reduced 42.2% in vitamin E-selenium supplemented versus unsupplemented controls. The duration of all intramammary infections in lactation was reduced 40 to 50% in supplemented heifers. Weiss et al. (1990) reported that clinical mastitis was negatively related to plasma selenium concentration and concentration of vitamin E in the diet.

Many new intramammary infections (IMI) occur in the 2 weeks before and after calving. Deficiencies of either vitamin E or selenium have been associated with increased incidence and severity of IMI, increased clinical mastitis cases, and higher somatic cell counts (SCC) in individual cows and bulk tank milk. Somatic cell counts are a primary indicator of mastitis and milk quality in dairy herds. The PMN is a major defensive mechanism against infection in the bovine mammary gland. A known consequence of vitamin E and selenium deficiency is impaired PMN activity and postpartum vitamin E deficiencies are frequently observed in dairy cows. Dietary supplementation of cows with selenium and vitamin E results in a more rapid PMN influx into milk following intramammary bacterial challenge and increased intracellular kill of ingested bacteria by PMN. Subcutaneous injections of vitamin E approximately 10 and 5 d before calving successfully elevated PMN α-tocopherol concentrations during the periparturient period and negated the suppressed intracellular kill of bacteria by PMN that commonly is observed around calving (Smith et al., 1997).

Diets of multiparous dairy cows were supplemented with either 0 or 1,000 IU vitamin E (as *dl*-α-tocopheryl acetate) during the dry period (Smith et al., 1984). Cows were additionally administered selenium at the rate of 0 or 0.1 mg per kg body weight via i.m. injection 21 days prepartum. No vitamin E or selenium were supplemented during lactation. Incidence of new clinical cases of mastitis was reduced by 37% in both groups receiving vitamin E compared to controls. The reduction in clinical mastitis was only 12% when cows were injected with selenium but not supplemented with dietary vitamin E. These authors also reported that clinical cases in the vitamin E supplemented-selenium injected cows were consistently of shorter duration than those occurring in all other groups. Erskine et al. (1989) investigated specific effects of selenium status of dairy cattle on the induction of mastitis by *E. coli*. Bacterial concentrations were significantly higher in selenium-deficient than in selenium-adequate cows and selenium supplementation reduced both severity and duration of clinical mastitis.

Plasma concentrations of α-tocopherol decreased at calving for cows fed dietary treatments with low or intermediate concentrations of vitamin E, but not for cows fed the high vitamin E treatment (Weiss et al., 1997). High dietary vitamin E increased concentration of α-tocopherol in blood neutrophils at parturition. The high vitamin E treatment was 1,000 IU/d of vitamin E during the first 46 d of the dry period, 4,000 IU/d during the last 14 d of the dry period, and 2,000 IU/d during lactation.

The percentage of quarters with new infections at calving was not different (32.0%) between cows receiving treatments that contained low and intermediate concentrations of vitamin E but was reduced (11.8%) in cows receiving the high vitamin E treatment. Clinical mastitis affected 25.0, 16.7 and 2.6% of quarters during the first 7 d of lactation for cows receiving the low, intermediate, and high vitamin E treatments, respectively. Cows with plasma concentrations of α-tocopherol <3.0 μg/ml at calving were 9.4 times more likely to have clinical mastitis during the first 7 d of lactation than were cows with plasma concentrations of α-tocopherol >3.0 μg/ml (Weiss et al., 1997).

ADDITIONAL BENEFITS OF VITAMIN E SUPPLEMENTATION

There have been more recent reports on benefits of vitamin E supplementation for livestock than any other vitamin (McDowell et al., 1996). Vitamin E was originally supplemented to poultry and livestock for prevention of exudative diathesis, encephalomalacia, white muscle disease, liver degeneration and other degenerative diseases. Recent research has revealed the benefits of improving disease resistance (see previous section) as well as improving product quality.

Supplementing vitamin E in well balanced diets has been shown to increase humoral immunity for ruminants (Hoffmann-La Roche, 1994) and monogastric species (Langweiler et al., 1983; Wuryastuti et al., 1993). These results suggest that the criteria for establishing requirements based on overt deficiencies or growth do not consider optimal health.

In a series of 28 day feedlot receiving trials, Lee et al. (1985) observed an improvement in early performance of newly arrived growing cattle supplemented with 450 IU vitamin E (as *dl*-α-

tocopheryl acetate) per head per day that were stressed by long distance shipment and changes from green forages to high grain feedlot diets. Perhaps depression of circulating cortisol concentrations may explain the improved gain and feed efficiency in this trial.

Gill et al. (1986) supplemented newly received feedlot cattle with 1,600 IU vitamin E (as *dl*-tocopheryl acetate) per head per day for the first 21 days and 800 IU vitamin E for the remaining 7 days of a 28 day trial. Average daily gain and gain to feed ratios were improved by 23.2 and 28.6%, respectively, for vitamin E supplemented stressed cattle. The number of sick pen days per head was reduced by 15.6%, and morbidity was reduced by 13.4% with vitamin E supplementation. The growth response to vitamin E could be related to the fact that young, rapidly growing animals are in a metabolically demanding state resulting from overall tissue growth, which has a high energy demand. Vitamin E is an integral part of this response via its ability to quench free radicals, which are generated during the course of metabolism.

Recent research has shown a beneficial response for vitamin E supplementation on male reproduction for bulls fed high concentrations of gossypol. Velasquez-Pereira et al. (1998) reported that bulls which received 14 mg free gossypol/kg body weight had a lower ($p<0.05$) percentage of normal sperm than those which also received supplemental vitamin E, 31 vs 55%, respectively (table 2). Likewise, sperm production per gram of parenchyma and total daily sperm production were higher ($p<0.05$) when gossypol treated animals also received vitamin E. Bulls receiving gossypol exhibited more sexual inactivity ($p>0.05$) than bulls in other treatments. Vitamin E supplementation to bulls receiving gossypol improved number of mounts in the first test and time of first service in the second test. The final conclusion of the Florida data is that vitamin E is effective in reducing or eliminating important gossypol toxicity effects for male cattle.

Many attempts have been made to control lipid oxidation in meats through the use of antioxidants. Dietary supplementation of vitamin E, and intravenous infusion of vitamin C immediately before harvest, are efficacious techniques for increasing the concentration of these vitamins in beef skeletal muscle (Schaefer et al., 1995). Meat with elevated levels of either and probably both of these antioxidant vitamins possesses greater stability of oxymyoglobin and lipid, which results in less discoloration and rancidity. Vitamin E would seem to be the most practical since it is administered dietetically. Vitamin E functions as a lipid-soluble antioxidant in cell membranes (Linder, 1985), thus protecting phospholipids and even cholesterol against oxidation. Increased dietary levels of vitamin E result in higher tissue α-tocopherol concentrations and greater stability of these tissues toward lipid oxidation. Buckley and Connolly (1980) reduced the rate of rancidity development in frozen pork by including vitamin E in the feed (80 mg per day per animal) for 7 d before slaughter of the pigs. Likewise, meat from turkeys raised on vitamin E-supplemented diets was more stable to rancidity development than meat from birds receiving control diets (Bartov et al., 1983).

Dramatic effects of vitamin E supplementation (500 IU per head daily) to finishing steers on the stability of beef color have been observed (Faustman et al., 1989a). Loin steaks of control steers discolored two to three days sooner than those supplemented with vitamin E. Supplemental dietary vitamin E extended the color shelf life of loin steaks from 3.7 to 6.3 days. This was most likely due to the increased α-tocopherol content of the loin tissue of the supplemented animals, which was approximately 4-fold greater than controls (Faustman et al., 1989a). Color is an extremely critical component of fresh red meat appearance and greatly influences the customer perception of meat quality. Steaks from cattle supplemented with vitamin E were preferred over control steaks by 91% of Japanese survey participants (n=10,941), and 58% of all participants identified muscle color as the most important factor in selecting beef products (Sanders et al., 1997).

In a subsequent report, Faustman et al. (1989b) observed that vitamin E stabilized the pigments and lipids of meat from the supplemented steers. Perhaps the vitamin E supplemented steers were able to incorporate a greater amount of vitamin E as an *in*

Table 2. Relationship of gossypol and vitamin E on semen characteristics of dairy bulls[a]

Item	Treatment		
	TRT1[b]	TRT2[c]	TRT3[d]
Normal, %	64.7±6.4[h]	31.4±7.4[i]	54.6±6.4[h]
Abnormal[e],%	4.4±1.3[h]	13.4±1.5[i]	4.8±1.2[h]
DSPG[f] ($\times 10^6$/g)	14.6±1.0[h]	10.2±1.0[i]	17.6±1.0[h]
DSP[g] ($\times 10^9$)	3.2±3.0[h]	2.2±3.0[i]	4.1±3.0[h]

[a] Least square means±SEM.
[b] Diet based on SBM, corn and 30 IU vitamin E/kg of supplement.
[c] Diet containing 14 mg free gossypol/kg BW/d and 30 IU vitamin E/kg of supplement.
[d] Diet containing 14 mg free gossypol/kg/BW/d and 4,000 IU vitamin E/bull/d.
[e] Midpiece abnormalities evaluated in isotonic formal saline.
[f] Daily sperm production per gram of parenchyma.
[g] Daily sperm production total.
[h,i] Means in a row with different superscript differ $p<0.05$.

vitro lipid stabilizer with effects on flavor and storage properties of various meats improved. Supplementing cattle with vitamin E resulted in steaks that exhibited superior lean color, less surface discoloration, more desirable overall appearance, and less lipid oxidation during retail display than control steaks (Sanders et al., 1997). Vitamin E also plays a role in controlling the color of veal calf meat. Combined feeding of monosodium phosphate and 100 IU of vitamin E per calf daily produced a light colored veal without making calves anemic (Agboola et al., 1990).

Feeding supplemental vitamin E at levels of 1,000 to 2,000 mg of naturally-occurring mixed tocopherols per cow per day increased the vitamin E content of milk and its stability against oxidized flavor (Neilsen et al., 1953). The vitamin E content of milk from cows fed stored feeds was lower than that of milk from cows on pasture and their milk was more susceptible to development of oxidized flavor. Feeding supplemental vitamin E as *dl*-α-tocopheryl acetate, providing an equivalent of 500 mg of *dl*-α-tocopherol per cow per day, increased the vitamin E content and oxidative stability of milk (Dunkley et al., 1967). Nicholson et al. (1991) suggest that adequate selenium improves the transfer of dietary tocopherol to milk.

The ability of vitamin E to affect growth, health and reproduction of animals is documented. A vitamin E supplementation program utilizing both parenteral and oral administration is often suggested, particularly when fresh green pasture is lacking. Mahan (1991) assessed the influence of low supplemental vitamin E (<16 IU/kg) to sows and offspring in three parities. Smaller litter size, sow agalactia and pig mortality during the 1st week after birth resulted from inadequate supplemental E to breeding sows. Chicks fed 100 IU per kg diet had increased weight gains and reduced mortality during coccidiosis challenge (Colnago et al., 1984).

Exercise has an influence on vitamin E requirements and needed supplementation (Valberg et al., 1993). For horses, dietary levels of vitamin E greater than the 80 IU/kg DM, and potentially approaching 300 IU/kg DM, are required to maintain blood and muscle vitamin E concentrations in horses undergoing exercise conditioning. The level of vitamin E recommended by the NRC for working horses, 80 IU/kg DM, will not maintain serum vitamin E levels.

The need for supplementation of vitamin E is dependent on the requirement of individual species, conditions of production, and in relation to available vitamin E in food or feed sources. The primary factors that influence the need for supplementation include (1) vitamin E- and/or selenium-deficient concentrates and roughages; (2) excessively dry ranges or pastures for grazing livestock; (3) confinement feeding where vitamin E-rich forages are not included or only forages of poor quality are provided; (4) diets that contain predominantly non-α-tocopherol and thereby are less biologically active; (5) diets that include ingredients that increase vitamin E requirements (e.g., unsaturated fats, waters high in nitrates); (6) harvesting, drying, or storage conditions of feeds that result in destruction of vitamin E and/or selenium; (7) accelerated rates of gain, production and feed efficiency that increase metabolic demands for vitamin E; and (8) intensified production that also indirectly increases vitamin E needs of animals by elevating stress, which often increases susceptibility to various diseases (McDowell and Williams, 1991; McDowell, 1992). After stress livestock may have reductions in α-tocopherol concentrations in certain tissues. Supplemental vitamin E may be required after stress to restore α-tocopherol in tissues (Nockels et al., 1996).

OPTIMUM VITAMIN ALLOWANCES

The National Research Council (NRC) and Agriculture Research Council requirements for a vitamin are usually close to minimum levels required to prevent deficiency signs and for conditions of health and adequate performance, provided sufficient amounts of all other nutrients are supplied. Most nutritionists usually consider NRC requirements for vitamins to be close to minimum requirements sufficient to prevent clinical deficiency signs and they may be adjusted upward according to experience within industry in situations where a higher level of vitamins is needed.

Allowances of a vitamin are those total levels from all sources fed to compensate for factors influencing vitamin needs of animals. These influencing factors include (1) those that may lead to inadequate levels of the vitamin in the diet and (2) those that may affect the animal's ability to utilize the vitamin under commercial production conditions. The higher the allowance the greater is the extent to which it may compensate for the influencing factors. Thus, under commercial production conditions, vitamin allowances higher than NRC requirements may be needed to allow optimum performance (Roche, 1979). Generally, the optimum supplementation level is the quantity that achieves the best growth rate, feed utilization, health (including immune competency), and provides adequate body reserves (Coelho, 1996).

The concept of optimum vitamin nutrition under commercial production conditions is illustrated in figure 1 (Roche, 1979).

The marginal zone in figure 1 represents vitamin levels that are lower than requirements that may predispose animals to deficiency. The requirement zones are minimum vitamin quantities that are needed

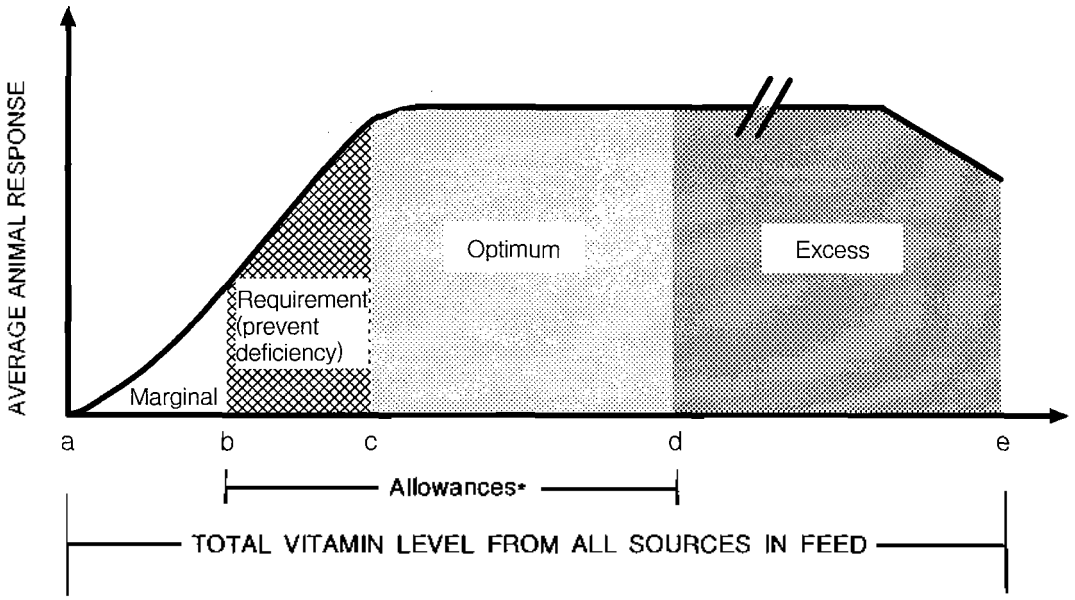

Figure 1.

to prevent deficiency signs, but may lead to suboptimum performance even though animals appear normal. The optimum allowances in figure 1 permit animals to achieve their full genetic potential for optimum performance. In the excess zone, vitamin levels range from levels still safe, but uneconomical, to concentrations that may produce toxic effects. Usually only vitamins A and D, under practical feeding conditions pose the possibility of toxicity problems for livestock. Optimum allowances of any vitamin are depicted as a range in figure 1 because factors influencing vitamin needs are highly variable and optimum allowances to allow maximum response may vary from animal to animal of the same species, type, and age within the same population and from day to day (Roche, 1979).

It should be emphasized that subacute deficiencies can exist although the actual deficiency signs do not appear. Such borderline deficiencies are both the most costly and the most difficult with which to cope, and often go unnoticed and unrectified, yet they may result in poor and expensive gains, impaired reproduction, or depressed production. Also, under farm conditions one will usually not find a single vitamin deficiency. Instead, deficiencies are usually a combination of factors, and often deficiency signs will not be clear-cut. If the NRC minimum requirement for a vitamin is the level that barely prevents clinical deficiency signs, then this level moves in relationship to the level required for optimum production responses. This means that if a greater quantity of a vitamin is required for an optimum response (because of the influencing factors), a greater quantity would also be required to prevent deficiency signs (figure 2). Similarly, if a lesser quantity is required for an optimum response, less would also be required to prevent deficiencies (Perry, 1978). Optimum animal performance required under modern commercial conditions cannot be obtained by fortifying diets to just meet minimum vitamin requirements. Establishment of adequate margins of safety must provide for those factors that may increase certain dietary vitamin requirements and for variability in inactive vitamin potencies and availability within individual feed ingredients.

The NRC requirements often do not take into account that certain vitamins have special functions in relation to disease conditions with higher than recommended levels needed for response (Cunha, 1985). In pigs artificially infected with *Treponema hyodysenteriae*, the agent causing diarrhea, high supplementation with vitamin E (200 mg/day) in combination with selenium (0.2 mg/day) markedly reduced the number of pigs that became clinically ill (Tiege et al., 1978). Clinical signs and pathological changes were less severe compared with vitamin E-deficient pigs. Thus, high doses of vitamin E increase resistance against disease. In practice, feeds contaminated with mycotoxins increase requirements for fat-soluble and other vitamins (e.g., biotin, folacin, and possibly others) and therefore supplementation should be increased above NRC minimum requirements. Apart from these fat-soluble vitamins, additions of folacin will also improve performance in

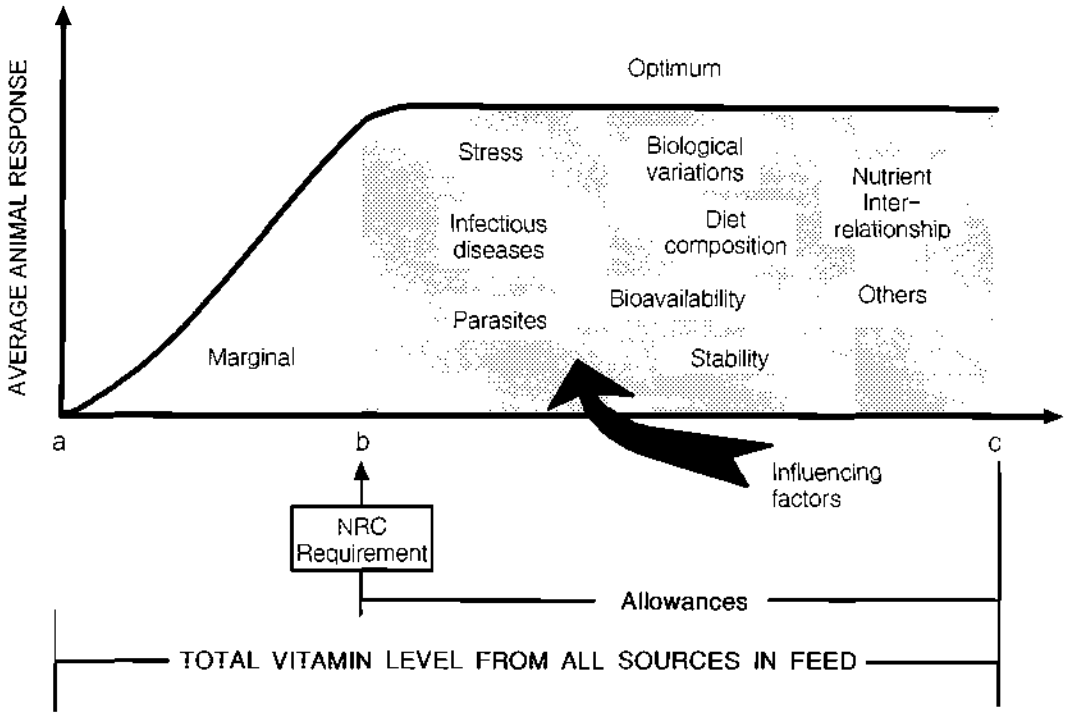

Figure 2.

pigs fed moldy grain (Purser, 1981) and of biotin for pigs fed feeds containing certain molds (Cunha, 1984). Besides other nutrients, vitamins play a major role in the immune response, the body s defense system against infectious disease. Vitamin supplementation above requirements has been shown to be required for optimum immune responses (Ellis and Vorhies, 1976; Cunha, 1985).

VITAMIN SUPPLEMENTATION MOST NEEDED BY LIVESTOCK

Vitamin requirements, as previously noted, are highly variable within the various species and classes of animals. Supplementation allowances need to be set at levels that reflect different management systems and that are high enough to take care of fluctuations in environmental temperatures, energy content of feed, or other factors that might influence feed consumption or the vitamin requirements in other ways (McGinnis, 1986). This section will briefly discuss vitamins that are normally provided in ruminant, poultry, swine, and horse diets.

Ruminants

Grazing ruminants generally only need supplemental vitamin A, if pastures are low in carotene, and possibly vitamin E (influenced by selenium status). Vitamin D is provided by ultraviolet light activity on the skin, while all other vitamins are provided by ruminal or intestinal microbial synthesis.

Ruminants housed under more strict confinement conditions generally require vitamins A and E and may require vitamin D if deprived of sunlight. Additional supplemental vitamin E would be needed to stabilize the meat color of finishing animals. Under specific conditions, relating to stress and high productivity, ruminants may be benefitted by supplemental B vitamins, particularly thiamin and niacin. Biotin deficiency has been linked to lameness in cattle (Budras et al., 1997; Distl and Schmid, 1994). Increased plasma biotin levels have been associated with hardness and positive confirmational changes in bovine hooves. Future research may find a need for carnitine supplementation. Adding a complete B-vitamin mixture to cattle entering the feedlot during the first month can reduce stress and increase gains. In one study, supplemental B vitamins given feedlot calves tended to reduce morbidity of animals (Zinn et al., 1987). Apparently under stress conditions of feedlots, the microbial population in the rumen is not synthesizing certain B vitamins at adequate levels.

Poultry

Poultry under intensive production systems are particularly susceptible to vitamin deficiencies (Scott et al., 1982). Reasons for this susceptibility are (1) poultry derive little or no benefit from microbial synthesis of vitamins in the gastrointestinal tract, (2) poultry have high requirements for vitamins and (3) the high density concentration of modern poultry operations places many stresses on the birds that may

increase their vitamin requirements. Typical grain-oilseed meal (e.g., corn-soybean meal) poultry diets are generally supplemented with vitamins A, D (D_3), E, K, riboflavin, niacin, pantothenic acid, B_{12}, and choline (Scott et al., 1982). Thiamin, vitamin B_6, biotin, and folacin are usually, but not always, present in adequate quantities in the major ingredients such as corn-soybean meal-based diets. Carnitine may be found to be of value in future studies.

Vitamins A, D, riboflavin, and B_{12} are usually low in poultry diets. However, adding other vitamins to poultry diets is good insurance. The vitamins D and B_{12} are almost completely absent from diets bases on corn and soybean meal. Vitamin K is generally added to poultry diets more than to those for other species because birds have less intestinal synthesis because of a shorter intestinal tract and faster rate of food passage. Birds in cages require more dietary K and B vitamins than those on floor housing because of more limited opportunity for coprophagy.

Swine

Vitamin supplementation of swine diets is obviously necessary with vitamin needs having become more critical in recent years as complete confinement feeding has increased. Swine in confinement, without access to vitamin-rich pasture, and housed on slatted floors, which limits vitamins available from feces consumption, have greater needs for supplemental vitamins. For swine, the vitamins most likely to be marginal or deficient in corn-soybean diets are vitamins A, D, E, riboflavin, niacin, pantothenic acid, and B_{12}, and occasionally also vitamin K and choline.

Almost all swine diets in the United States are now fortified with vitamins A, D, E, B_{12}, riboflavin, niacin, pantothenic acid, and choline. An increasing number of feed manufacturers are adding vitamins K and biotin, and some are adding B_6 to diets. Diets are fortified with these vitamins even though not all experiments indicate a need for each of them. Most feed manufacturers add them as a precaution to take care of stress factors, subclinical disease level, and other conditions on the average farm that may increase vitamin needs (Cunha, 1977). It appears that carnitine supplementation of weaning pigs has potential (Newton and Burtle, 1992).

Horses

There is a lack of experimental information on the level of vitamins required in well-balanced horse diets, as well as on which vitamins need to be added (Cunha, 1980). The vitamins most likely deficient for all classes of horses are vitamins A and E, with vitamin D also deficient for horses in confinement. Inadequate vitamin D may be provided to racehorses that are exercised only briefly in the early morning, when sunlight provides less antirachitic protection. Requirements for vitamins A, D, and E can be met with a high quality (e.g., green color) sun-cured hay. Deficiencies of vitamin K and the B vitamins appear to be less likely in the mature horse than in other monogastric species as many vitamins are synthesized in the cecum of the horse. It is not known, however, how much of the vitamins synthesized in the cecum are absorbed in the large intestine. Since it is difficult to depend on intestinal synthesis, many horse owners use B-vitamin supplementation of diets for the young horse and those being developed for racing or performance purposes (Cunha, 1980).

In recent years, vitamin supplementation has become more critical to the horse as the trend toward total confinement has increased. Presently, few horses receive a high level of vitamin intake from a lush, green pasture or from a high-quality, leafy, green hay. Cunha (1980) suggested that a vitamin premix for horses contain vitamins A, D, E, K, thiamin, riboflavin, niacin, B_6, pantothenic acid, folacin, B_{12}, and choline. Biotin supplementation is also recommended as Comben et al. (1984) showed a benefit of the vitamin for hoof integrity. Recently, there is a suggestion that carnitine supplementation is beneficial for horses.

FUTURE RESEARCH

A great deal of research is needed to further understand the metabolism and functions of all vitamins. Mechanisms of actions of vitamins A, D, E, K, and C are particularly not clear. Interrelationships of vitamins with each other and other nutrients as well as the significance of vitamin carriers and tissue receptors require concentrated studies. From a practical viewpoint for livestock producers, what are the requirements for vitamins under diverse conditions and how do requirements differ on the basis of functions (e.g. growth, reproduction, optimum immune response)? Bioavailability of different forms of vitamins need study as well as the many factors that reduce stability of vitamin in feeds as well as vitamin supplements.

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