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For M. Sc. Biochemistry Sem I

Structure and Properties of Vitamins

Vitamins are a group of organic nutrients, required in small quantities for a variety of biochemical functions. Plants can synthesize all vitamins but animals can synthesize only few of them. Therefore animals depend on plants and microbes for their vitamin needs. Vitamins carry out functions in very low concentrations. Hence the total daily requirement is very small.

Classification

Vitamins have been classified into two categories; fat soluble and water soluble. Fat soluble vitamins are vitamin A, D, E and K. water soluble vitamins are vitamin B complex (vitamins B1, B2, B3, B5, B6, B7, B9 and B12) and the vitamin C.

Vitamin A

Vitamin A is also called as antixerophthalmic factor or the bright eyes vitamin because of its involvement in visual process. Fish liver oil is the richest source of vitamin A. Other sources are butter, milk and eggs, vegetables and fruits.

Vitamin A is present in two forms A1 and A2 (Figure 1 & 2). Carotenoids such as α, β and ϒ-carotenes and cryptoxanthinact as provitamin form of vitamin A. Among these β-carotene is the most potent provitamin form. β-carotene is made up of eight 5-carbon isoprenoid units liked to form a long chain of 40 carbon atoms with an ionone ring at each end. Hydrolysis of β-carotene yields two moles of vitamin A1. Cleavage occurs at the midpoint of the carotene in the polyene chain connecting the two ionone rings. Conversion of β-carotene into vitamin A takes place in liver of fishes and mammals. Vitamin A is a complex primary alcohol called retinol. The terminal –OH group is mostly esterified with fatty acid.

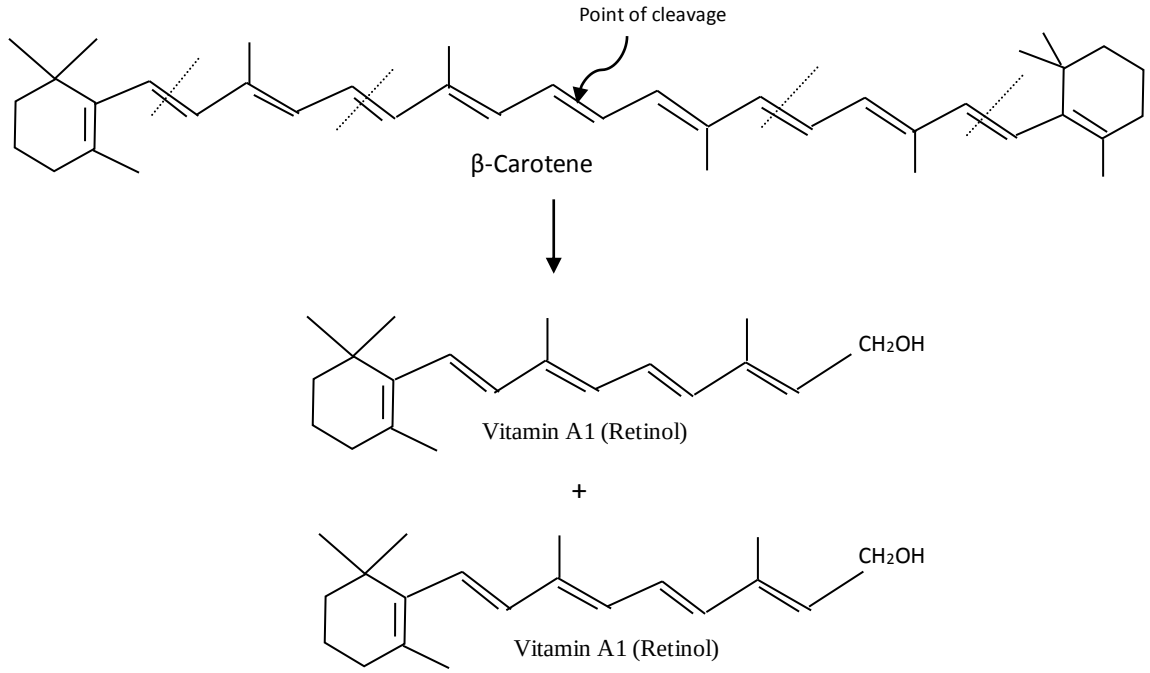

Figure 1: Hydrolysis of β-carotene

Another form of vitamin A is A2 which in contrary to A1 (found in salt water fishes) is found in fresh water fishes. The difference between the two forms is that ionone ring in vitamin A2 contains an additional conjugate double bond between carbon atoms 3 and 4.

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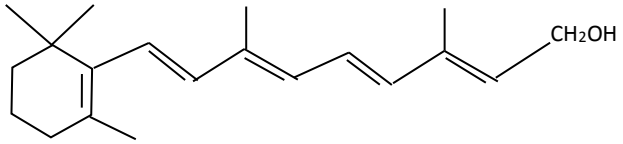


Figure 2: structure of vitamin A2 (3-dehydroretinol)

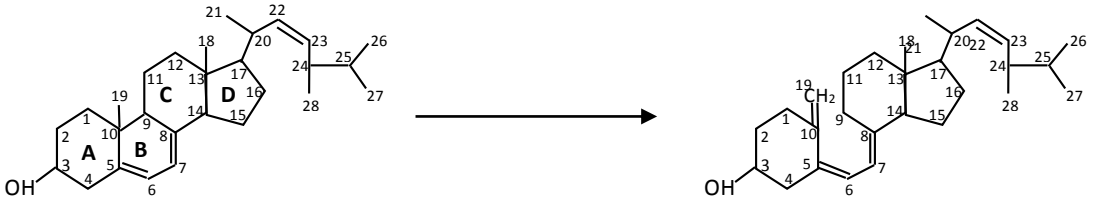
In the tissues, the metabolic transformation of retinol is carried out by enzymes. The β-carotene in the ingested food is split into retinal by intestinal enzyme. Retinal is then reduced to retinol enzymatically. Retinol is then converted into retinyl ester by reacting with fatty acid like palmitic acid. The retinyl ester can enzymatically hydrolysed into retinol which is resterified with palmitic acid to produce retinyl ester. This retinyl ester is stored in liver. The storage form of vitamin A in the liver is retinyl ester, but the form of vitamin A that circulates in the blood is retinol which is bound to a specific carrier protein called retinol binding protein (RBP). Liver can also successively convert retinol to retinal and retinal to retinoic acid. Retinoic acid is quickly absorbed from the intestine through the portal system and rapidly excreted back into the intestine through the bile.

Retinoic acid which is a derivative of retinol acts as hormone and binds through receptor protein in the cell nucleus. There it regulates the gene expression in the development of epithelial tissues particularly of skin. Retinoic acid is an active ingredient in drug tretinoin (Retin-A), used in treatment of severe acne and wrinkled skin. Retinal which is also a derivative of retinol is the bile pigment. It initiates the response of rod and cone cells of the retina to light and produces a neuronal signal to brain.

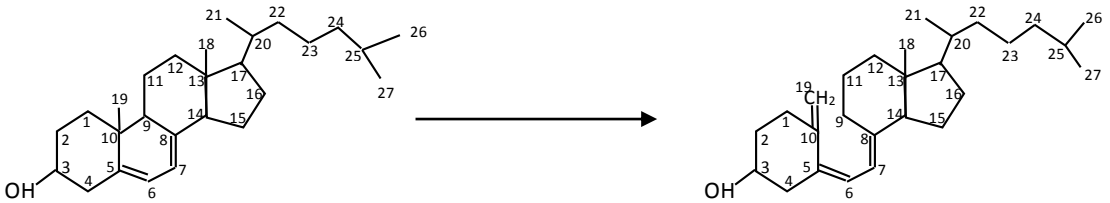
Vitamin D

Because of its prevention action on rickets, vitamin D is called antirachitic factor. Fish liver oil is excellent source of vitamin D. It is also called sunshine vitamin as its provitamin form present in human skin is converted into active vitamin D by irradiation with UV light. Two forms namely vitamin D2 (ergocalciferol) and vitamin D3 (cholecalciferol) are present (Figure 3). Vitamin D like vitamin A is absent in vegetables fats and oils.

Ergosterol is converted to vitamin D2 by a series of steps whereas 7-dehydrocholecalciferol which is also a provitamin found in animals is converted intocholecalciferol by a series of steps. During the activation of the provitamin, the ring B is cleaved between C9 and C10 to produce vitamin D2 and D3.



Ergosterol Vitamin D2 (Ergocalciferol)



7-Dehydrocholesterol Vitamin D3 (Cholecalciferol)

Figure 3: Structure of vitamin D1 and D2 and their precursors.

Vitamin D3 is produced in skin by UV irradiation of 7-dehydrocholesterol, which breaks the bond between C9-C10. In the liver, a –OH group is added at C25. In the kidney, a second –OH is added at C1 which produces the active hormone 1α, 25-dihydroxy vitamin D3. This hormone regulates the metabolism of calcium in kidney, intestine and bone.

Vitamin E

Vitamin E is also known as antisterility factor because its deficiency may cause sterility in animals. It was first isolated from wheat germ and named it α, β-tocopherols. After that five other tocopherols were obtained from various cereal grains like wheat germ, corn oil, rice etc. Other sources of vitamin E are cottonseed, rice, corn, soybean, coconut, and peanut. Among all α-tocopherol is most common and has greatest activity. Tocopherols are derivatives of 6-hydroxychroman (also called tocol) bearing an isoprenoid side chain at C2 (Figure 4).

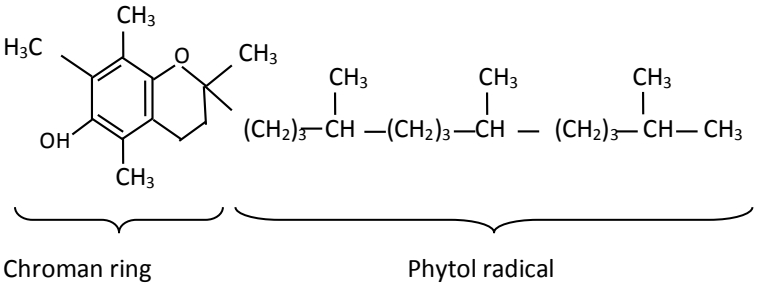


Figure 4: Structure of α-tocopherol (5, 7, 8- trimethyltocol)

Tocopherols are powerful antioxidants. They prevent oxidative damage of other lipid molecules such as vitamin A and fats present in food. Due to this antioxidizing property vitamin E is commercially added to foods to retard their spoilage. Its antioxidising property is stimulated by vitamin C and phenols. Vitamin E also protects mitochondrial system from inactivation by lipid peroxides. It acts as an antioxidant of peroxidation.Breakdown of α-tocopherol involves both oxidative cleavage of the chroman ring to yield quinine or hydroquinone like compounds and the degradation of the isoprenoid side chain.

Vitamin K

Vitamin K is also known as coagulation vitamin or antihemorrhagic factor due to its role in blood clotting. Two forms of vitamin K naturally occur, vitamin K1 (Figure 5) and K2 (Figure 6). Vitamin K1 is present in green leafy vegetables such as cabbage, spinach etc. and K2 is present in putrified fish meat.

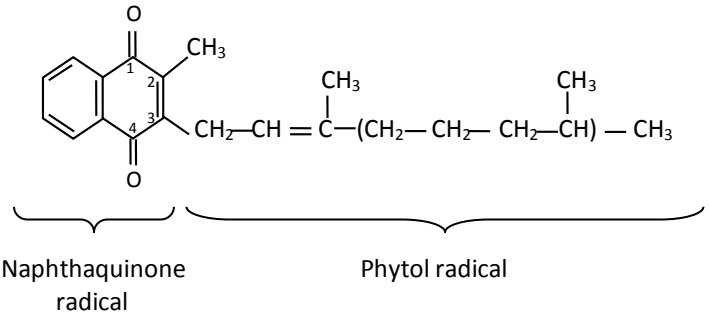


Figure 5: Structure of (A) vitamin K1 (phylloquinone)

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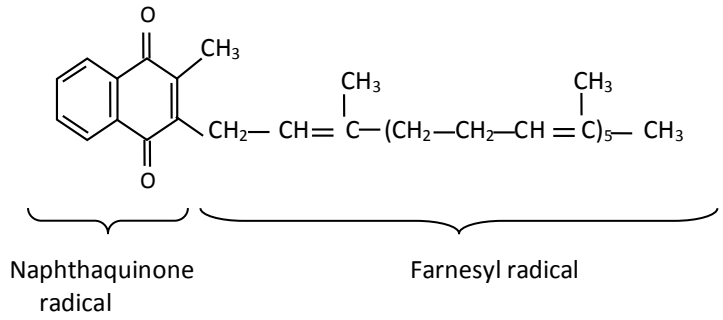


Figure 6: Structure of vitamin K2 (menaquinone)

Vitamin K is derivative of naphthoquinone. The C3 of quinone ring has phytol radical in vitamin K1 whereas this position is occupied by difarnesyl radical in K2. Vitamin K1 has four isoprene units in its side chain whereas K2 contains six isoprene units each having double bond. Vitamin K also plays role in electron transport system (ETS) and in oxidative phosphorylation. The probable specific site of action of vitamin K in ETS is between NADH and cytochrome b.

Water soluble vitamins

Vitamin B complex

Vitamin B complex consists of a group of vitamins such as B1, B2, B3, B5, B6, B7, B9 and B12 (Table 1). All these members of vitamin B complex are not related either chemically of physiologically but they possess some common features:

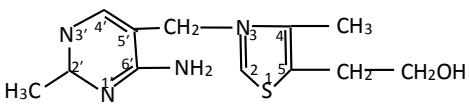
a. All of them are water soluble.
b. Most of them act as coenzymes that take part in metabolic pathways.
c. Most of them can be obtained from the same source that is liver and yeast.
d. Most of them can be synthesized by intestinal bacteria.

Table 1: Coenzyme derivatives of water soluble vitamins.

S. No.	Vitamin	Systematic name	Coenzyme form
1.	Vitamin B1	Thiamine	Thiamine pyrophosphate (TPP)
2.	Vitamin B2	Riboflavin	Flavin mononucleotide (FMN), Flavin adenine dinucleotide (FAD)
3.	Vitamin B3	Pantothenic acid	Coenzyme A (CoA)
4.	Vitamin B5	Niacin	Nicotinamide adenine dinucleotide (NAD), Nicotinamide adenine dinucleotide phosphate (NADP),
5.	Vitamin B6	Pyridoxine	Pyridoxal phosphate (PLP)
6.	Vitamin B7	Biotin	Biocytin
7.	Vitamin B9	Folic acid	Tetrahydrofolate (THFA)
8.	Vitamin B12	cyanocobalamin	Deoxyadenosylcobalamine

Vitamin B1

Thiamine is known as vitamin B1 as it was the first member of vitamin B complex to be identified. It is known as anti beriberi factor due to its curing action against beriberi. It is also known as antineuritic factor or heat labile factor. Vitamin B1 is found in all plants and animal foods. In cereals outer layers of seeds are especially rich in thiamine. The milling of wheat lowers the thiamine content. Milk also contains thiamine although in relatively low amounts. Thiamine is 2,5-dimethyl-6-aminopyrimidine bonded through a methylene linkage to 4-methyl-5-hydroxyethyl thiazole (Figure 7).



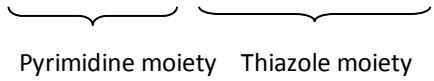


Figure 7: Structure of vitamin B1 or Thiamine.

Thiamine is phosphorylated with ATP to form thiamine pyrophosphate (TPP).

Thiamine + ATP ⟶ Thiamine pyrophosphate (TPP) + AMP

TPP, in association with lipoic acid forms the prosthetic group for the enzyme carboxylase. TPP participate in many reactions such as decarboxylation of α-keto acids such as pyruvic acid and α-ketoglutaric acid.

Vitamin B2

Vitamin B2 is known as riboflavin. It is popularly known as yellow enzyme because of its colour. It is found naturally as two flavin coenzymes namely flavin mononucleotide (FMN) and flavin adenine dinucleotide (FAD). Various sources of riboflavin are milk, cheese, eggs, and yeast. Leafy vegetables are richer in riboflavin than they are in thiamine. Riboflavin consists of a sugar alcohol, D-ribitol, attached to a chromogenic dimethyl isoallaxazine ring at N9 (Figure 8).

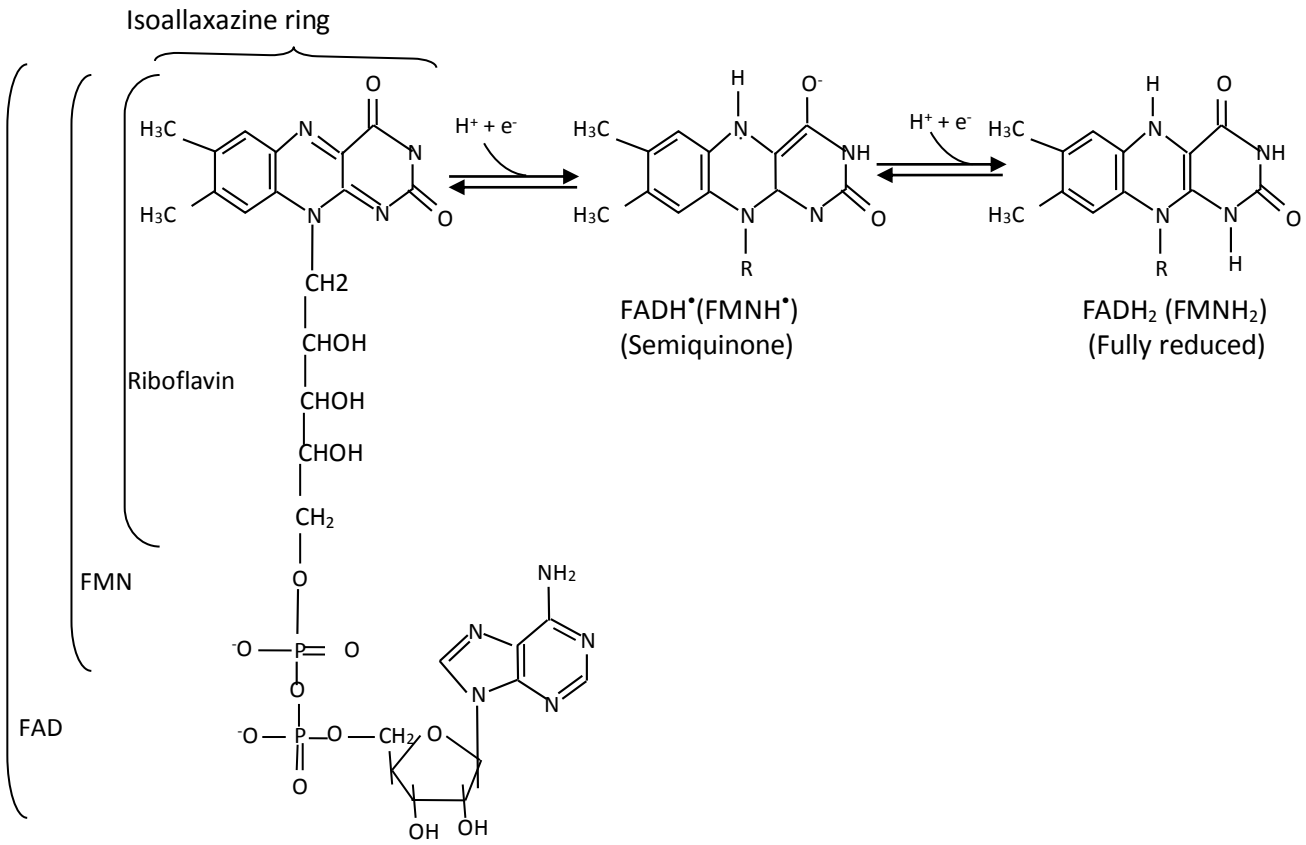


Figure 8: Structure of riboflavin, FMN and FAD.

Flavin containg proteins (flavoproteins) are enzymes that catalyse oxidation reduction reactions using either FMN or FAD as coenzymes (Table 2).

Table 2: some flavoproteins that uses flavin nucleotide coenzymes.

Enzyme	**Flavin nucleotide**
Acetyl CoA dehydrogenase	FAD
Dihydrolipoyl dehydrogenase	FAD

Succinate dehydrogenase	FAD
Glycerol-3-phosphate dehydrogenase	FAD
NADH dehydrogenase	FMN
Glycolate oxidase	FMN

FMN and FAD are synthesized from riboflavin by FMN kinase and FAD synthetase, respectively.

Riboflavin + ATP ⟶ FMN + ADP
FMN + ATP ⟶ FAD + PPi

FMN and FAD coenzymes undergo reversible oxidation-reduction in presence of the enzyme and a suitable substrate (Table 2). The fused ring structure of flavin nucleotides is known as isoallaxazine ring which undergoes reversible reduction. It is reduced by accepting one or two electrons in the form of one or two hydrogen atoms (each atom has an electron plus a proton) from a reduced substrate. The fully reduced forms are abbreviated as FADH2 and FMNH2. When a fully oxidized flavin nucleotide accepts only one electron (one hydrogen atom) the semiquinone form of the isoallaxazine ring is produced which is abbreviated as $FADH^{\bullet}$ and $FMNH^{\bullet}$. Because the flavin nucleotides have ability to participate in either one or two electron transfers therefore flavoproteins are involved in a greater diversity of reactions than the NAD(P) linked dehydrogenases.

The flavin nucleotide in most flavoproteins is bound covalently to the protein as prosthetic group. Flavoenzymes play a key role in cell metabolism. They function in accepting hydrogen atoms from reduced pyridine nucleotides. They participate in the enzymatic oxidation of glucose, fatty acids, amino acids and purines. Some flavoproteins play quite different roles as light receptors. Riboflavin and flavoproteins play significant role in phototropic curvature of various plant organs. Riboflavin is synthesized by all green plants, most bacteria, yeast and moulds. Animals do not synthesise riboflavin. In human the ingested riboflavin is largely passed out as such or as its coenzymes, the FMN.

Vitamin B3

Vitamin B3 is also known as pantothenic acid. The coenzyme form of vitamin is coenzyme A (Co A). Pantothenic acid is widely present in yeast, liver and eggs. Pantothenic acid is an amide of pantoic acid (α,γ-dihydroxy-β-dimethyl butyric acid) and β-alanine (Figure 9).

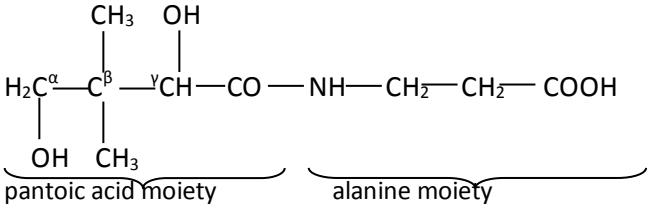


Figure 9: Structure of vitamin B3.

Vitamin B3 is synthesized by plants and microorganisms but not by animals. Therefore, it is required in diet to serve as starting point for CoA. The function of CoA is in acylation reactions. CoA in presence of ATP, acetate and suitable enzyme converted into acetyl CoA. Acetyl CoA is an important coenzyme in carbohydrate and lipid metabolism.

Vitamin B5

Vitamin B5 is known as nicotinic acid or niacin. The term nicotinic acid is less commonly used to avoid any association with the alkaloid nicotine of tobacco. Niacin is widely distributed in plants and animal tissues as its amide called niacinamide. Niacin is most abundantly found in yeast. Other sources of niacin are liver, salmon, poultry and red meat, ground nut, sunflower oil. The conversion of niacin to nicotinamide takes place in kidney, brain and liver if glutathione is present. In human and other animals niacin is synthesized from amino acid tryptophan. Nicotinamide is also synthesized from NAD by amidation and subsequent degradation.

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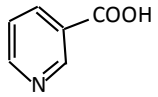
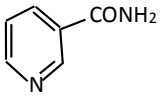
The two pyridine nucleotide coenzymes namely, nicotinamide adenine dinucleotide (NAD) and nicotinamide adenine dinucleotide phosphate (NADP) contain niacinamide as their structural constituent. Niacin is a pyridine derivative (Figure 10).



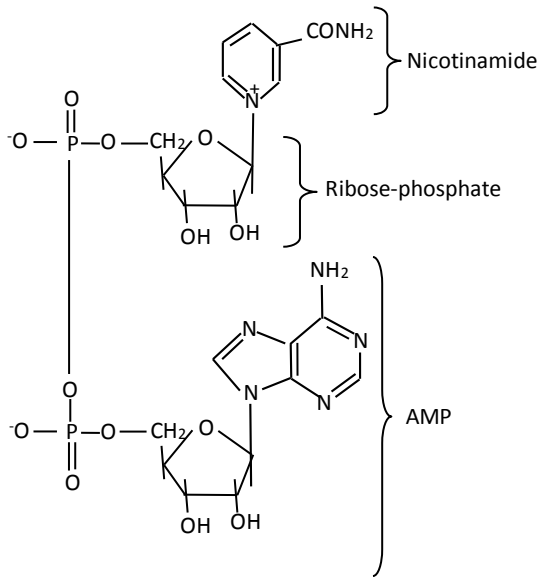
Nicotinic acid (niacin)

(A)

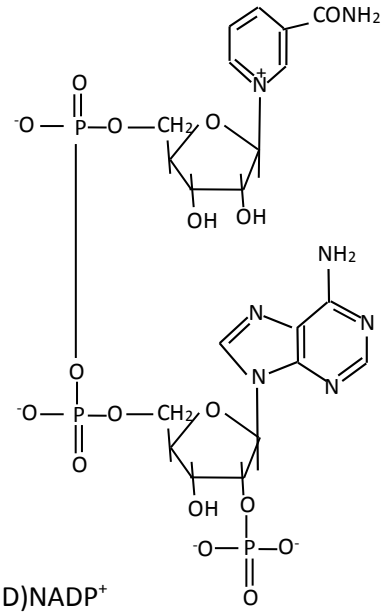


Nicotinamide (niacinamide)

(B)



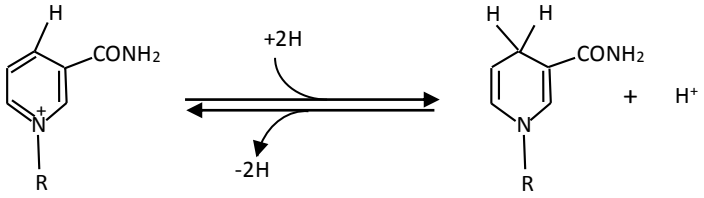
(C)NAD$^+$



(D)NADP$^+$

Figure 10: Structure of (A) niacin, (B) niacinamide, (C) NAD$^+$ and (D) NADP$^+$.

These coenzymes are present in two forms. NAD$^+$ and NADP$^+$ are oxidizing agents; they accept electrons from other molecules and get reduced into NADH and NADPH respectively (Figure 11). The NADH and NADPH then act as reducing agents and donate electrons to other molecules.



NAD(P)$^+$ (oxidized) NAD(P)H (reduced)

Figure 11: Redox rections of NAD$^+$ and NADP$^+$

NAD$^+$ and NADP$^+$ play an essential role in many biochemical reactions, especially redox reactions (oxidation-reduction reactions) in which oxidoreductase enzymes transfer hydrogen. For example in a redox reaction catalysed by alcohol dehydrogenase two hydrogen atoms and two electrons (the two electrons of the C-H bond) are removed from the ethanol molecule, one as proton (H^+) and the other as hydride ion ($H:^-$).The hydride ion and both electrons are transferred to NAD$^+$, generating NADH and proton is released in the medium. The hydrogen of NADH is donated to acetaldehyde to reduce it into ethanol by same enzyme alcohol dehydrogenase (Figure 12). Enzymes that use NAD$^+$ rarely use NADP$^+$ and vice versa.

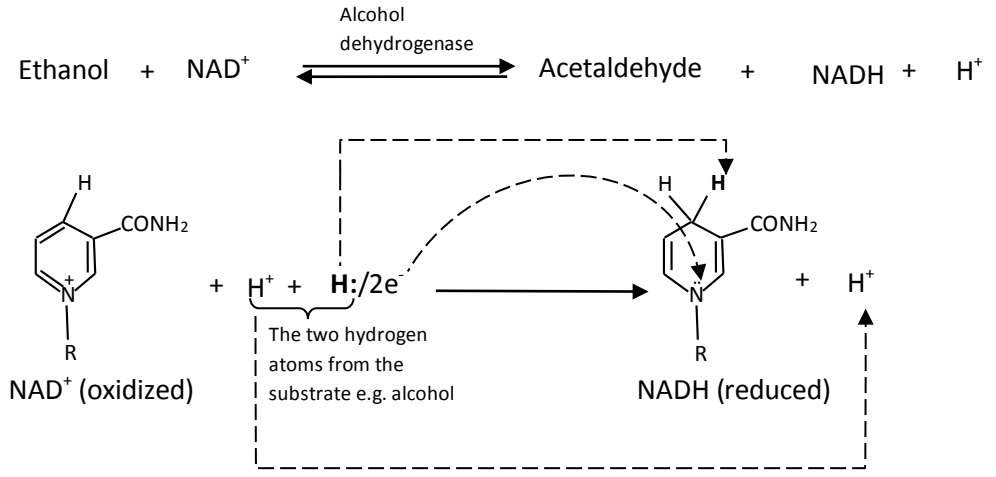


Figure 12: Redox reaction catalysed by alcohol dehydrogenase.

Vitamin B6

Vitamin B6 is also known as antidermatitis factor. There are three compounds in vitamin B6 group;pyridoxine, pyridoxal and pyridoxamine. Vitamin B6 is rich in cereals, peas, sprouts, carrots, potatoes, bananas and yeast. It is also found in milk, egg yolk, salmon, chicken, fish, pork and liver. Pyridoxal andpyridoxamine also occur in nature as their coenzymes namely pyridoxal phosphate and pyridoxine phosphate respectively, respectively. Vitamin B6 is pyridine derivative. The three forms of vitamin B6 differ from each other in the nature of substituents attached at C4 of the ring (Figure 13).

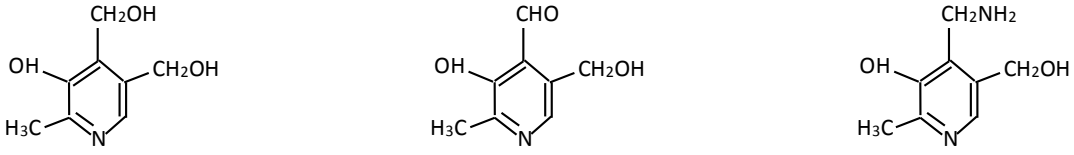


Figure 13: Structure of vitamin B6 compounds

Pyridoxine can be converted into either pyridoxal or pyridoxamine but neither of them can be converted to pyridoxine. Pyridoxal-5'-phosphate (PLP) act as coenzyme (Figure 14) in many biochemical reactions such as metabolism of amino acids e.g. transamination, decarboxylation and racimization reactions. PLP-dependent enzymes are also involved in other essential biological processes, such as hemoglobin biosynthesis, fatty acidmetabolism.

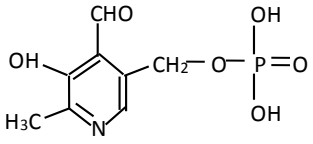


Figure 14: Structure of coenzyme pyridoxal-5'-phosphate (PLP).

In the brain, the PLP-dependent enzyme aromatic L-amino acid decarboxylase catalyzes the synthesis of two major neurotransmitters: serotonin from the amino acid tryptophan and dopamine from L-3,4-dihydroxyphenylalanine (L-Dopa). Other neurotransmitters, including glycine, D-serine, glutamate, histamine, and γ-aminobutyric acid (GABA), are also synthesized in reactions catalyzed by PLP-dependent enzymes.

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Vitamin B7

Vitamin B7 is known as biotin is sometimes referred to as vitamin H. it is produced by intestinal bacteria as well as found in yeast, liver, kidney, milk and molasses. Biotin is present in nature in combined state called biocytin linked with a peptide bond with amino acid lysine (Figure 15). Removal of biotin from biocytin and recycling of biotin from biotin-dependent enzymes requires the activity of the enzyme biotinidase. Biotin is the cofactor required for enzymes that are involved in, decarboxylation.

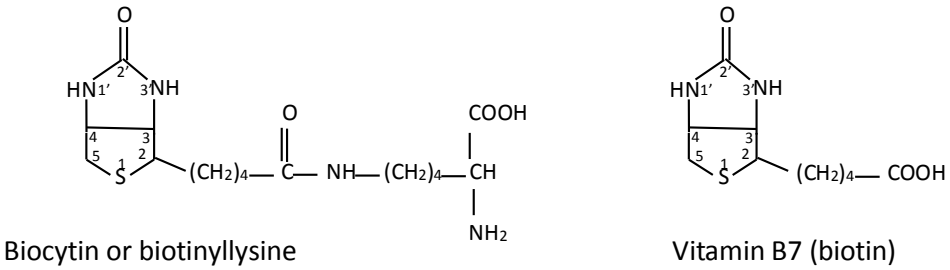


Figure 15: Structure of biotin.

Biotin consists of a fused imidazole ring and thiophene ring with a fatty acid side chain. The oxybiotin in which sulfur atom of biotin is replaced by an oxygen atom has same activity. Biotin and thiamine are the only sulfur containing vitamins. Biotin serves as prosthetic group for many enzymes which catalyse carboxylation, decarboxylation and transcarboxylation reactions in prokaryotes and eukaryotes. The CO_2 is carried as carboxylic group attached to one of the ureido nitrogen atoms of biotin, forming N-carboxybiotin complex (Figure 16). In humans, the biotin-requiring enzymes include acetyl-CoA carboxylase (ACC), pyruvate carboxylase (PC), propionyl-CoA carboxylase (PCC). The enzyme ACC is a cytosolic enzyme that is the rate-limiting enzyme of fatty acid synthesis. PC and PCC are mitochondrial enzymes; PC catalyzes the critical first reaction in the pathway of gluconeogenesis and PCC is involved in the metabolism of several amino acids and in oxidation of fatty acids with an odd number of carbon atoms.

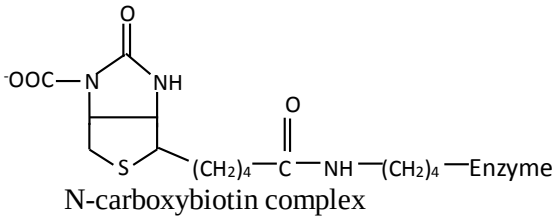


Figure 16: Structure of N-carboxybiotin

Vitamin B9

Folic acid and its derivatives (tri- and hepta-glutamyl peptides) are widely distributed in biological world. It is present in liver, kidney, yeast, dates and spinach. Like thiamine with improper cooking, folic acid content is destroyed. Folic acid consists of three units, glutamic acid, p-aminobenzoic acid and pterin which is a derivative of heterocyclic fused ring compound (Figure 17).

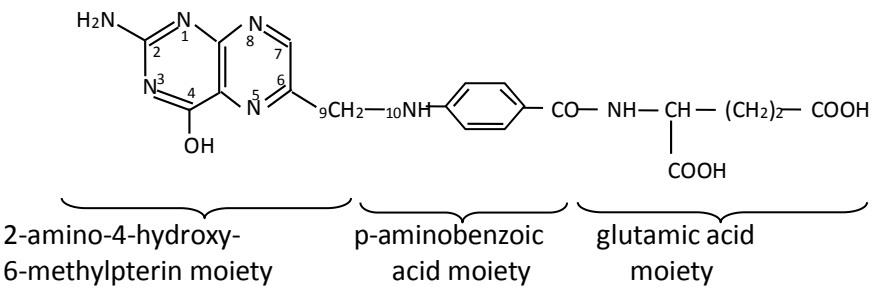
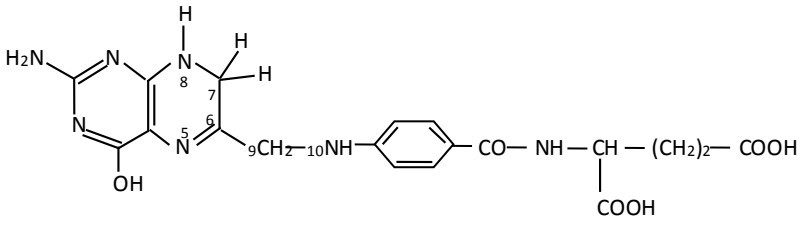
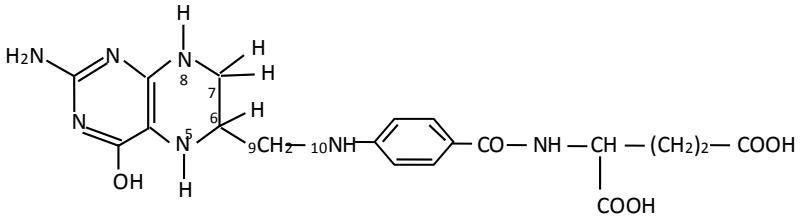


Figure 17: Structure of vitamin B9 or folic acid

The number of glutamic acid residues varies in various vitamin B9 derivatives. The additional glutamic acid groups being conjugated in peptide linkage. The coenzymes of folic acid are dihydrofolate (DHFA or FH_2) and tetrahydrofolate (THFA or TH_4) (Figure 18).



7, 8-dihyrohydrofolic acid(DHFA)



5, 6, 7, 8-tetrahydropfolic acid (THFA)

Figure 18: Structure of DHFA and THFA.

DHFA is synthesized from folic acid by enzyme DHFA reductase (also known as folate reductase). DHFA can further be reduced by dihydrofolic reductase into 5,6,7,8 tetrahydrofolate (THFA). Reduction of THFA from folate is associated with oxidation of NAPDH or NADH and requires the presence of ascorbic acid. Drugs trimethoprim, methotrxate and aminopterin are inhibitors of DHFA reductase. Similar to two carbon transfer reactions performed by CoA, vitamin B9 is involved in one carbon transfer reactions.

Vitamin B12

Vitamin B12 is the last vitamin of B complex. It is known as cyanocobalamin. The coenzyme form of this vitamin is known as deoxyadenosylcobalamin or cobamide coenzyme. Vitamin B12 is found only in animals. Major source of vitamin B12 is liver, less amount is present in milk, meat, eggs, fish. It is synthesized by intestinal microorganisms. Cyanocobalamin is not present in plant foods except in spirulina, which is blue green algae. Animals and plants do not synthesize this vitamin. Only microorganisms especially aerobic bacteria synthesise cyanocobalamin.

Structure of vitamin B12 is one of the most complex structures known (Figure 19). Cyanocobalamin is a pigment similar to the tetrapyrrole ring structure of the porphyrins e.g. chlorophyll and haem. It contains a heavy metal atom cobalt in its trivalent state. This is unique feature of this vitamin as there is no other cobalt containing organic molecule exists in nature. Cobalt atom is located in the central and is surrounded by a macrocytic structure of four reduced pyrrole rings (A, B, C and D) collectively called corrin. Out of six coordinate valences of the cobalt atom (Co^{2+}), four are satisfied by four nitrogens of the reduced tetrapyrrole, fifth and sixth valency is satisfied by a nitrogen atom of 5,6-dimethylbenzimidazole and a cyanide ion, respectively. Ring A and D are directly linked to each other and corrin has lower degree of unsaturation with only six double bonds. Other two rings B and C are linked through a single methane carbon. Another unique feature of this vitamin is the presence of a loop of the isopropanol, phosphate, ribose and 5, 6-dimethylbenzimidazole in that order. The end of the loop is attached with the central cobalt atom.

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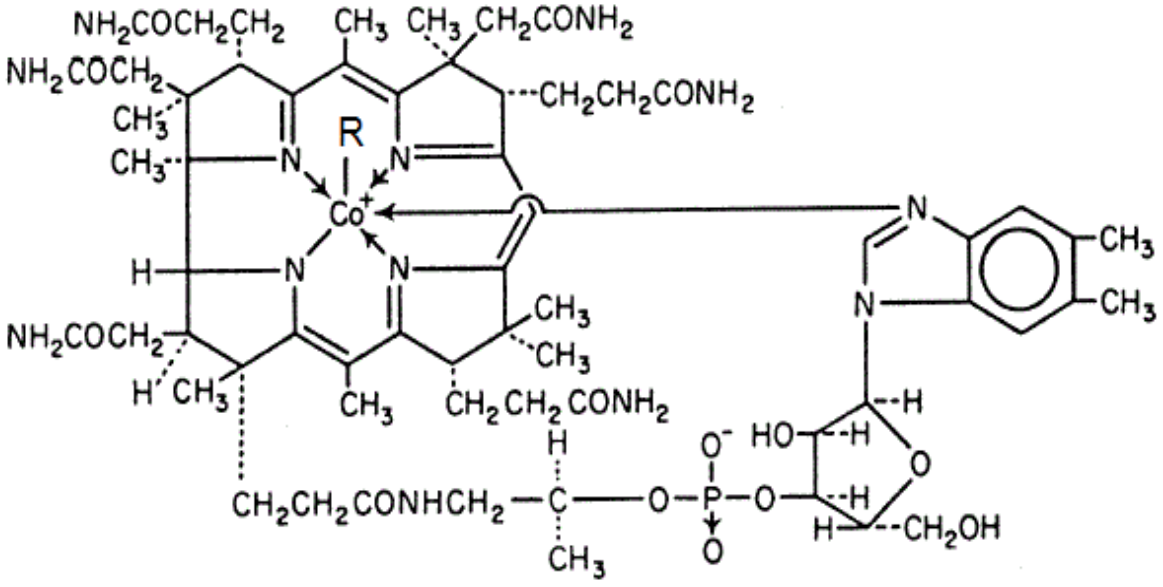
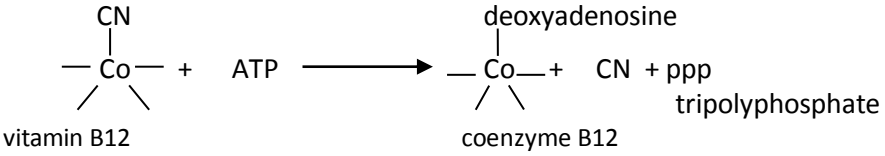


Figure 19: Structure of Vitamin B12 (R = CN, Me, and Coenzyme B12).

The structure of the vitamin B12 and coenzyme B12 (5′-deoxyadenosyl cobalamin) are similar except that the CN group in B12 coenzyme is replaced by adenosine and linking with cobalt atom takes place at 5′ carbon atom of the ribose of adenosine. Vitamin B12 coenzyme is the only known example of a carbon-metal bond in a biomolecule. Vitamin B12 is converted to coenzyme B12 by extract from microorganisms supplemented with ATP.

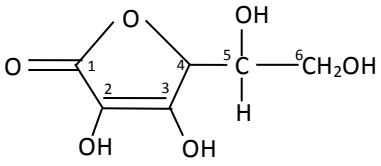


Adenosylcobalamin take part in following biochemical reactions such as 1, 2 shifts of a hydrogen atom, carrier of a methyl group, isomerization of dicarboxylic acids and dismutation of vicinal diols.

Vitamin C

Vitamin C is also known as ascorbic acid and antiascorbutic factor because of its curing action against scurvy. It is present in all fresh fruits and vegetables. Citrus fruits such as orange, lemon are richest source of vitamin C. It is also present in amla, guavas, tomatoes, raw cabbage and green pepper. Vitamin C is synthesized by most animals, but not by primates (e.g. ape, human)and guinea pigs, therefore they acquire it from their diets. It is good reducing agent, it is lost under oxidizing conditions like aeration and heating.

Ascorbic acid is derivative of hexose L-gulose (Figure 20). Only its L-isomer has anti ascorbutic property. It is readily oxidized in presence of copper and iron but not in aluminium. Because of this the foods cooked in copper utensils lose vitamin C quickly.



Ascorbic acid

Figure 20: Structure of vitamin C.

Alkali also destroy vitamin C, therefore baking soda has deleterious effects more than steam cooking. Freezing has no detrimental effect. Vitamin C is powerful reducing agent as it oxidizes rapidly.

Plants also follow this biosynthetic pathway of ascorbic acid. The inability to synthesize vitamin C by human, primates and guinea pigs is due to lack of enzyme L-gulono oxidase. The oxidation of ascorbic acid into dehydroascorbic acid takes place in presence of metal ion. Dehydroascorbic acid is even much more reducing agent by virtue of its unpaired electron. Dehydroascorbate can be reduced back into ascorbic acid in presence of H_2S or cysteine. The reduced form (ascorbate) and oxidised form (dehydroascorbate) are equally potent for metabolic functions and present in plasma at a ratio of 15:1, respectively. Dehydroascorbic acid may be hydrated to 2, 3-diketo-L-gulonic acid which is biologically inactive and can not be converted to either of the two active forms in the body (Figure 21).

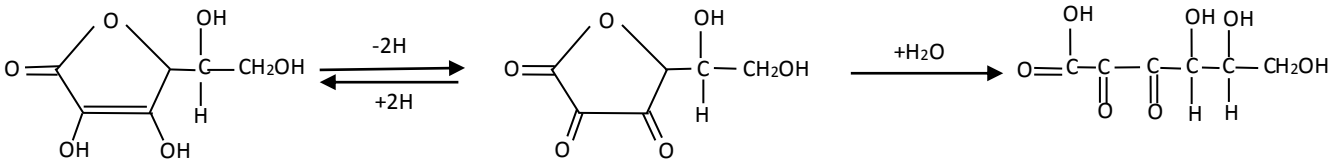


Figure 21: Metabolism of ascorbic acid

In plants ascorbic acid plays important role in germination, growth, metabolism and flowering. Vitamin C stimulates amylase, protease and RNase activity. Vitamin C acts as coenzyme for two groups of hydroxylation. One is copper containing hydroxylases and second is α-ketoglutarate-linked iron containing hydroxylases. Among copper containing enzymes is dopamine β-hydroxylase which catalyses synthesis of catecholamines (norepinephrine and epinephrine) from tyrosine in adrenal medulla and central nervous system. In this reaction Cu^{+} is oxidized to Cu^{2+}. Ascorbic acid is specifically required for reduction of Cu^{2+} back into Cu^{+}. In this redox reaction ascorbic acid is oxidized to monodehydroascorbate (Figure 22).

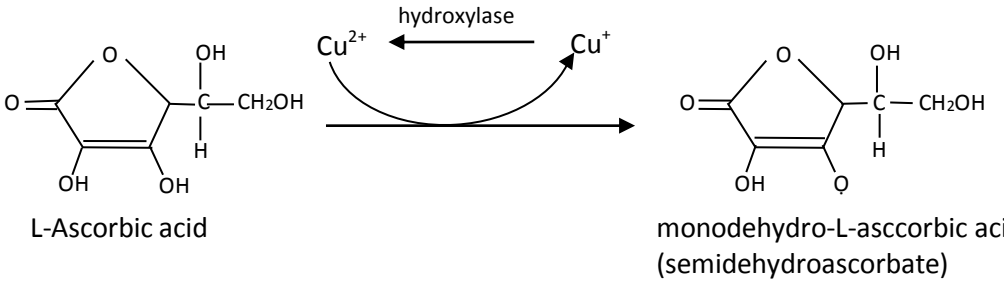


Figure 22: Reduction of copper by ascorbic acid.