

Studies in Biology no. 101

# **Sulphur in Biology**

**John W. Anderson**



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The Institute of Biology's  
Studies in Biology no. 101

# **Sulphur in Biology**

**John W. Anderson**

Ph.D.

Reader, School of Biological Sciences,  
La Trobe University, Victoria, Australia

**Edward Arnold**

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*First published 1978*

by Edward Arnold (Publishers) Limited  
41 Bedford Square, London, WC1B 3DQ

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### **British Library Cataloguing in Publication Data**

Anderson, John W

Sulphur in biology. – (Institute of Biology.  
Studies in biology; no. 101; 0537-9024).

1. Sulphur in the body 2. Sulphur –  
Physiological effect 3. Plants, Effect of  
sulphur on

1. Title II. Series  
574.1'921 QP535.S1

ISBN 0-7131-2711-2

Printed and bound in Great Britain at  
The Camelot Press Ltd, Southampton

## General Preface to the Series

Because it is no longer possible for one textbook to cover the whole field of biology while remaining sufficiently up to date the Institute of Biology has sponsored this series so that teachers and students can learn about significant developments. The enthusiastic acceptance of 'Studies in Biology' shows that the books are providing authoritative views of biological topics.

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Readers' comments will be welcomed by the Education Officer of the Institute.

1978

Institute of Biology  
41 Queen's Gate  
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## Preface

Sulphur is one of the major elements essential for life and has recently been the subject of much biological interest. In many parts of the world the concentration of sulphur in the soil is too low for maximum plant productivity and also adversely affects the nutritional quality of plant foodstuffs which are used for human and animal consumption. But man's interest in the effect of sulphur on organisms has been roused by other events too, such as the burning of fossil fuels which releases toxic gaseous sulphur oxides into the atmosphere.

The issues mentioned above raise fundamental biological questions. Why is sulphur essential for organisms? What forms of sulphur satisfy their nutritional requirements? How is sulphur cycled from one organism to another? What are the world's reserves of sulphur? Will the toxic sulphur oxides accumulate in the atmosphere? This booklet aims to establish certain principles pertinent to the role of sulphur in biology and to show that sulphur is in a state of dynamic equilibrium between organisms in much the same way as nitrogen and carbon. This information is relevant to the questions posed above and hopefully it will stimulate an interest in this important element.

I would like to express my gratitude to Dr R. E. Williamson for many helpful comments in preparing this booklet.

Melbourne, 1977

J. W. A.

# Contents

General Preface to the Series	iii
Preface	iii
<b>1 Requirements of Organisms for Sulphur</b>	<b>1</b>
1.1 Sulphur as a constituent of proteins 1.2 Other sulphur-containing metabolites 1.3 Environmental sources of sulphur, carbon and nitrogen for organisms 1.4 Bioenergetics of reducing sulphate, carbon dioxide and nitrate 1.5 Biological cycling of sulphur, carbon and nitrogen	
<b>2 Transformations of Inorganic Sulphur by Organisms</b>	<b>11</b>
2.1 Oxidation states of sulphur 2.2 Major types of inorganic sulphur transformations catalysed by organisms 2.3 Assimilatory sulphate reduction 2.4 Dissimilatory sulphate reduction 2.5 Oxidation of sulphur by chemoautotrophic bacteria 2.6 Oxidation of sulphur by photoautotrophic bacteria 2.7 Formation of inorganic sulphur from organic sulphur compounds by heterotrophic organisms	
<b>3 Sulphur Nutrition and Metabolism of Plants and Animals</b>	<b>23</b>
3.1 Sulphur nutrition of plants 3.2 Synthesis of cysteine and methionine by plants 3.3 Sulphur nutrition of monogastric animals 3.4 Methionine and cysteine content of foodstuffs 3.5 Increasing the world supply of sulphur amino acids 3.6 Sulphur nutrition of ruminant animals	
<b>4 Cycling of Sulphur</b>	<b>36</b>
4.1 Sulphur reserves of the world 4.2 Anthropogenic additions of sulphur to the biosphere 4.3 Addition of sulphur to the biosphere by natural physical processes 4.4 Removal of sulphur from the biosphere 4.5 Volatilization of sulphur by organisms 4.6 Global cycling of sulphur 4.7 Sulphur cycling in aquatic systems 4.8 Sulphur cycling in pastures and livestock	
<b>5 Man's Disturbance of the Sulphur Cycle and its Consequences</b>	<b>49</b>
5.1 Effect of atmospheric sulphur dioxide on organisms 5.2 Uses of sulphur by man 5.3 Effect of sulphur fertilizers on organisms 5.4 Some examples of the effect of sulphur-containing wastes on organisms 5.5 Detoxification and sulphur tolerances of organisms	
Further Reading	60

# 1 Requirements of Organisms for Sulphur

Sulphur is one of the elements essential for the life of all organisms – plants, animals and microorganisms. The requirement of an organism for sulphur can be demonstrated by depriving it of its appropriate sulphur source. Under these conditions the organism will either fail to grow, or, if it contains appreciable reserves of sulphur (e.g. seeds of plants), it will exhibit a slow growth rate, loss of mass or deficiency symptoms compared with a control organism supplied with sulphur. For our purposes, some idea of an organism's requirement for sulphur can be gained from the elemental composition of organisms. Sulphur accounts for approximately 0.2–0.7% of the dry mass of most organisms. On a molar basis several other elements are present in substantially higher concentrations (Table 1).

**Table 1** Typical values for the elemental composition of some organisms. All values are expressed as atoms of the element relative to one atom of sulphur. Some of the trace elements are not included. Gaps in the table indicate that values were not determined in conjunction with those for the elements shown.

Element	Organism		
	<i>Saccharomyces cerevisiae</i> (yeast)	<i>Zea mays</i> (maize)	<i>Homo sapiens</i> (man)
Hydrogen		1175	306
Carbon		684	191
Oxygen		523	37.5
Nitrogen	47.5	19.6	27.3
Potassium	4.57	4.43	1.14
Calcium	0.08	1.08	4.78
Phosphorus	3.12	1.21	4.12
Magnesium	0.49	1.40	0.27
Sulphur	1.00	1.00	1.00
Chlorine		0.74	0.54
Iron	0.02	0.27	0.009
Sodium	0.52		0.84

## 1.1 Sulphur as a constituent of proteins

Carbon, hydrogen and oxygen are associated with almost all of the large number of compounds found in biological matter. The two most

fundamental compounds essential for life are the nucleic acids, which also contain nitrogen and phosphorus, and the proteins, which contain nitrogen and sulphur. Cells contain a large number of different proteins which fulfil several essential functions. Some proteins, called enzymes, catalyse the multitude of different chemical reactions associated with the generation of cellular energy and its use in cellular maintenance, growth, development, regulation and reproduction. Other proteins do not have catalytic activity but serve a structural function. Typical of this latter group are some of the proteins associated with membranes such as those of nuclei, mitochondria, chloroplasts and the plasma membrane. Another group of proteins act as a reserve of amino acids and energy.

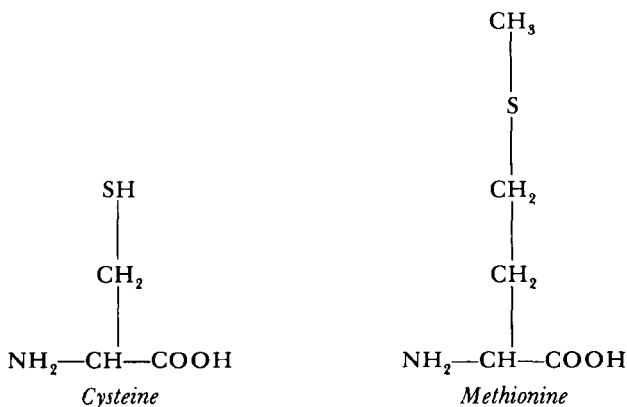
Proteins are made up of amino acids. The structure of two typical amino acids found in proteins can be written as



where R is different for each amino acid. In proteins the  $-\text{COOH}$  group of one amino acid is linked to the  $-\text{NH}_2$  group of another. The  $-\text{CO}-\text{NH}-$  bond formed is known as a peptide bond.

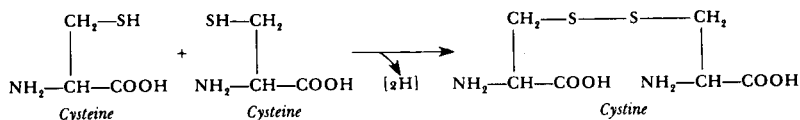
Proteins vary in their size. The animal hormone corticotrophin for example contains 39 amino acid units, the enzyme ribonuclease from ox pancreas contains 124, and many more complex enzymes contain more than 1000. Although there are many thousands of proteins in any one organism, all are built up from about twenty different amino acids. Proteins differ only in the proportion of the twenty amino acids and in the sequence in which they are joined together.

Two of the protein amino acids, cysteine and methionine, contain sulphur in the R-side chain:



If all twenty amino acids were present in a protein in equal molar amounts then the proportion of any single amino acid would be 5% and the cumulative proportion for the two sulphur amino acids would be 10%. For the majority of proteins the proportion of the sulphur amino acids is less than this (typically 3–7%), but the proportions can vary greatly. Keratin, the fibrous protein of hair and wool, contains a very high proportion of cysteine (12%), whereas collagen, a fibrous protein of skin and cartilage, contains no cysteine and only a very small amount of methionine. Nevertheless, it can be said that virtually all proteins contain at least one of the sulphur amino acids. Although sulphur has other essential roles in organisms (see section 1.2), it is the occurrence of sulphur in the protein amino acids cysteine and methionine which constitutes the basic biological importance of this element in all organisms.

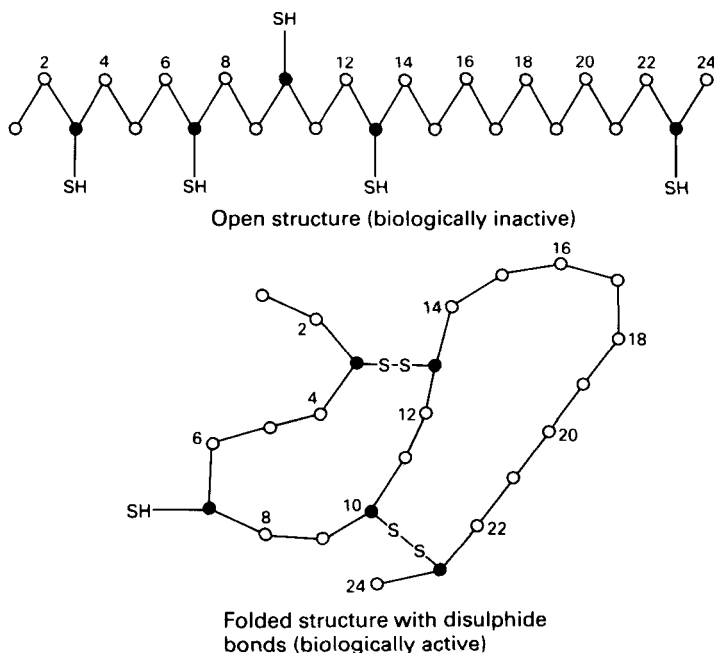
Sulphur occurs in cysteine in a —SH group (also known as a thiol or sulphhydryl group). Two aspects of its chemistry are relevant to the role of cysteine in proteins. The —SH group of cysteine, together with the —SH group of another molecule of cysteine, readily oxidizes to form a molecule of cystine. The two molecules are linked by a disulphide bond (—S—S—):



The same process can occur between two non-adjacent cysteine units within a protein except that in this case the process of oxidation is carefully controlled by the cell. If two cysteine units within a protein are linked together by a —S—S— bond then this will cause the protein to fold (Fig. 1–1). Disulphide linkages are therefore important in determining the configuration of proteins. This in turn is directly relevant to the catalytic or structural properties of the protein.

The other important feature of the chemistry of cysteine is that the —SH group readily reacts with a group of compounds known as —SH group reagents (e.g.  $\text{Hg}^{2+}$ ,  $\text{Pb}^{2+}$ , *p*-chloromercuribenzoate, *N*-ethylmaleimide). It follows that any —SH groups in the protein which are not oxidized as described above will react with —SH group reagents. It is found that the catalytic activity of a large number of enzymes (perhaps as many as 40%) is destroyed or inhibited by —SH group reagents. This implies that the —SH groups of cysteine are involved in the catalytic function of these enzymes. Incidentally, the reactivity of  $\text{Hg}^{2+}$  and  $\text{Pb}^{2+}$  with the —SH groups of proteins largely explains the toxicity of mercury and lead.

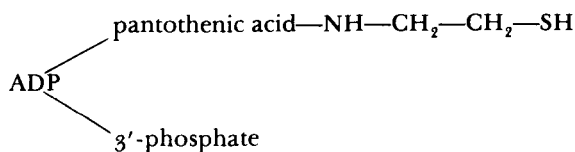




**Fig. 1-1** Folding of a hypothetical protein chain by oxidation of the —SH groups of cysteine units in the protein. The precise nature of the folding is determined by the amino acid sequence in the protein. The —SH groups of cysteine at positions 3 and 10 have oxidized with those at positions 13 and 23 respectively to form disulphide bonds (—S—S—) but the —SH group at position 7 has not been oxidized. The unfolded form of the protein is biologically inactive; the folded form is active. If the protein was an enzyme which was completely inhibited by —SH group reagents, we would conclude that the unoxidized —SH group at position 7 was associated with the catalytic function of the enzyme. (●) cysteine units, (o) other amino acid units.

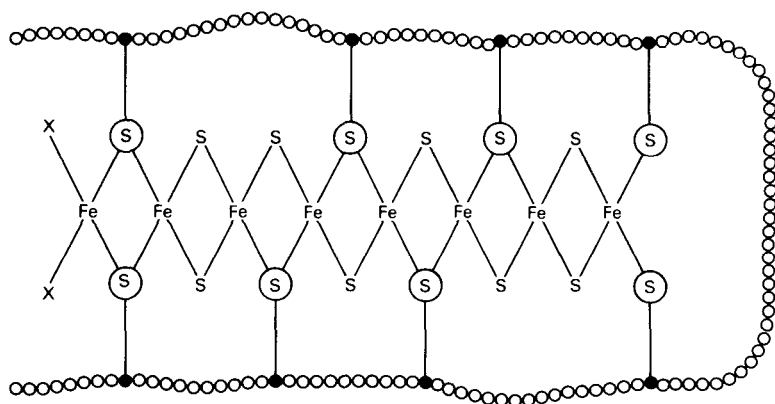
## 1.2 Other sulphur-containing metabolites

Organisms contain other metabolites, in addition to cysteine and methionine, which contain sulphur. Some of these serve important metabolic roles. Coenzyme A is probably the most important of these. It is a complex molecule whose structure is shown below.



Aminoethane thiol ( $\text{NH}_2\text{—CH}_2\text{—CH}_2\text{—SH}$ ), which can be viewed as decarboxylated cysteine, is linked via its  $\text{—NH}_2$  group to pantothenic acid leaving the  $\text{—SH}$  group free at the terminal end. For this reason coenzyme A is frequently written as CoASH. The biological importance of coenzyme A is that it reacts via its  $\text{—SH}$  group with carboxylic acids in a series of enzyme-catalysed reactions to form the corresponding thioethers (e.g. acetate is metabolized as acetyl-coenzyme A,  $\text{CoA—S—CO—CH}_3$ ). The metabolic machinery of cells is geared to metabolize many carboxylic acids as their thioethers of coenzyme A. For example, many parts of such basic processes as the oxidation and synthesis of fatty acids, the synthesis of amino acids and the oxidation of certain intermediates of the tricarboxylic acid cycle (carbohydrate metabolism) all involve the formation of the corresponding thioethers of coenzyme A. It is evident that coenzyme A is as intrinsic to metabolism as ATP itself. Since the aminoethane thiol present in the coenzyme A molecule is formed by decarboxylation of cysteine, this is another reason for the importance of this sulphur amino acid in organisms.

The group of compounds known as the ferredoxins (a type of non-haem iron sulphur protein) merit special attention. They are proteins of low molecular weight and contain a higher proportion of cysteine units than usual. The relevance of the ferredoxins to this section rather than section 1.1 relies on the fact that they contain equal numbers of sulphur and iron atoms in addition to the sulphur contained in the cysteine and methionine units in the protein chain. The number of iron and additional sulphur atoms in a ferredoxin molecule depends on the source; the ferredoxin from *Clostridium pasteurianum* (a bacterium) contains eight whereas that from spinach chloroplasts contains two. The exact spatial arrangement of the iron and additional sulphur atoms is not known, though it seems likely that the atoms of iron are linked together via the additional sulphur atoms and that this association is in turn linked to the protein chain via the sulphur atoms of cysteine units in the chain. A typical model for ferredoxin is shown in Fig. 1–2. This configuration confers on the protein a highly negative redox potential, the most negative known for a biological compound; i.e. the reduced form of ferredoxin can, in theory, effect the reduction of oxidized forms of other redox pairs having a more positive redox potential (e.g. reduction of NADP to  $\text{NADPH}_2$ ). In plants the importance of ferredoxin lies in the fact that the oxidized form is the recipient of electrons ejected from chlorophyll during photo-oxidation of chlorophyll in the light reactions of photosynthesis (i.e. ferredoxin is reduced). Reduced ferredoxin is probably the eventual source of reducing power for the reduction of  $\text{CO}_2$  in the dark reactions of photosynthesis,  $\text{NADPH}_2$  acting as an intermediate in this process. Reduced ferredoxin also serves as the reducing agent in other cellular processes including nitrogen fixation in



**Fig. 1-2** A proposed structure for ferredoxin from the nitrogen-fixing organism *Clostridium pasteurianum*. The outer series of circles enclosing the structure represents the protein chain; cysteine units and other amino acids in the chain are shown by the symbols (●) and (○) respectively. Sulphur atoms enclosed in a circle (S) represent the sulphur atoms of cysteine units. (Redrawn from HUGHES, M. N. (1972). *The Inorganic Chemistry of Biological Processes*. John Wiley and Sons, Inc., New York.)

some nitrogen-fixing organisms. Other iron-sulphur proteins also form part of the electron transport chain of mitochondria.

Further examples illustrating the role of sulphur-containing compounds in metabolic processes could be cited. Some of these are summarized in Table 2.

**Table 2** Functions of some sulphur-containing compounds found in organisms.

Compound	Function
Cysteine, methionine, co-enzyme A and ferredoxin	See the text.
S-Adenosyl methionine	Methyl group donor for methylation reactions.
Glutathione	Reducing agent, especially important in the reductive detoxification of certain metabolites injurious to cells.
Lipoic acid	Cofactor required in the oxidation of oxo acids in the TCA cycle of aerobic organisms.
Biotin	Cofactor for various carboxylation reactions.
Sulpholipid	Structural material of chloroplast membranes.
Thiamine pyrophosphate	Cofactor for decarboxylation of oxo acids and transketolase reactions.
Formyl methionine	Amino acid of N-terminal end of proteins during synthesis; often cleaved subsequently.

### 1.3 Environmental sources of sulphur, carbon and nitrogen for organisms

Since all organisms contain sulphur, carbon and nitrogen in organic compounds it follows that at least some organisms must be able to utilize sources of these elements which are freely available in the environment in which they grow. All three elements occur in a variety of forms in geological deposits (e.g. carbon as limestone,  $\text{CaCO}_3$ ; sulphur as metal sulphides,  $\text{FeS}$ ,  $\text{CuS}$ ; nitrogen as saltpetre,  $\text{KNO}_3$ ), but these are not available to the majority of organisms because of their geographic localization and their depth below the earth's surface. The sources of carbon, sulphur and nitrogen which are widely available to organisms are located in the top few metres of the earth's crust, the oceans and the gases of the atmosphere. All three elements most frequently occur in these media in oxidized forms: sulphur as sulphate, carbon as  $\text{CO}_2$  and nitrogen as nitrate. However, most organic molecules found in cells contain all three elements in reduced forms or, more correctly, low oxidation states (Table 3). This implies that those organisms which can

**Table 3** Most common forms of sulphur, carbon and nitrogen in the physical environment used by organisms, and some examples of the forms found in organic compounds in organisms.

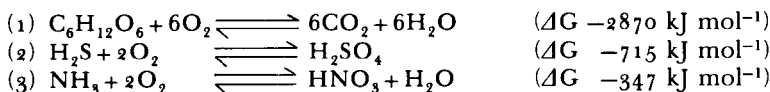
<i>Element</i>	<i>Form found in environment</i>	<i>Forms found in organisms</i>	
Sulphur	$\text{SO}_4^{2-}$	—SH —S—	cysteine methionine
Carbon	$\text{CO}_2$ , $\text{HCO}_3^-$	—HCOH— — $\text{CH}_2$ —	sugars fats
Nitrogen	$\text{NO}_3^-$	— $\text{NH}_2$ —NH—	amino acids proteins

use the oxidized forms (high oxidation states) present in the environment must possess mechanisms for reducing them. The formation of sugars from  $\text{CO}_2$  (reduction) is mainly achieved by photosynthetic organisms. Those organisms which can reduce the sulphur in sulphate to lower oxidation states (e.g. to sulphite and sulphide) are discussed in Chapter 2.

### 1.4 Bioenergetics of reducing sulphate, carbon dioxide and nitrate

The biological reduction of sulphate,  $\text{CO}_2$  and nitrate are all energy-requiring processes. The energy requirements of photosynthesis (reduction) and the energy yield of respiration (oxidation) are probably well known to most students; here they will be briefly compared to the

oxidation and reduction of sulphur, carbon and nitrogen to establish a common principle. Considering the oxidation reactions first, glucose, which can be assumed for the purpose of discussion to be the product of photosynthesis, can be oxidized by molecular oxygen in a bomb calorimeter and its change in free energy measured. Heat energy is released in the process implying that the reaction products contain less free energy than the substrates. There has therefore been a loss of free energy (negative  $\Delta G$ ) and the reaction is said to be exergonic. Similarly  $\text{H}_2\text{S}$  and  $\text{NH}_3$  (low oxidation state forms of sulphur and nitrogen respectively) can also be oxidized in exergonic reactions:

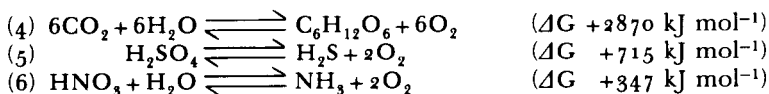


The magnitude of the  $\Delta G$  values indicates how far the reactions lie to the right since  $\Delta G$  is related to the equilibrium constant ( $K_{\text{eq}}$ ) by the equation:

$$\Delta G = -5.7 \log_{10} K_{\text{eq}}$$

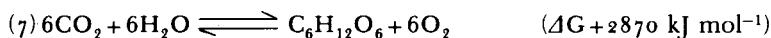
Thus if  $\Delta G$  is  $-5.7 \text{ kJ mol}^{-1}$ ,  $K_{\text{eq}}$  is 10; if  $\Delta G$  is  $-11.4 \text{ kJ mol}^{-1}$ ,  $K_{\text{eq}}$  is 100. Conversely, if  $\Delta G$  is  $+5.7 \text{ kJ mol}^{-1}$ ,  $K_{\text{eq}}$  is 0.1; and if  $\Delta G$  is  $+11.4 \text{ kJ mol}^{-1}$ ,  $K_{\text{eq}}$  is 0.01. It follows from this analysis that the substrates in reactions (1) to (3) are almost completely oxidized at chemical equilibrium. In cells, these reactions can serve as sources of energy. Most cells have energy-generating mechanisms based on the aerobic and/or anaerobic oxidation of glucose or related compounds (respiration) but some organisms described in the next chapter use the oxidation of  $\text{H}_2\text{S}$  (and other forms of sulphur with low oxidation states) as energy-generating mechanisms. The same principle applies to the oxidation of forms of nitrogen with low oxidation states.

Now consider reactions (1) to (3) in the opposite direction:

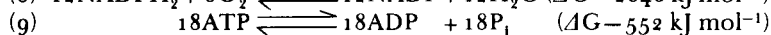


The free energy changes of these reactions are positive and the reactions are said to be endergonic. It follows from the equation relating  $\Delta G$  and  $K_{\text{eq}}$  that it is not possible to produce significant amounts of the products in reactions (4) to (6). Yet it is known that some organisms reduce sulphate to  $\text{H}_2\text{S}$  and incorporate it into the sulphur amino acids. It is also known that photosynthetic organisms form sugars and fats from  $\text{CO}_2$  whilst some organisms reduce nitrate to  $\text{NH}_3$  and incorporate it into amino acids. Clearly, organisms cannot carry out these reductions by the single step reactions shown in reactions (4) to (6) since good yields of product can only be obtained by reactions with a negative  $\Delta G$ . The ability of

organisms to carry out these seemingly impossible reactions lies in their capacity to couple the endergonic reaction (positive  $\Delta G$ ) to exergonic reactions (negative  $\Delta G$ ). Whilst this might be achieved by a series of complex reactions, the  $\Delta G$  of the overall process is readily calculated by summing the component  $\Delta G$  values. Using photosynthesis as an example: the endergonic reaction



is coupled to the exergonic reactions



The net  $\Delta G$  when reactions (7) to (9) are summed is  $-322 \text{ kJ mol}^{-1}$ , thus ensuring that a good yield of glucose is obtained at chemical equilibrium. Glucose has therefore been synthesized at the expense of hydrolysing ATP and oxidizing NADPH<sub>2</sub> which in this example are products of the light reactions of photosynthesis. The important point is that metabolic energy has been expended to effect the formation of glucose from CO<sub>2</sub>. The same principle is equally true for the reduction of oxidized forms of sulphur and nitrogen to lower oxidation states.

### 1.5 Biological cycling of sulphur, carbon and nitrogen

The brief treatment of the bioenergetics of sulphur, carbon and nitrogen brings us to the point at which the biological cycles for these elements can be established. Some organisms can, in energy-requiring reactions, use oxidized forms of the elements present in the physical environment to make the organic molecules of life. The energy for these processes can come from the sun, or, in some cases, from the oxidation of other materials present in the environment. Green plants belong to this category and are unique in being able to use sulphate, CO<sub>2</sub> and nitrate as their sources of sulphur, carbon and nitrogen respectively. The reduced forms of the elements, made by these organisms, can in turn be oxidized by a second class of organisms in energy-generating reactions and then used as a source of energy for growth. Animals belong to the latter class. However, it should be noted that many organisms fall into one class with respect to one element but another class with respect to another element. The examples cited in Table 4 illustrate this point. Finally, it should be pointed out that organisms belonging to the first class with respect to a particular element are dependent on the second class for regenerating the oxidized forms of the element for re-use. The two classes of organisms are therefore dependent on each other for the alternate formation of oxidized and reduced forms.

Organisms which can use CO<sub>2</sub> as their sole source of carbon are referred to as autotrophs (*auto*, Gk., self; *trophikos*, Gk., nourishment).

Theoretically this nomenclature could be used for referring to organisms which use sulphate and nitrate as their sources of sulphur and nitrogen for growth (e.g. S-autotrophs and N-autotrophs), but this nomenclature would be very confusing particularly for those organisms which can use sulphate as their sulphur source but cannot use  $\text{CO}_2$  as a source of carbon (Table 4). There are other complications too. Some anaerobic bacteria

**Table 4** Forms of sulphur, carbon and nitrogen used by some organisms.

<i>Organism</i>	<i>Sulphur</i>	<i>Carbon</i>	<i>Nitrogen</i>
Plants	$\text{SO}_4^{2-}$	$\text{CO}_2$	$\text{NO}_3^-$
Monogastric animals	Organic S	Organic C	Organic N
Ruminant animals	Organic S and $\text{SO}_4^{2-}$	Organic C	Organic N and $\text{NH}_4^+$
<i>Penicillium</i> (a fungus)	$\text{SO}_4^{2-}$	Organic C	$\text{NO}_3^-$
<i>Thiobacillus</i> (a bacterium)	$\text{S}^{2-}$ , $\text{S}_2\text{O}_3^{2-}$	$\text{CO}_2$	$\text{NO}_3^-$
<i>Chlorobium</i> (a bacterium)	$\text{S}^{2-}$	$\text{CO}_2$	$\text{N}_2$ , $\text{NH}_4^+$

use sulphate as a terminal electron acceptor (thereby effecting its reduction) in a process analogous to the reduction of oxygen by respiration in aerobic organisms; they produce far more sulphide than they require for the synthesis of the sulphur amino acids. Accordingly, in this book, the form of sulphur used by an organism will always be specified.

Organisms which require forms of carbon more complex than  $\text{CO}_2$  (i.e. reduced forms of carbon) are referred to as heterotrophs; they must derive their supply of carbon either directly or indirectly from autotrophs. Here again there is an analogy between sulphur and carbon; some organisms are unable to synthesize the sulphur amino acids from any form of inorganic sulphur regardless of the oxidation state. Such organisms are entirely dependent on those that can.

## 2 Transformations of Inorganic Sulphur by Organisms

In the previous chapter it was established that organisms catalyse two fundamental transformations of sulphur: oxidation, an energy-generating process, and reduction, an energy-requiring process. It was also noted that most organisms capable of reducing oxidized forms of sulphur incorporate the sulphur they reduce into the sulphur amino acids and that these organisms provide a supply of cysteine and methionine for those organisms incapable of using inorganic sulphur. This chapter is concerned with the organisms that catalyse interconversions of inorganic sulphur, the reactions involved, the importance of the reactions in the life of the organisms and how the reactions are possible in relation to the principles of bioenergetics. In addition it will be seen that the growth of the various organisms is restricted to those habitats which provide suitable conditions for the operation of the appropriate biological reactions that they catalyse.

### 2.1 Oxidation states of sulphur

Sulphur can exist in a large number of oxidation states. Some of these are shown in Table 5. Sulphate is the most oxidized form of sulphur

**Table 5** Some inorganic forms of sulphur and the changes in free energy associated with their oxidation to sulphate by molecular oxygen.

<i>Form</i>	<i>Formula</i>	<i>Oxidation state</i>	<i>ΔG of oxidation to 1 mol of sulphate (kJ mol<sup>-1</sup>)</i>
Sulphate	SO <sub>4</sub> <sup>2-</sup>	+6	0
Dithionate	S <sub>2</sub> O <sub>6</sub> <sup>2-</sup>	+5	-139
Sulphite	SO <sub>3</sub> <sup>2-</sup>	+4	-200
Disulphite	S <sub>2</sub> O <sub>5</sub> <sup>2-</sup>	+4	
Dithionite	S <sub>2</sub> O <sub>4</sub> <sup>2-</sup>	+3	-327
Thiosulphate	S <sub>2</sub> O <sub>3</sub> <sup>2-</sup>	+2	-497
Elemental sulphur	S <sup>0</sup>	0	-502
Sulphide	S <sup>2-</sup>	-2	-715

(oxidation state +6) and therefore can only act as an oxidizing agent. It is one of the most stable forms of sulphur and is the most abundant form of sulphur available in the physical environment for use by organisms.



Under specialized local conditions other forms of sulphur can be present in substantial amounts. Waterlogged (anaerobic) soils, for example, frequently contain sulphur in lower oxidation states (e.g. sulphide and thiosulphate) and they contribute to the unpleasant smell of these soils. However, sulphur in lower oxidation states is not normally present in significant amounts in well-drained soils.

The free energy changes associated with the oxidation of the various forms of sulphur to sulphate by molecular oxygen are shown in Table 5. All these reactions, have a negative  $\Delta G$ , the value becoming increasingly more negative with decreasing oxidation states. Incidentally, oxidation does not imply that sulphate is formed; oxidation only entails an increase in oxidation state (e.g. thiosulphate to sulphite, sulphide to thiosulphate, etc.).

The sulphur amino acids essential for life contain sulphur in oxidation state  $-2$ . The same oxidation state is found in  $H_2S$  and the sulphides. It follows therefore that if an organism uses an inorganic sulphur source with an oxidation state greater than  $-2$  for the synthesis of the sulphur amino acids then the sulphur must first be reduced to oxidation state  $-2$ . Organisms that use oxidized forms of sulphur carry out the reduction and then subsequently incorporate sulphide into an acceptor molecule to form the sulphur amino acid cysteine. It follows that the input of free energy required to obtain a given yield of sulphide is greatest for those forms of sulphur with the highest oxidation states.

## 2.2 The major types of inorganic sulphur transformations catalysed by organisms

Organisms catalyse a wide variety of sulphur interconversions involving both oxidation and reduction. Each conversion must comply with the principles of bioenergetics. Clearly it is erroneous to consider, for example, the oxidation of sulphide to sulphate by one organism as the opposite process to the reduction of sulphate to sulphide in another. As in the formation of sugars from  $CO_2$  in photosynthesis and the oxidation of sugars to  $CO_2$  in aerobic respiration, the processes involved in sulphur oxidation and reduction involve completely different biological processes. Indeed, even the biological reduction of sulphate can be achieved by two distinctly different processes. The transformations of inorganic sulphur catalysed by organisms can be classified according to the biological and bioenergetic principles involved; these are summarized in Table 6.

## 2.3 Assimilatory sulphate reduction

The process of assimilatory sulphate reduction involves the expenditure of metabolic energy to reduce inorganic sulphate (or any