SCIENCE EDUCATION SERIES
No. 1

MINERAL NUTRITION OF PLANTS

by

M. A. T. DE SILVA
BSc, MSc, (Lond)

NATIONAL SCIENCE COUNCIL OF SRI LANKA
47/5 Maitland Place
Colombo 7.

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PREFACE

This review was prepared in response to an invitation by the Statutory Working Committee on Science Education Research of the National Science Council of Sri Lanka. It provides basic information on an important aspect of plant life. The Mineral Nutrition of Plants cover what may be called the inorganic phase of the nutrition of plants. Its coverage is very wide and hence only the most important principles have been treated in this treatise, illustrating wherever possible with examples drawn from the Sri Lankan scene.

The illustrative examples are chosen largely from the work on the coconut palm with which the author has been associated for over 20 years. Apart from reflecting the intimate knowledge of the subject in relation to this crop, it does not intend to belittle the enormous contributions made by many scientists working on other crops.

The presentation of subject matter is in a sequential order commencing with the sources of raw materials. Although this review is meant to provide supplementary reading material for G.C.E. Advanced Level students, it could also be useful for teachers and undergraduates.

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FOREWORD

The dissemination of scientific information is one of the main functions of the National Science Council. The National Science Council Journal provides a medium for the publication of scientific research papers, while "Vidurava," the quarterly science bulletin of the National Science Council, contains scientific articles of a general nature which are of interest to the public.

There is still a wide gap in the availability of reading material on scientific subjects of local interest. One result of this is that science students confine their reading only to their school notes and to the few available text books which are mostly published abroad. In an attempt to improve this situation, the Science Education Research Committee (SERC) of the National Science Council decided to publish a series of booklets on scientific topics of local interest and supplementary reading material for students and for general public. The authors who have been selected by the Committee to prepare these booklets are experts in there respective fields. The manuscripts that were submitted by the authors were examined by referees before being accepted for publication. The views expressed in these publications are those of the authors and not necessarily those of the National Science Council.

In conclusion I must thank the Science Education Research Committee of the National Science Council, and in particular its Hony. Director, Prof. K. Jayasena, for the work they have put in to make this project a success.

R. P. Jayewardene
Secretary-General
NATIONAL SCIENCE COUNCIL OF SRI LANKA

14 November, 1980.

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Chapter 1

INTRODUCTION

1.1 Historical

The inquiry into processes and factors which control plant life can be traced back to ancient times. These were indeed the simple trials on agricultural practices such as ploughing and tilling which brought about measurable increases of crop yields.

Van Helmot who lived from 1577 to 1644 A.D. is considered to be the first to conduct scientific experiments on plant life to investigate the factors which affect growth. He grew a willow shoot in soil moistened with rain water and determined its increase in weight after five years of growth. Although his main conclusions on the observations he made from these experiments were incorrect, his work provided the stimulus for further investigations. During the years that followed several other chemists and botanists continued their investigations, without still altering the age-old idea that earth, fire, air, water and nitrate should be the basic ingredients of plant growth.

The rapid developments in the field of chemistry in the nineteenth century opened a new chapter in the study of soils and plants. By the beginning of the century Theodore de Saussures had shown that carbon and elements of water combine together in the plant, and that nitrogen which was so essential for growth was obtained from the soil. He also noted that the composition of plant ash differed with the age of the plant and the type of soil in which it grew. Years later based on extensive observations, Liebig contributed a theory of mineral nutrition, in which he stated that crop production in a field increased or decreased in exact proportion to the increase or decrease in the supply of mineral matter from manure. He also propounded what is known as the Law of the Minimum, in which he stated that the deficiency or absence of one essential constituent, while all others being present, makes that soil infertile for all those crops for which that one constituent is indispensable.

By the end of the century the classical experiments of Lawes and Gilbert in Rothamsted, England and that of Boussingault of France had clearly established the fundamentals of plant nutrition. By this time the strong influence of nitrogen (N), phosphorus (P) and potassium (K) on plant growth was well recognized.

Further progress on plant nutrition awaited the development of new techniques of growing plants under controlled conditions in sand and water cultures. With these developments during the first quarter of the twentieth century, the essentiality of the 10 major elements, C,H,O,N,P,K,Ca,Mg,S and Fe became firmly established. During this period the giant strides made in the fields of organic and physical chemistry, stimulated intensive studies which finally resulted in the understanding of the more important physico-chemical and bio-chemical process which take part in nutrient metabolism.

1.2 Criteria of essentiality of mineral elements

The introduction of nutrient culture procedures for the study of mineral nutrition provided a convenient method to determine the extent to which an element is essential to normal plant growth. Nevertheless, even without such precise methods, the early chemists were able to determine the indispensable nature of the ten major elements, chiefly because of the larger requirements of these for plant growth. However, the turn of the present century saw the rapid increase in a list of elements which were essential for normal growth of plants, but required in amounts less than 1.0 part per million in solution cultures. These were referred to as trace elements. The essentiality of these had to be established by very precise methods and this led Arnon[*] in 1950 to outline the criteria for recognising essentiality. These requirements briefly are as follows:

(a) The absence of that element should prevent normal growth and reproduction of a plant.

(b) The function of that element cannot be performed by any other element.

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[*] D.I. Arnon, Criteria of essentiality of inorganic nutrients for plants with special reference to molybdenum. *Lotsya* 3, 31 - 38 (1950)

(c) The effect of that element must be direct, and not be the result of effects of other elements.

Although, in a general sense these criteria were adequate, a few special cases required a further explanation before the universal nature of essentiality could be established. Thus, it was soon realised that some elements could be at least partially replaced by others of similar valency. For instance even a major element such as potassium, has been partly replaced by sodium in certain plants. There are also certain elements such as silicon, aluminium, vanadium, chloride and cobalt which are beneficial for certain species of plants only. Molybdenum which is generally considered universally essential for plant growth can be replaced almost completely with vanadium in certain species of Azotobacter, while in the algae Scenedesmus, molybdenum can be totally done away with if nitrogen is supplied as urea instead of as nitrate. Such exceptional circumstances had also to be given consideration, before essentiality of an element could be firmly established.

1.3 General classification and nomenclature

As pointed out earlier the essentiality of C,H,O,N,P,K,Ca,Mg,S and Fe were clearly recognised by the beginning of the present century. However, with the discovery that elements such as manganese, copper, zinc, boron and molybdenum were also equally important and essential for normal growth, but required in smaller quantities, a broad classification of essential elements was introduced. In this classification, C,H,O,N,P,K,Ca,Mg,S and Fe were generally referred to as 'major' elements while Mn,Cu, Zn,B and Mo were called 'rare' 'trace' or 'minor' elements, implying that the former group was more 'important' than the latter group.

Arnon* however, explained that Mn, Cu, Zn, B and Mo were indispensable to plant growth and were required in measurable quantities. Therefore they were neither "trace" elements nor elements of minor importance. Further these elements were also not "rare" elements in a chemical sense.

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*D. I. Arnon. A memorandum regarding nomenclature. *Lotsya* 3, 40 (1950)

On these arguments, he said that the first group of elements should best be referred to as Micronutrients while the latter could be called Micronutrients. Micronutrients were defined as those nutrients which were required in amounts less than 1.0 part per million in culture media. Under this classification iron had to be considered as a micro element because it has been shown that, provided supplies are replenished at reasonable intervals, plants will grow normally with about 1.0 part per million of iron in sand and water culture media. The undisputed distinction between these two groups of essential elements in quantitative terms, is indeed the main reason for the universal acceptance of this classification.

1.4 Fundamental features of plant nutrition

The essential feature in the nutrition of plants is the ability of living plant organisms to take up from soil, water and air, the necessary primary ingredients and transform these into complex compounds. The chain of events which take place during this process involves complex physico-chemical reactions, some of which are only partly understood. The fact that no less than fifteen elements (viz. C,H,O,N,P,K,Ca,Mg,S,Fe,Mn,Cu,Zn,B and Mo) participate in these processes indicates the magnitude and complexity of the mechanisms involved. Among the essential elements, carbon, hydrogen and oxygen are obtained almost entirely from water and air, and are hence not regarded as mineral nutrients. Mineral nutrition of plants would therefore involve only those chemical elements which are normally taken up by plants from the soil.

The sequence of events which take place during the mineral nutrition of plants can be conveniently divided into four stages, each of which is governed by a given set of principles.

In the first stage, by a series of physical and chemical process the essential chemical elements present in the soil are transformed and made available to plants. The soil in which most plants grow is an enormous store of chemical elements, some of which exists in a relatively free state and others in a combined state. Elements which are the most abundant are not the elements which are most needed for plant growth. Hence the plant has to use a special mechanism to screen and take up only those elements it requires most. The second step is therefore the process by which essential nutrients are selectively absorbed or taken up by the roots of plants.

In the next step the nutrients taken up may be metabolised by the tissue of the roots, or these may be translocated to the shoot.

In the final stage depending on the functions, the nutrients are either converted into complex chemical compounds, or they catalyse biochemical reactions, or are involved in the maintenance of ionic balance in cells and tissues.

In the following sections it is proposed to review briefly the four stages referred to above, which constitutes the story of the mineral nutrition of plants.

Chapter 2

CHEMICAL COMPOSITION OF SOILS

2.1 Chemical composition of the earths crust

Some 14 chemical elements make up 99.5 per cent of the earths crust. Of these, oxygen and silicon make up about 74 per cent in the average composition. If considered by volume, oxygen makes up 90 per cent of the earths crust, and most of it is combined with silicon and aluminium in minerals as shown in the table below.

TABLE I

Average chemical composition of the earths crust*

Element	%	Oxide	%
O	46.5	SiO_2	59.07
Si	27.6	Al_2O_3	15.22
Al	8.1	Fe_2O_3	3.10
Fe	5.1	FeO	3.71
Ca	3.6	CaO	5.10
Mg	2.1	MgO	3.45
Na	2.8	NaO	3.71
K	2.6	K_2O	3.11
Ti	0.6	TiO_2	1.03
P	0.12	P_2O_3	0.30
Mn	0.09	MnO	0.11
S	0.06	H_2O	1.30
Cl	0.05		
C	0.04		

*Data from F. W. Clarke and H. S. Washington. U.S. Geol. Survey Prof. Paper 127 (1924). Quoted by M. L. Jackson *in* "Chemistry of the Soil" (*ed.* F. E. Bear) p 74. Reinhold Publishing Corp. (1964)

2.2 Soil formation and soil minerals

The inorganic constituents of soils are mainly present in a limited number of inorganic compounds of definite crystal structures. These are generally referred to as soil minerals. Soil minerals are formed from the parent rock material, through a process called weathering which is in fact a combination of physical, chemical and mechanical process. The composition of a soil mineral can vary greatly, because the different elements or ions present in a given crystal structure can be substituted by isomorphous elements. Many of the so called micronutrients are present in soil minerals by isomorphous substitution.

As the process of weathering proceeds the rate of release of inorganic elements (in ionic state) begin to slow down and finally in soils with highly weathered minerals the release of exchangeable ions becomes too slow and insufficient to support intensive agriculture. It is at this stage that fertilizers are required to increase the yields of agricultural crops.

2.3 Availability of mineral nutrients

The soil is a heterogenous medium made up of solid, liquid and gaseous components in different proportions. In most common soils the solid component which is made up of the minerals and organic matter, makes up about one half of the soil volume. The other half is made up of the soil solution and air (See Figure 2.0).

A small but an important fraction of the various elements in the soil minerals occur in a form in which they can be replaced by other elements. This fraction in the soil, usually referred to as "exchangeable ions", play a very important role in plant nutrition. The supply of this easily exchangeable fraction of ions is maintained by the gradual weathering of rock minerals; but the rate at which this occurs, and the chemical 'activity' of the ions which go into solution depends on the nature of minerals present. Hence it can be said that the mineral composition of the soil can have a very important bearing on the fertility of a soil.

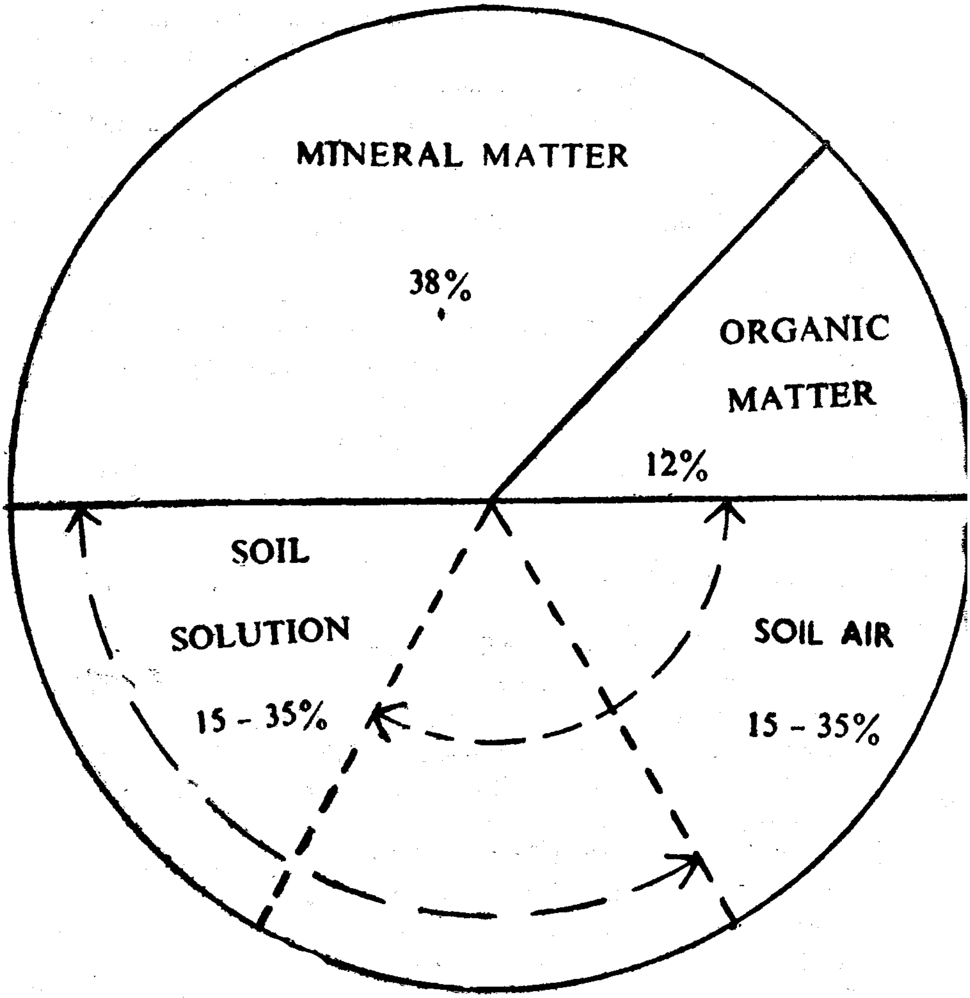

Figure 2.0 Diagram showing broadly the distribution of materials in the Earths Crust

However, the 'activity' or the concentration of a cation in solution does not provide any information on the supplying power of these nutrients. Since at the same 'activity' of a given cation, the clay-mineral association of a soil can supply the plant much more of that cation than from a true solution. This is chiefly because apart from the nature and concentration of ions present in the medium, their availability to plants is governed by several other factors, of which the following may be considered the more important:–

(a) Nature of the soil colloid
(b) Cation and Anion exchange phenomena
(c) Soil pH
(d) Fixation
(e) Effect of complementary ions

2.3.1 Soil colloid

The important chemical properties of soils are due to a fraction called the soil colloid which is made up of inorganic and organic matter. The inorganic fraction is contributed by the clay particles, i.e. those inorganic particles with a diameter $< 2\mu$. On the other hand the organic fraction is contributed by dead plant matter together with the excretions and remains of soil micro-organisms.

The clay particles or clay minerals as they are better known possess the property of adsorption* and exchange of cations, and it is this unique property which largely determines the capacity of a soil to store the essential plant nutrients. These properties of the soil of course depends on the type of mineral, size of the particles and the binding forces which exist in the colloid.

The chemical, physical and biological properties of soils are also affected by the organic matter content. Its importance lies in its ability to increase the exchange capacity of cations and anions in soils. The organic fraction in the soil also assists in increasing the solubility

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*Adsorption is a physico-chemical process in which one or more ions accumulates on a solid, caused by exchange of ions or other reactions.

of phosphorus in soils and making it available to plants which would otherwise be converted to non-available forms.

2.3.2 Cation and anion exchange phenomena

The cations and anions present in the soil reversibly exchange places between the solid particles and the liquid phase, and also among solid particles. This property of ion exchange is almost entirely due to the unique physical and chemical properties of the soil colloid.

The soil colloid normally has a predominant negative charge, but in many of its chemical properties it behaves as an amphoteric medium, because it attracts and binds both negatively charged and positively charged ions. The common cations which take part in ion exchange are Ca^{++}, Mg^{++}, H^{+}, $Na,^{+}$ and NH_4^{+} while the common anions which take part in this process are SO_4^{--}, Cl^{-}, NO_3^{-}, $H_2PO_4^{-}$, $H\ PO_4^{--}$, HCO_3^{-}.

An important measure of the chemical activity of the soil is the Cation Exchange Capacity (CEC), which is defined as the amount of a cation (in milligram equivalent) bound to 100 grams of a given soil at pH 7. The CEC of some typical soils of Sri Lanka are given in Table II.

The exchange property of cations varies with the size, charge and hydration of the cations. Often these are adsorbed on the broken chemical bonds of silica-alumina units of mineral particles, or may replace hydrogen of available hydroxyl (OH) groups. The ability of cations to replace another in the soil colloidal particles depends on the type of cation, its concentration, the nature of the anion associated with the cation, and nature of the colloidal particle. It has been shown that ions with higher valency have a greater replacing power, and are also more firmly adsorbed. It has also been shown that among ions with similar valency, the replacing power is greater in the larger ions. However, hydration of an ion decreases this power of replacement.

Except for information on the phosphate radical, less is known on the exchange and adsorption properties of anions. Adsorption of anions on clay minerals probably take place partly through the replacement of OH groups, and partly through other anion-exchange sites. A change of pH has a profound effect on the exchange of anions. The capacity of anions for exchange and adsorption also seem to be affected by the presence of compounds of aluminium and iron.

2.3.3 Soil pH

The acidity of a soil is due to the presence of hydrogen ions. The pH of soils vary from about 4.0 in the highly acidic soils to over 9 in the soils, formed from coral or other calcarious materials. The pH of some of the typical soils of Sri Lanka are given in Table III. As would be expected the pH of the soil has a profound influence on the availability of plant nutrients. In general the availability of iron, manganese, copper, zinc and boron increase with decrease of pH up to about 4.5. Macro-nutrients on the other hand are more available in the pH range 6 to 8. The chart prepared by Emil Troug to show the change in the availability of plant nutrients with change of pH is given in Figure 2.1.

2.3.4 Fixation

Cations and anions in the soil colloid, reversibly exchange positions during weathering of soil minerals. However under certain conditions ions present in the soil solution can enter irreversibly the crystalline structure of minerals and become unavailable for plants. This process by which plant nutrients are changed to less soluble and less available forms is called "fixation". Phosphorus is one of the important plant nutrients which undergo such fixation. It is believed that fixation of phosphorus takes place in two stages. In the first stage the phosphate radical is adsorbed on the colloidal particles, and later undergoes isomorphous substitution with radicles in the crystal structure. In this condition phosphate is not available to plants.

The rate and magnitude of fixation of an element depends on several factors, of which one is the type and chemical character of the soil. In a study carried out in Sri Lanka* on two red-yellow soils, it was found that the phosphorus fixation capacity of one soil (red-yellow podsol) was more than thrice that of the other soil (red-yellow latosol).

Among cations potassium, magnesium and ammonium are known to be fixed more readily than calcium and sodium.

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*C. S. Weeraratne and V. Premakumar. Some Studies on phosphorus fixation in soils. *Proc. Ceylon Assoc. Advan. Sci.* Part I, 59 (1973)

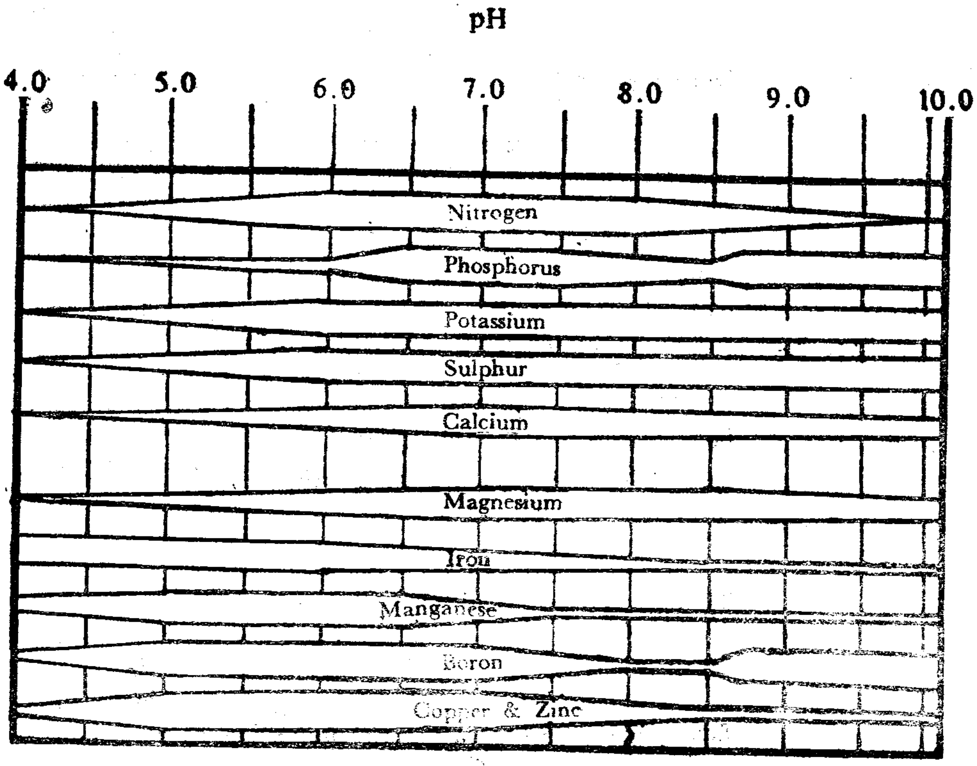

Figure 2.1 Diagramatic representation of the availability of nutrients with change of pH (After Truog*)

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*E. Truog. Lime in relation to availability of plant nutrients. *Soit Sci.* 65, 1 - 7 (1948).

2.3.5 Complementary ion effect

During absorption of nutrients by plant roots, the soil solution gets replenished by exchangeable ions from the soil colloid. However, the ease with which this occurs depends on the nature of other ions present in the colloid. In other words, the release of ions to the soil solution from the exchange sites of colloidal particles is controlled to some extent by the other ions present in these colloidal particles. This is called the "complementary ion-effect" According to the complementary ion-principle, the proportion of a given cation released from exchange sites of a colloid, increases with the strength of the chemical bond holding a complementary ion on this colloid. This shows that, higher the strength of the chemical bond of the complementary ion, the greater the release of the required cation.

The ease with which cations may be released from exchange sites of natural soils can be placed in the following order: Na > K > Mg > Ca. From this it can be inferred that a soil containing higher exchangeable calcium will favour the release of a greater proportion of potassium than magnesium. This may be one of the reason for the frequently noted deficiency of magnesium seen when available potassium is high.

TABLE II

Cation exchange capacities of some soil groups of Sri Lanka*

	Soil group	General distribution (districtwise)	CEC m e /100g soil
1	Reddish Brown Earth	Anuradhapura, Puttalam, Moneragala, Vavuniya, Trincomalee, Hambantota	10 - 20
2	Solodized Soloetz	Mannar, Jaffna, Trincomalee, Puttalam	15 - 30
3	Solonchaks		10 - 25
4	Non-Calcic Brown Soils	Amparai, Batticaloa, Polonnaruwa, Trincomalee	5 - 15
5	Immature Brown loam	Kandy, Kegalle, Kurunegala	10 - 20
6	Red Latosols	Jaffna, Mannar, Puttalam Vavuniya	2 - 6
7	Yellow Latosols		
8	Calcic Red Latosols	Jaffna	15 - 20
9	Grumusols	Mannar, Jaffna	55 - 65
10	Soils or recent marine marine calcareous sediments	Jaffna	1 - 25
11	Alluvil Soils	All districts	5 - 50
12	Regosols	Batticaloa, Amparai, Puttalam, Mannar, Trincomalee, Jaffna	<2 —
13	Red-Yellow Podzolic Soils	Kandy, Nuwara Eliya, Badulla, Kegalle, Matale, Ratnapura, Moneragala, Colombo, Kalutara, Galle, Kurunegala, Matara	8 - 15
14	Reddish-Brown Latosolic Soils		2 - 20

TABLE III

pH values of some soils of Sri Lanka

	Location	Soil type	Soil pH (1:50H O)
1	Lunuwila	Sandy loam	5.6
2	Kudaweva	Cinnamon sand	5.8
3	Galewela	Brown loamy soil	6.1
4	Lunuwila	Clay loam	5.2
5	Bingiriya	Sandy loam	5.7
6	Nattandiya	Lateritic loam	5.5
7	Kottawa	Lateritic gravelly soil	4.5

*After K. A. de Alwis and C. R. Panabokke Handbook of the soils of Sri Lanka (Ceylon). *J. Soil Science Society of Ceylon,* 2 (1973)

Chapter 3

SOIL-PLANT RELATIONSHIP

3.1 The root environment

One of the most elusive problems in the study of mineral nutrition of plants is the mechanism by which plants take up nutrients. The phenomenon of nutrient uptake is intimately associated with the chemical environment of the plant root in the soil. The plant root as it grows, penetrate the soil medium and hence comes in close contact with both the solid soil particles and the liquid soil solution. On theoretical assumptions, a convincing explanation of ion absorption by plants would be the straightforward diffusion of ions from the solution to the root through its plasma membrane. However, experiments have shown that a knowledge of the concentration of cations in the soil solution does not provide any information about the supplying power of these ions to plants.

It is now recognised that roots take up nutrients from three possible sources, i.e. (a) the soil solution, (b) the exchangeable ions and (c) the easily decomposable minerals. The importance of each of these sources as a supplier of plant nutrients varies with the different nutrients. For example for nitrogen, the amount of nitrate present in the soil solution and its rate of replenishment is more important than the total nitrate present in the soil. While for potassium the requirement has to be met both from the soil solution and the exchangeable K. In the case of phosphate which is present in the soil solution in minute quantities (about 1.0 part per million), rapid renewal from other sources becomes necessary to maintain growth of plants.

3.2 Movement to cations to root surfaces

In 1962, Viets* introduced the idea of chemical pools in soils. In general, he said that nutrients exist in 5 different forms in the soil. These he illustrated by concentric circles as shown in Figure 3.0.

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*F. G. Viets. Chemistry and availability of micronutrients in Soils. *J. Agric. Food Chem.* 10, 174 - 178 (1962)

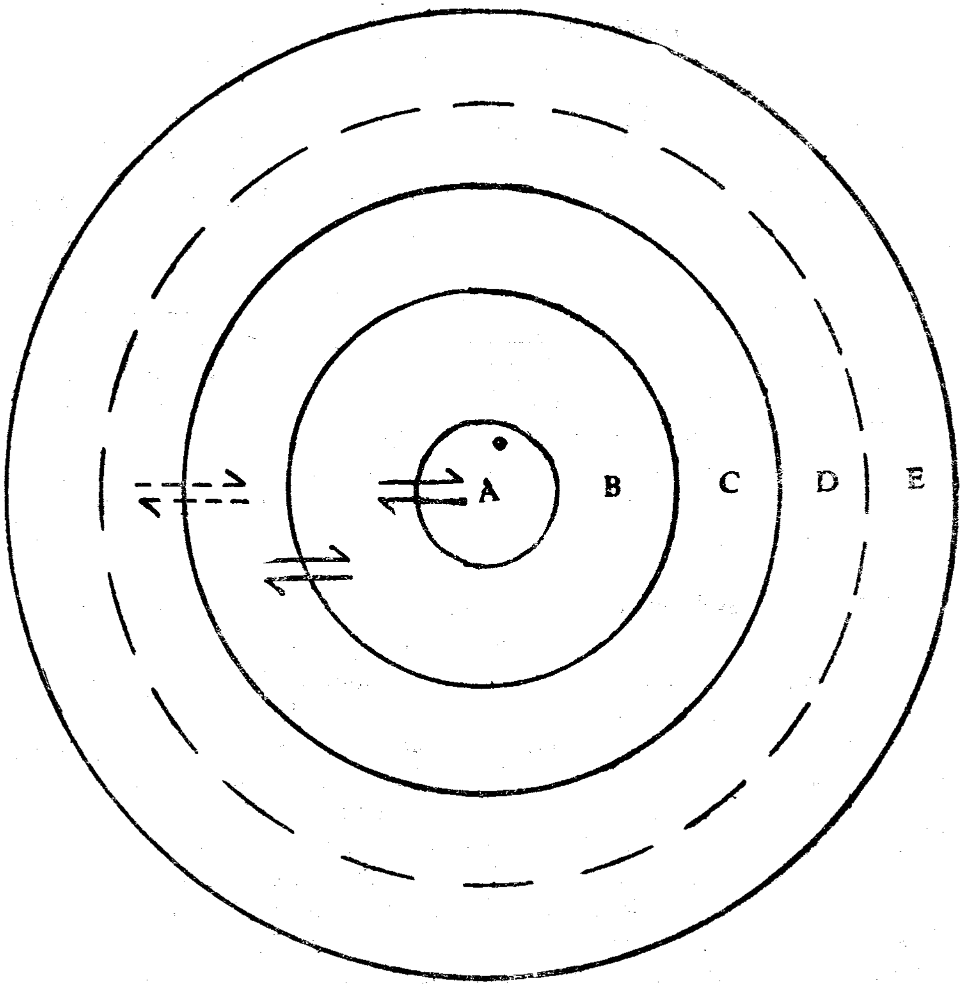

***Figure* 3.0 Diagramatic representation of the pools of nutrients available to plants. (After Viets)*

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*F. G. Viets. Chemistry and availability of micronutrients in soils. *J. Agric. Food Chem.* 10. 174 - 178 (1962).

Pool C. probably represent a part of the readily decomposable minerals. According to this author, the pools A, B and C are in reversible equilibrim and are hence the most vital for plant absorption. When the plant root takes up bases and anions from the soil solution, the equilibrim shifts and exchangeable ions are released into the solution. This in turn is replenished from the pool C, and to a lesser extent from pool D.

Within the soil medium, nutrients are believed to reach the root surface through the operation of three processes, i.e. (a) root interception, (b) mass flow and (c) diffusion. Root interception is the growth of roots towards nutrients. Mass-flow is the process by which nutrients are brought to upper layers by the mass movement of soil water, while diffusion is the slow process by which cations are brought near the root surface by exchange phenomena on soil particles.

3.3 Cation exchange capacity of roots

The discovery of the existance of a cation exchange property in roots of plants have provided a clue to the mode by which nutrients get adsorbed on the root surface and finally get absorbed. The cation exchange capacity of roots has been attributed to the presence of an acidic colloid on the root surface, which is generally referred to as the "root-colloid". Thus in this process cations are believed to be exchanged between the soil colloid and the so-called root colloid, resulting in an accumulation of cations on the root surface. The cation exchange capacity of roots is generally high in dicotyledons than in monocotyledons, and has been shown to increase with increase in available nitrogen.

Plants with higher cation exchange capacities in roots show a greater affiniting for divalent than for monovalent cations. This is one of the main reasons for a greater uptake of calcium and magnesium by dicotyledonous plants. In such plants therefore monovalent cations such as potassium would require a higher concentration(or activity) in the soil to enable their entry into the root. The reciprocal effects are seen in monocotyledonous plants, where the lower cation exchange capacities in roots results in a higher attraction for monovalent cations.

It is well recognised that nutrient absorption by plants vary to a considerable extent among the different species, and for that matter even within the same species of plants, varietal differences could exist. This fact was elegantly demonstrated by J. C. Brown and his colleagues in 1958*. In their experiments they grew two varieties of soya bean called PI and "Hawkeye" in highly alkaline soils, and after the primary laves had emerged, the shoot of one variety was grafted to the root stock of the other variety (inter-varietal grafts). They discovred that the shoots growing on the "Hawkeye" root stocks were green, while those on PI root stocks had developed chlorosis due to a deficiency of iron. These results showed that when available iron was low due to alkaline soil conditions, the root stock of the "Hawkeye" variety was more efficient than the root stock of the PI variety of soya bean, in the absorption of iron.

Similar examples could be found in many other plants. For instance in tea plants differences have been seen between clones, of their ability to absorb nitrogen from the supplying solution**. Similarly it has been observed in coconut palms (var. *typica*), that the absorption of magnesium by one progeny was distinctly more efficient than that of another progeny, indicating the existence of two genotypes.***

3.4 Mechanism of ion absorption by roots

One of the unique features in the nutrition of plants is the ability of their absorbing organ (roots) to take up ions selectively from the growth medium. It is thought that the root colloid and soil colloid compete with each other for cations, and hence the direction in which cations move, will depend on the differences in the cation exchange capacities of the root and soil.

The uptake of ions by plant roots takes place in two stages. In the first stage, due to the operation of the CEC s' of the root and

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*J. C. Brown *et al.* Iron chlorosis in soya bean as related to the genetype of root stock. *Soil. Sci.* 56, 75-82 (1958).

**S. Krishnapillai and U. Pethiyagoda. The nitrogen nutrition of young tea plants in sand culture. *Proc. Ceylon Assoc. Adv. Sci.* Part I, 43 (1972).

***M.A.T. de Silva. *et al.* Nutritional studies on initial flowering of coconut (var *typica*). I The effect of magnesium deficiency and Mg-P relationship. *Ceylon Cocon. Q.* 24, 107-113 (1973).

soil, cations are adsorbed on the root surface. This process takes place by normal physico-chemical methods and is not related to the metabolic activities of the plant. Hence this stage is generally referred to as "non-metabolic" uptake of a nutrient. The second stage in nutrient uptake is called ion accumulation. This process is governed by metabolic activities of the plant, and more specially by respiration or the energy producing process of metabolism. Hence this phase is generally referred to as "metabolic" uptake.

The mechanism by which ions adsorbed and accumulated on the root surface is transported through the cell wall into the cells and finally to the conducting tissues is not fully understood. It has been suggested that certain chemical compounds rich in energy, assist in the transfer of ions across permeability barriers. Experiments have shown that among the many organic compounds present in the cell walls or roots, the concentration of malic acid is the most easily affected during the process of ion absorption. It has been implied that this substance may be partly responsible for the translocation of absorbed ions.

Chapter 4

TRANSLOCATION AND DISTRIBUTION OF NUTRIENTS IN PLANTS

4.1 Ionic interactions

It has been pointed out that the abundance of mineral nutrients in the soil was not an index of their availabilitiy. Likewise the magnitude of nutrient uptake is not always a measure of their availability. This is chiefly because, the mechanism of absorption of nutrient ions is not entirely governed by simple physico-chemical laws.

One of the important factors which affect the uptake of nutrient ions is the interference caused by ionic interactions. Although the concept of chemical activities of nutrient elements has been used to explain the driving force for the movement of ions from the soil medium to the root tissue, the causes for ionic interactions are not fully understood. Clearly different mechanisms are responsible for the various examples of ionic interactions.

When the absorption of one nutrient is increased by the presence of another, the relationship is called "synergism". The opposite effect, where the increasing presence of one element tends to decrease the absorption of another is called "antogonism". It so happens that on certain occasions two elements which are antogonistic in one plant, or under a given set of conditions can be synergistic in another plant or under a different set of conditions in the same plant.

Almost all mineral elements required by plants are subject to ionic interactions during absorption, which results in disproportionate uptake of nutrients. A few common examples are: potassium versus magnesium, nitrogen versus potassium or phosphorus and iron versus manganese. In the following sections an attempt will be made to illustrate these reactions from observations made in Sri Lanka.

4.1.1 Interaction of potassium with magnesium

In the exchange capacity of a soil a 2:1 ratio for K:Mg is considered optimum for the proportionate uptake of these two nutrients. If the ratio exceeds this value in the soil then the plant uptake of magnesium decreases. Such situations occur frequently through indiscriminate use of fertilizers and also as a result of leaching*.

During the period 1950 to 1960 magnesium deficiency became evident in several localities in the South and South-western regions of Sri Lanka, where traditionally coconut palms have been grown without any fertilizer treatments. In the early 1950's when a scheme was introduced to provide fertilizers for coconut plantations at subsidized prices, the use of inorganic manures containing exclusively nitrogen, phosphorus and potassium became very popular. The liberal use of such fertilizers in a heavily eroded lateritic gravely soil, thus provided conditions for reducing the availability of magnesium.

The causes of this disturbance can be explained fairly well by the "valency effect" discussed earlier. Thus the coconut palm being a monocotyledenous plant, would take up preferentially more of the monovalent potassium than the divalent magnesium. In such circumstances to compete and displace potassium, the divalent nutrients need a higher concentration; which is evidently not available in the leached wet zone soils.

In these investigations it was interesting to note that regardless of the concentration of individual ions, the sum total of K, Mg and Ca in milligram equivalents per 100 grams of plant material was remarkably constant, indicating that under such conditions, unbalanced uptake of cations occur probably to ensure electrical neutrality of the system. The data given in Table IV, from an experiment carried out at the Coconut Research Institute of Sri Lanka illustrates this phenomenon.

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*Leaching is the process in which soluble nutrients are dissolved, specially during heavy rains, and drained off from the surface soil.

4.1.2 Interaction of nitrogen with phosphorus

The interaction of nitrogen with phosphorus has been frequently observed in plantations which have been opened up in recently cleared forest lands. Such lands are generally rich in nitrogen, which leads to an imbalance in the uptake of nitrogen in relation to phosphorus. Young coconut palms growing under such situations become prone to infections of fungul diseases. Hence the manifestation of a N-P interaction is the occurence of a weakened and vulnerable condition resulting in foliar infestations of fungal diseases such as "leaf blight".

4.1.3 Interaction of nitrogen with potassium

The relationship of nitrogen with potassium is of particular interest in the nutrition of coconut palms, because at times this interaction appears to be antogonistic, while at other times, it appears to be synergistic. Thus when the availability of potassium is low, a relatively higher uptake of nitrogen occur in coconut palms causing a decline in the production of fruits. On the other hand when the available potassium is high, increasing quantities of available nitrogen bring about a striking increase in the yield. The data from an experiment on coconut palms summarised in the Table V, illustrate this interaction.

4.1.4 Inter-relationships of iron and manganese

The relationship between Fe and Mn in the nutrition of plants has been the subject of an intensive investigation. Though most of the observations indicated a strong antogonistic effect between these two elements, there have been a few reports where the reverse effects have been observed. The investigations of Somers and Shive* with soya bean plants and their interpretation of the results aroused deep interest. They claimed that iron is active in the ferrous form in plants, but if iron is absorbed in the

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*I.I. Somers and J. W. Shive. The iron-manganese relation in plant metabolism. *Plant Physiol.* 17, 582-602 (1942)

TABLE IV

Mean leaf nutrient contents of fronds (6th frond) taken from magnesium deficient coconut palms*

Location	Condition of palms	Fertilizer treatment	Mean leaf nutrient content in milli equivalents per 100g.			
			K	Ca	Mg	K+Ca+Mg
Mattegoda Estate, Polgasowita	Healthy	NPK	39.8	10.7	12.6	63.1
	Yellow	None	26.2	15.0	27.1	68.3
do	Yellow	NPK+MgSO	35.7	12.9	12.3	60.9
do	Yallow	NPK+Dolmite	35.9	13.3	13.3	62.5
do	Yellow	NPK+Cattle manures	37.4	10.6	13.3	61.4
Walgama Estate, Pannipitiya	Yellow	NPK only	46.6	16.8	4.1	67.4
do	Yellow	NPK+1.0lb. MgSO	32.9	19.7	14.6	67.2
do	Yellow	NPK+2.0lb. $MgSO_4$	34.9	12.6	15.4	62.8
do	Yellow	NPK+3.0lb. $MgSO_4$	32.6	11.4	13.8	57.7

TABLE V

Results of a fertilizer experiment on coconut palms showing the effect of an interaction between nitrogen and potassium on yields of copra (given in Kg per hectare)**

Nitrogen treatments / Potassium treatments	No Nitrogen	0.227 Kg Nitrogen	0.454 Kg Nitrogen	0.681 Kg Nitrogen
No Potassium	1415	1213	1220	1046
0.681 Kg Potassium	1723	1902	2051	1881

ferric form, it is rapidly reduced to the ferrous form by a powerful reducing agent, which they said was none other than manganese. These research workers went a step further and said that the symtoms of iron *deficiency* were similar to that of manganese *toxicity* and *vice versa*, and concluded that the two types of symptoms were identical being produced by the same disorder,– the disturbed iron to manganese ratio.

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* After M. A. T. de Silva. Magnesium deficiency and nutrient imbalance in coconut palms. *Proc. Ceylon. Associ. Adv. Sci. Part* I, 20 (1965)

b**After T. S. Balakrishnamurti. Report of the Soil Chemistry Division. *Ceylon Cocon. Q.* 24, 23 - 29 (1972).

These arguments were strongly contested by several scientists among whom was E. J. Hewitt.* The convincing and critical evidence provided by Hewitt indeed disproved almost entirely the theory enunciated by Shive and Somers. Nevertheless the fact remained that the behaviour of iron in plant nutrition specially in relation to manganese remained unexplained and was a setback to the understanding of events in metabolism. It became evident however, that the antogonistic effects between iron and manganese was observed only in plants such as soya bean and oats, which were susceptible and sensitive to small changes in availability of these nutrients.

In recent years similar studies have been initiated with coconut seedlings to study the effects of iron and manganese on growth and uptake.** Special techniques were used to extract non-combined ferrous and ferric forms of iron from root tips of treated plants. By this means it was demonstrated that in the case of coconut palms, excess of iron taken up in the ferrous form, is converted to the less soluble ferric form and is held back in the root. In this condition iron is said to be immobilized in the roots.

4.2 Translocation of nutrients

Translocation is the process by which nutrients are moved or transported from the point of absorption (i.e. the root in most cases) to the point where these are metabolized. However, it can also mean the movement of nutrients within the plant from one site to another. The organs of active metabolism are usually the feeder roots, leaves, apical buds and the reproductive shoots. Although the methods by which nutrients are translocated are not fully understood, it is possible that several mechanisms are involved in this process.

The absorption and movement of phosphate were investigated in coconut palms using the modern techniques of radio-active isotopes***. The fact that the coconut palm can produce a continuous flow of sap (toddy) from its spadices on tapping, rendered it uniquely amenable to this investigation.

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*E. J. Hewitt. The role of mineral elements in plant nutrition. *Ann. Rev. Plant Physiol* 2, 25-52 (1951)

**M. A. T. de Silva. Some observations on the iron and manganese nutrition of coconut seedlings. *in* "Coconut Research and Development", (*ed.* N. M. Nayar) Wiley Eastern Indio Ltd., New Delhi (1980).

***D. A. Nethsinghe. Reoport of the Soil Chemist. *Ann. Rept. Cocon. Res. Inst. for* 1960. 12-31 (1962)

In the experiments carried out in 1960, 2.5 litres of a solution containing 5 millicuries of radio-active phosphorus (P_{32}) in 14 per cent KH_2PO_4, were sprinkled round the base of an adult coconut palm which was being tapped for toddy. The specific activity of phosphorus (i.e. the ratio of active to non active phosphorus) in the exudates clearly showed that for a 25 foot tall palm the applied phosphorus could be translocated from the root to the crown within 2 hours of its application. This experiment convincingly demonstrated the high mobility of phosphorus in plant tissues.

Several other significant observations were made in this experiment, Thus it was found that the absorbed phosphorus accumulated mostly in the young spadices and more specially in the female flowers (buttons) and spikes. In developing fruits, accumulation occured more readily in the immature than in the mature ones.

4.3 Mobility of nutrients

When plants are adequately provided with their requirements of mineral nutrients there is no cause for concern about the mobility of ions within the plant. However, when the supply of a nutrient becomes inadequate to meet the normal requirements, the ability of such a nutrient element to move from an area where it is less useful to an area where it is in greater demand (i.e. its mobility) becomes very important.

At times this mobility may assume such proportions that tissues from which a nutrient is withdrawn may become deficient in that nutrient resulting in the appearance of externally visible symptoms. Thus the appearance of visual symptoms of deficiency in mature plants tissues, is indicative of the deficiency of a *mobile* element. Likewise the appearance of deficiency symptoms in tender immature tissues is indicative of the deficiency of a *immobile* element. Among macro-nutrients nitrogen, potassium and magnesium are considered to be mobile, while phosphorus and calcium are relatively immobile. In the case of micro-nutrients though not much work has been done, iron has been considered by some scientists to be very immobile.

As early as in 1916, Gile and Carrero* demonstrated by means of very simple experiments the immobile nature of iron. For example, in one experiment they transferred plants growing in an iron-containing medium to a minus-iron medium, and showed that the newly produced leaves were chlorotic (yellowish in colour) due to the immobility of iron from older leaves to the newer ones. In another experiment they painted half of a young chlorotic leaf with a dilute solution of iron and showed that restoration of the green colour occured only on the painted part of the leaf.

However, recent studies indicate that mobility of a nutrient ion is governed mostly by factors such as pH, occurrence and concentration of other ions, and presence of complex organic molecules or radicles.

4.4 Distribution and accumulation of nutrients

An evaluation of the chemical composition of various plant components is the basic step in the study of the mineral nutrition of a plant. The significance of such data in diagnosing and correcting nutrient disorders will be discussed in greater detail in the final section of this monograph. But for the present the general order in the distribution of nutrient elements will be examined partly to illustrate the overall patterns, and partly to demonstrate the distortions that may occur as a result of other factors.

By the use of radio-active isotopes it has been possible to obtain a fairly accurate picture of the distribution and accumulation of phosphorus in the crown of the coconut palm**. The Table VI gives the specific activity of phosphate in leaflets from fronds of different degrees of maturity.

The results clearly show that the youngest and the most mature fronds have the lowest specific activity, while in leaf positions 3 - 13 the content remains fairly uniform.

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*P. L. Gile and J. O. Carrero. Immobility of iron in the plant. *J. Agric. Res.* 7, 83 - 87 (1916)

**D. A. Nethsinghe. Report of the Soil Chemist. *Ann. Rept. Cocon. Res. Inst. for* 1961. 11-24 (1963).

TABLE VI

Specific activity of phosphate in coconut leaflets, in counts per minute per mg P_2O_5*

Section of frond \ Leaf position	1 Youngest	2	3	4	6	9	13	Mature
Tip	20	70	95	92	89	91	85	33
Middle	13	45	74	73	80	81	80	19
base	13	17	53	49	65	68	61	13

In this same series of experiments, a study on coconut water (sometimes referred to as 'coconut milk', liquid endosperm etc.) showed that the specific activity of phosphate 30 days after application increased with decrease in maturity of fruit up to the "kurumba" stage.

Although the mineral composition of plant components in a given species takes a regular pattern often this pattern is disturbed due to the influence or inter-action of external factors such as the pH of the soil medium, availability of nutrients and ionic interactions. The observations of two experiments carried out on coconut seedlings in sand cultures is given in Figures 4.0 and 4.1 to illustrate the changes that occur in the distribution of nutrients in plant components when subjected to, (a) deficiency of a nutrient and (b) a change of pH.

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*D. A. Nethsinghe. Report of the Soil Chemist. *Ann. Rept. Cocon. Res. Inst. for* 1961 11 - 24 (1963).

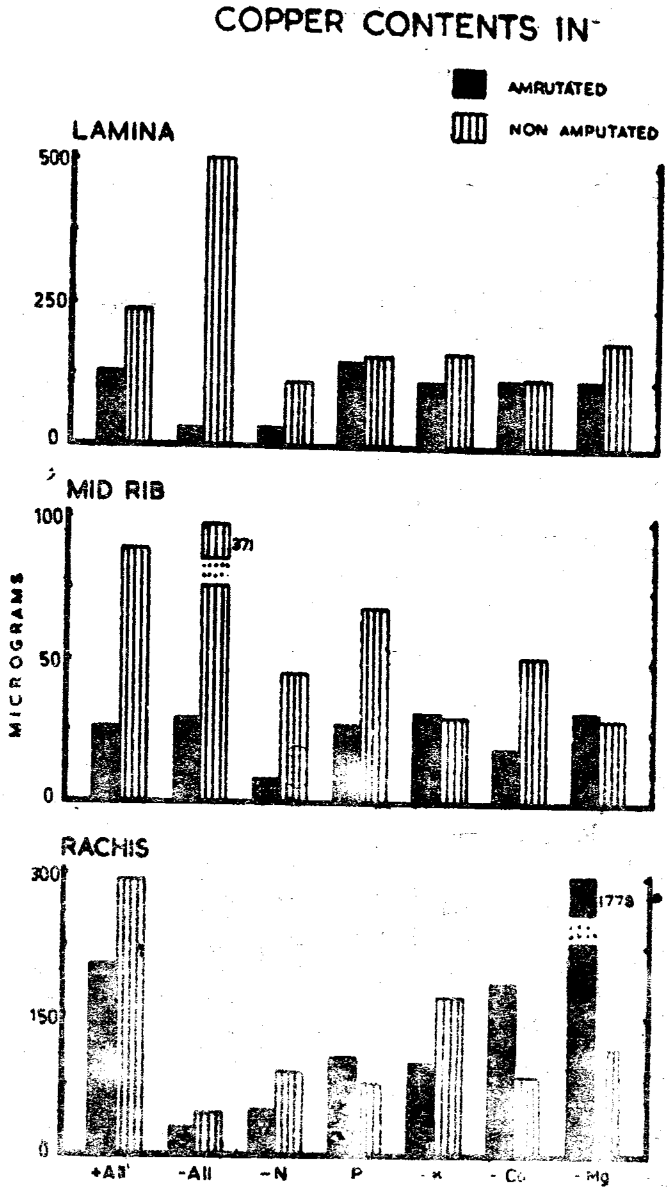


Figure 4.0 Histograms showing the distribution of copper in the laminae, midribs and rachis of coconut seedings subjected to macro nutrient deficiencies.

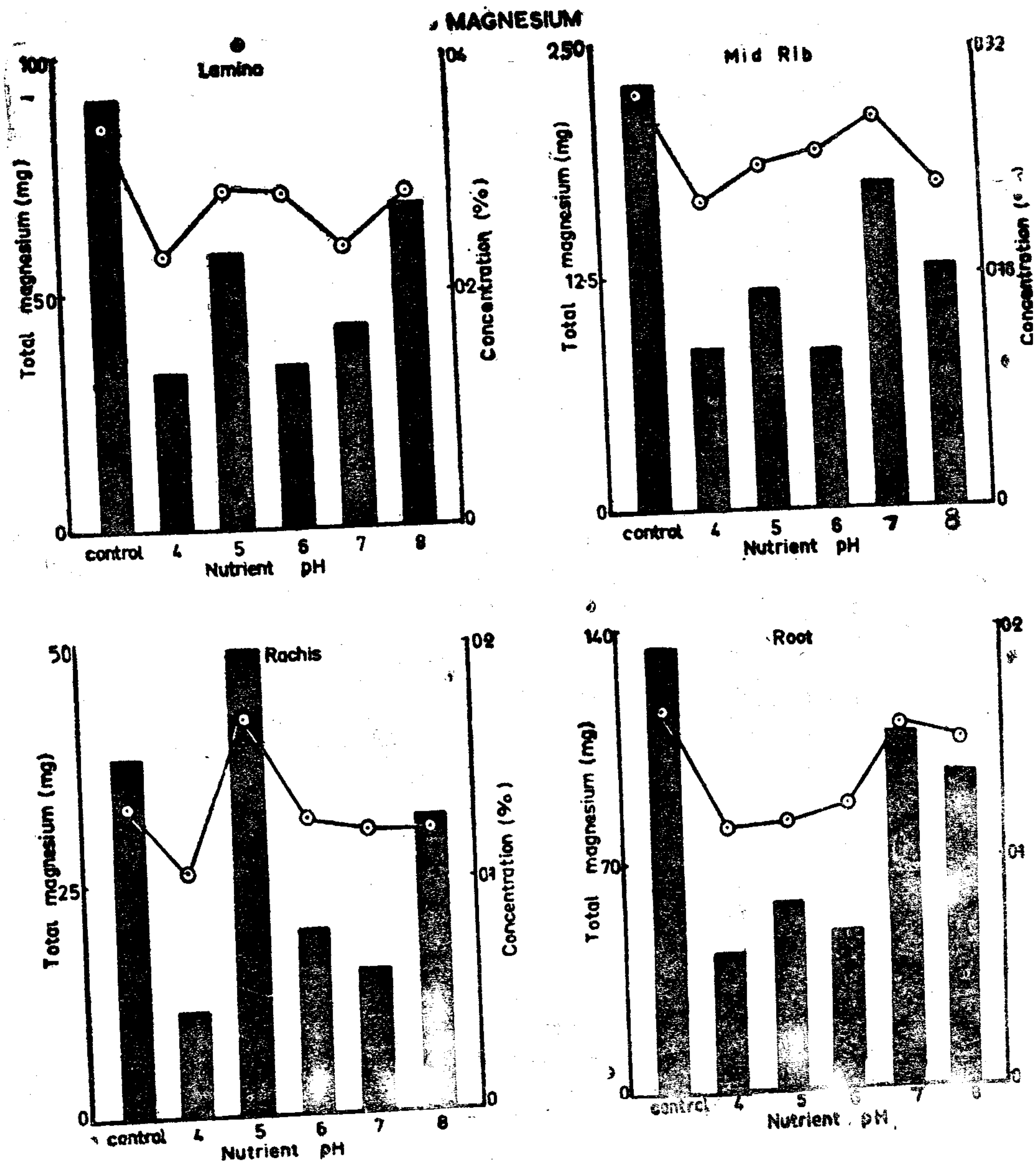


Figure 4.1 Histograms showing the distributon of magnesium in plant components of coconu seedings subjected to nutrient solutions of different pH values

Chapter 5

FUNCTIONS OF MINERAL NUTRIENTS

5.1 General considerations

The proof that an element is essential for the normal growth of a plant implies that such an element has a definite and an indispensable function to be performed in the plant. It has been shown that many elements which are not essential for normal growth of plants have been able to substitute essential elements partly, and in this capacity such elements also deem to perform some of the functions of the essential elements. An extreme example is the role of rubidium which can replace and perform almost all the functions of potassium in some varieties of *Chlorella.* Recent work on coconut have also indicated that sodium may at least partly replace potassium in its nutrition. This observation is of special significance to Sri Lanka, because for ages farmers have refused to believe that table salt was not a fertilizer for coconut plantations.

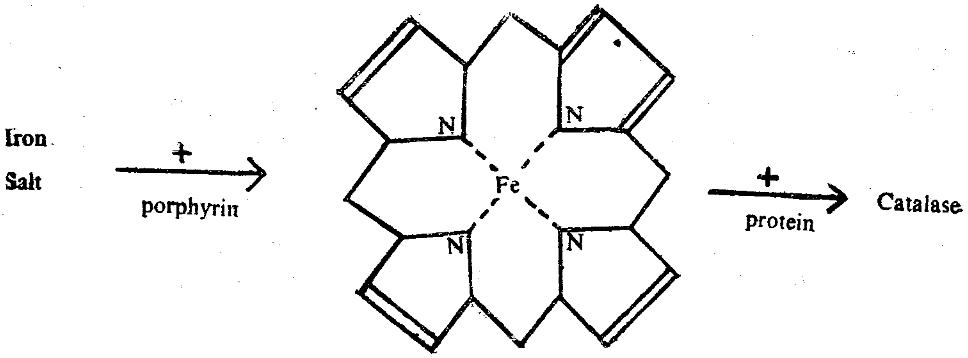
On the basis of the functions performed by mineral nutrients, these elements could be broadly classified into three main groups. The first of these have as their main function the formation of structural units in cell building. Members of this group are nitrogen and sulphur. The second group has both a structural as well as a catalytic function in metabolism. Elements in this group are phosphorus, calcium and magnesium. The third group comprises of elements which have almost exclusive catalytic functions in plants. All the micronutrients except probably boron falls into this category.

5.2 Catalytic functions of nutrient elements

The nutrient elements which have a catalytic function are associated with enzymes, and these enzymes again are broadly classified into two groups: (i) the metal-activated enzymes, and (ii) the metallo-enzymes. The following are the characteristics of the two classes of enzymes associated with metals.

Metal-activated enzymes	Metallo-enzymes
1. Metal reversibly bound to enzyme	– Metal firmly bound to enzymes
2. Dissociation constant is measureable	– Dissociation constant very small
3. Metal/protein ratio variable	– Metal/protein ratio a small integer
4. Metal/enzyme activity ratio variable	– Metal/enzyme ratio constant
5. Metal is not specific	– Metal is specific
6. Enzyme activity may exist without the metal	– No enzyme activity without metal

Among essential elements manganese and magnesium function in many enzyme reactions as activators. On the other hand zinc, iron, copper and molybdenum are often found to be bound firmly to enzymes and functions as metallo enzymes. With regard to the catalytic functions of enzymes, it is interesting to note that in most instances the metal ion associated with an enzyme can perform a catalytic function in its inorganic state in the absence of the protein component. It is thus said that these elements in their inorganic state possess in a rudimentary or primitive form the functions that they perform so efficiently when combined or associated with an organic radicle. An example is the oxidation of ascorbic acid by salts of copper. When copper forms part of the enzyme called ascorbic acid oxidase, its catalytic function increases a 1000 fold. A more striking example is the behaviour of iron in the enzyme catalase. Catalase is the enzyme which splits hydrogen peroxide to water and oxygen. This property of catalase is present in a very mild form in inorganic iron salts. In the formation of catalase, iron initially enters an organic ring molecule called porphyrin. This iron porphyrin has the catalase activity which is 1000 times greater than the iron salt. When this iron porphyrin (also referred to as heme) now combines with a specific protein to form the enzyme catalase, this activity increases further by a million times.



5.3 Functions of macronutrients

5.3.1 Nitrogen

Nitrogen is taken up by plants mostly as nitrates, ammonia, urea, or some derivative of these compounds. However, plants with symbotic bacterial nodules or other microbial associations can take up nitrogen in the elemental form. Whatever the source of nitrogen, during transformations within the plant, ammonia is produced as one of the inorganic intermediate products of metabolism. The ammonia thus formed is received by organic carboxylic acids, forming ultimately amino acids. These are so to say, the building blocks of proteins.

Apart from proteins and amino acids, nitrogen enters into a large number of biologically important compoonds, among which are the compounds known as purines and pyrimidines. The proteins also lead to the formation of enzymes and co-enzymes. By entering such a vast range of biologically important compounds in the plants, nitrogen thus plays a major role in cell building and growth.

5.3.2 Phosphorus

Phosphorus enters the plant as the ortho-phosphate radicle and remains so in both the inorganic and organic compounds of plants. It enters into a large number of compounds and plays a key function in the transfer of energy during the various metabolic processes. In glycolysis the sugars carrying phosphate radicles play a very important role and enters several intermediary breakdown products. It is also associated with several genetically important compounds called nucleic acids. Each nucleic acid is made up of three distinct components:– an organic base, a sugar and a phosphoric acid residue. Two such important nucleic acids are ribonucleic acid (RNA) and deoxyribonucleic acid (DNA). Phosphate is generally concentrated in metabolically active tissues and also in regions where rapid cell division takes place. In the storage tissue of seeds etc. it is accumulated as a substance called phytin which is an organic compound with six phosphoric acid groups.

In many plants it has been shown to assist in early flowering, and consequently in early bearing (See Fig. 5.0).

5.3.3 Potassium

Although potassium is a macro-element and hence required in large quantities, it has not been observed to form any metabolically important compound. In the plant it exists largely as soluble inorganic salts, and to a smaller extent as soluble organic salts. Its absence or deficiency causes many visible symptoms to occur. In coconut palms potassium has been found not only to increase the overall yield of crops but also to increase the size of fruits. In spite of its major importance in plant nutrition it has not been assigned any functions for which its presence is indispensable.

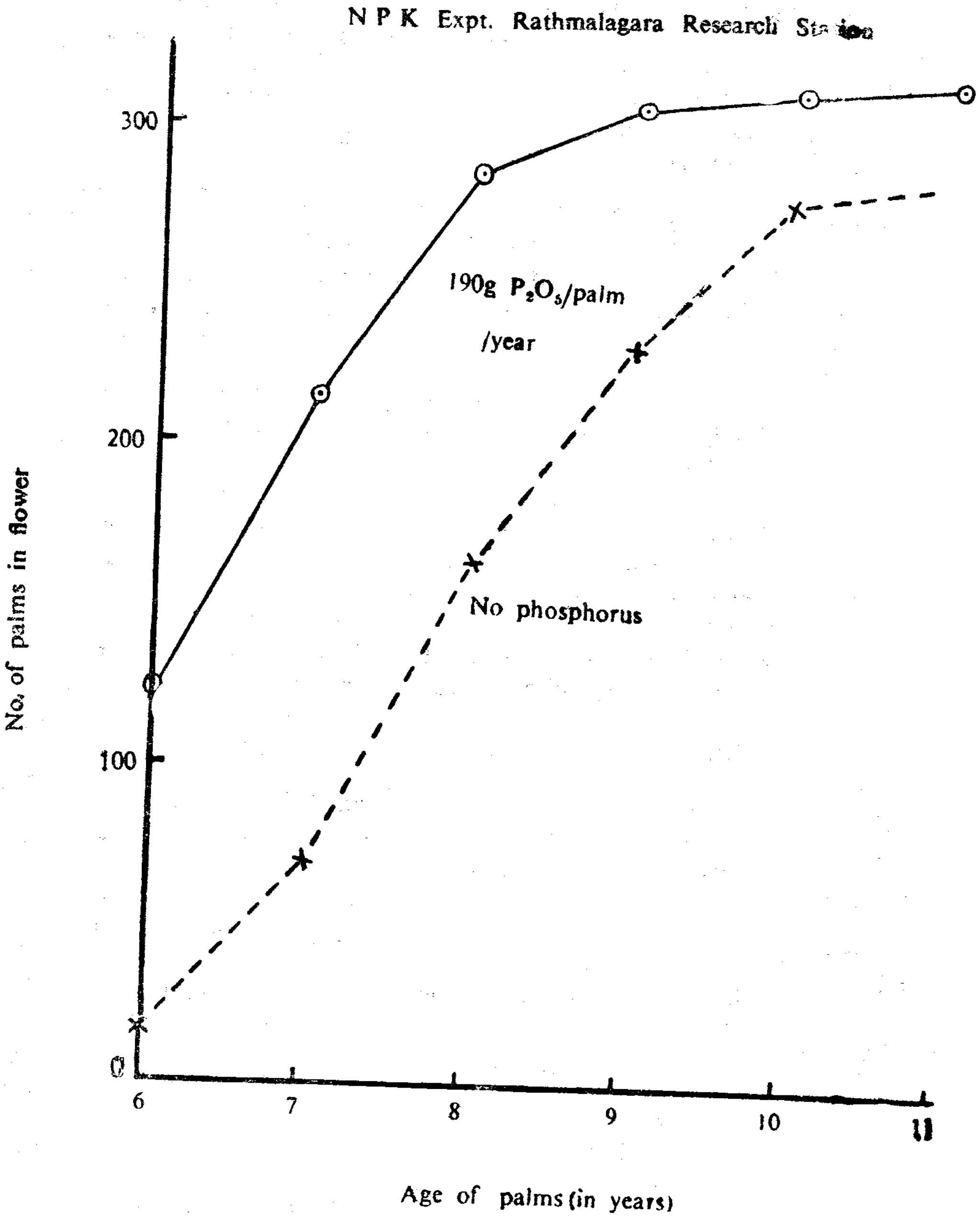


Figure 5.0 Diagram showing the effect of phosphorus on the age of initial flowering in coconut palms.

However, it has been fairly well established that its presence is necessary for (a) maintaining the organization, permeability and hydration of cells, and (b) assisting in the efficient utilisation of iron. It has also a role to play as an activator of enzymes and in the opening and closing movements of stomota.

5.3.4 Sulphur

Sulphur is taken up by plants mostly from the soil in the form of sulphate. However, if the sulphur dioxide content in the air increases appreciably it may be taken up in the gaseous state through leaves.

Sulphur is a constituent of the amino acids, cystine, cysteine and methionine, and hence enter into the composition of proteins. The fact that sulphur exists in the various organic compounds as the $>$S-H group, indicates that it has to undergo reduction in the plant before entering the organic compounds.

A deficiency of sulphur has been shown to produce a soft "rubbery" type of copra from coconut kernels.

5.3.5 Calcium

Although calcium is taken up by plants in relatively large quantities its role is not clearly understood. Being a very immobile element, its deficiency shows a marked effect on the growth and development of young shoots. Curling of young leaves and appearance of chlorotic patches on leaves are typical symptoms of calcium deficiency. Calcium starved plants show retarded root development which consequently weaken the anchorage of plants.

Earlier it was believed that calcium through the formation of pectate, enters directly into the constitution of the cells. However, later evidence have failed to confirm this view. Nevertheless it seems certain that calcium is associated in some way during cell division in the stabilizing of chromosomes. Calcium ions have also been shown to function as an activator of a number of enzymes, and in fact in the case of the enzyme amylase, calcium has been found to stabilize its molecular structure.

5.3.6 Magnesium

Ten percent of the magnesium present in the leaf is contained in chlerophyll. It is the only metal constituent in the chlorophyll molecule. Deficiency of magnesium results in a loss of the yellow pigments xanthophyll and carotene in addition to chlorophyll. The fact that chlorosis due to a deficiency of magnesium begins with mature leaves indicates that it is a very mobile element. Chlorosis due to magnesium deficiency is very characteristic since it is almost always interveinal in nature.

Magnesium is known to play a very important role in enzyme activities, although a few other elements like manganese can substitute magnesium at least partly in these activities. Magnesium has been implicated to assist the movement of phosphorus from the root to shoot. Studies on coconut palms seems to confirm this finding.* In other words magnesium functions as a "carrier" for phosphorus and *vice versa*. In this capacity magnesium probably promotes early flowering by assisting the transport of phosphorus.

5.4 Functions of micronutrients

5.4.1 Iron

Iron has several important functions to perform in the plant and its absence or deficiency can be easily demonstrated with nutrient culture experiments. As has been pointed out earlier iron functions through the formation of a complex ring compound called iron porphyrin (or heme) which by association with specific proteins forms a series of very important enzymes and activators as shown below:

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*M. A. T. de Silva *et al.* Nutritional studies on initial flowering of coconut (var *typica*). I The effect of magnesium deficiency and Mg-P relationship. *Ceylon Cocon. Q.* 24, 107-113 (1973).

$Fe \longrightarrow Heme$
$+$
porphyrin

Enzyme	Occurrence
Plant haemoglobin	Rhizobium legume nodules
Catalase	Many plants
Peroxidase	Many plants
Cytochrome c peroxidase	Yeast
Cytochrome a	Yeast
Cytochrome a_1	*B. pasteurianum*
Cytochrome a_2	*E. coli*
Cytochrome a_3	Yeast
Cytochrome b	Yeast
Cytochrome b_1	*E. coli*
Cytochrome b_2	Yeast
Cytochrome c	Yeast
Cytochrome f	Plant cells

Catalase is involved in the splitting of hydrogen peroxide with the release of oxygen. Peroxidase activates H_2O_2 to function as a powerful oxidizing agent. The presence of haemoglobin in legume root nodules is significant because neither the root nodule cells nor the nitrogen fixing bacteria (Rhizobium) could separately produce haemoglobin. Haemoglobin is probably associated with the transport of oxygen in fixation of nitrogen. Most of the other derivatives of the heme are believed to be associated with the transport of electrons during enzyme reactions.

Iron is also known to occur in forms other than as the heme. For example in the enzyme zanthin oxidase. In general, in many of its reactions involving electron transfer• iron is believed to function through the reversible oxidation, reduction change.

$$Fe^{++} \rightleftharpoons Fe^{+++}$$

5.4.2 Manganese

Quite unlike iron, manganese has been known to function only as an activator of enzyme systems. Although it has been shown to be associated with several enzymatic reactions, in many of these the metal ion can be partly or wholly substituted with other metallic cations. However, it is certain that manganese is the most important metal in the enzymatic reactions of the citric acid cycle. There is at least one reaction in plant metabolism in which Mn appears to be indispensable in its function. This is the oxygen evolving step of the Hill reaction.

Manganese seems to be very closely associated with the manufacture of the chloroplasts and chlorophyll. In this role it behaves somewhat similar to iron. Manganese is also associated with molybedenum in the synthesis of amino acids from nitrates.

5.4.3 Zinc

One of the most important functions of zinc is its relationship to auxin. Zinc not only functions in the formation of auxin, but also assists the relevant enzymes to synthesis the auxin, A deficiency of zinc therefore causes a severe reduction of auxin, which in turn alters many of the growth and developmental process in plants. For example flower production and setting of seeds are severely affected.

Zinc is known to be a constituent of a number of enzymes of which alcohol dehydrogenase and carbonic anhydrase are the most common. The latter enzyme catalyse the reaction, $H_2O + CO_2 \rightleftharpoons H_2CO_3$.

5.4.4 Copper

Copper is a constituent of several enzymes, some of which catalyse the oxidation of substances directly by oxygen. As has been pointed out earlier this property of copper containing enzymes is already present in simple copper salts in a very mild form. When the metallic copper enters a specific protein to form an enzyme, this catalytic property of the ionic salt is increased several times. A common example is the copper bound enzyme ascorbic acid oxidase which catalyse the oxidation of ascorbic acid to a substance called dehydroascorbic acid and water. It is thought that copper in these enzymes function through the cyclic conversion of cupric to cuprous and back. Other copper enzymes found in plants are, polyphenol oxidase, laccase and probably cytochrome oxidase.

5.4.5 Boron

Boron has frequently been associated with calcium in its physiological role. Deficiency of boron results in necrosis and severely retarded growth of the apical tissues. In coconut seedlings boron deficiency caused shoots to take a cabbage-like formation. Calcium deficiency is also known to produce similar symptoms. Although some physiological relationship between boron and calcium has been observed, the exact function of boron has not been elucidated. Like calcium, boron has also been implicated to affect the formation of cell walls, and in cell division.

Boron is also thought to be associated with the translocation of sugars.

5.4.6 Molybdenum

The importance of molybdenum is seen mostly in relation to the metabolism of nitrogen. In leguminous plants molybdenum has been found to be essential for fixation of atmospheric nitrogen, through the symbiotic association of azotobacter with tissues of the leguminous plant roots.

Molybdenum is also required for nitrate assimilation in plants, and this occurs through the enzyme nitrate reductase, which has molybdenum as one of its specific components. It is interesting to note that molybdenum not only enters the composition of the enzyme nitrate reductase, but also directly assists in its formation.

Molybbdenum is also a component of the enzyme system which helps to break down nitrates to nitrites with the release of energy. In this case molybdenum appears to be associated with an enzyme, which has iron in addition to Mo in its composition.

Chapter 6

NUTRIENT REQUIREMENTS OF PLANTS

6.1 Methods for the study of nutrient requirements

Simultaneously with the search for factors which control plant growth, efforts were directed to a search for a simple and convenient method to determine the nutrient requirements of plants. Extensive studies during the past 150 years or so have resulted in the near perfection of several interesting techniques to evaluate nutrient requirements in plants. Some of the more important procedures are; (a) fertilizer experimentation, (b) bio-assay experiments, (c) sand and water culture experiments, (d) soil analysis, (e) plant analysis and (f) foliar sprays.

6.2 Fertilizer experimentation

The earliest attempts to study under field condition the mineral requirements of plants were simple observation experiments, in which the response of the plant to the addition of a particular fertilizer was studied. The results of such experiments, though overwhelmingly convincing at times, are only useful to a limited extent. The reason for this is that such experiments do not take into account the inherent variability of materials under investigation, and furthermore the effect of other factors cannot be elucidated. As pointed out in an earlier chapter, soil is a heterogenous material and its chemical and physical properties can vary considerably even within a small area of a few square meters. Unless adequate safeguards are taken, such factors are bound to influence the results of field experiments.

To overcome these effects, during the early part of this century, various experimental procedures were tested; the outcome of which is the development of mathematical designs for laying out experiments. Modern field experimentation therefore involves an initial planning of the field layout based an statistical considerations. The essential feature of these new methods of field experimentation is that a choice can be made to estimate, or even eliminate the effects of undesirable factors which may affect the accuracy of the results. Furthermore these techniques provide a means of observing the effects of several factors simultaneously.

In Sri Lanka the Tea Research Institute at Talawakelle and the Coconut Research Institute at Lunuwila, share the honour of being the pioneering institutions in applying the method of scientific experimentation to perennial crops. The experiment at Lunuwila on adult coconut palms was laid out by Salgado* in the year 1935. Its objectives were to test the effects of nitrogen, phosphorus and potassium on the growth and yield of adult coconut palms. This experiment which was concluded in 1965, after 30 years of work, is considered to be the oldest and the longest continuous record of any experiment of this kind. The present day recommendations on fertilizer treatment of coconut palms is still based on some of the findings of this experiment.

Although results of field experiments are useful in studying the manurial requirements of agricultural crops, there are certain limitations. Firstly, it has to be remembered that the results obtained under a given set of conditions would not have universal application. This is chiefly because the variability in soil and climate (generally referred to as agro-climate) even within a small area can be so wide that no one experiment will be able to provide answers all possible situations. Secondly, an experiment becomes manageable only if a few factors are tested. Under these circumstances it would not be known whether the results had been, or could be influenced by factors which are not being tested. Thirdly, experiments on tree crops such as rubber and coconut, require large extents of land which limits the controlof experimental conditions.

Nevertheless field experimentation has come to stay, as this is one of the direct methods of studying fertilizer requirements of plants.

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*M L. M. Salgado. Report of the Soil Chemist. *Ann. Report of Cocon. Res. Scheme of Ceylon for* 1949 (1951)

6.3 Bio-assay technique

The so called bio-assay technique employs a test plant to investigate the fertility of a soil in pot experiments. Generelly, plants which are quick growing and fairly sensitive to changes in nutrient levels of soils are chosen as the test plants. The procedure is based on the method proposed by Mitscherlich* at the begining of the century. Some years later modifications to this method were introduced by Neubauer* who grew a definite number of seedlings in a given weight of soil and observed the increase in dry weights of plants.

In Sri Lanka, Paltridge and Santhirasegaram** used the bio-assay technique to study the chemical characteristics of some of the soils of the North-Western Province. They used as test plants, a pasture grass (*Paspalum commersonii*) and two legumes (*Phaseolus lathyroides* and *Medicago sativa*). On the results obtained they went on to predict the requirement of fertilizers for these soils (lateritic gravel, lateritic loam, lateritic sands, white cinnamon sands).

It has however, to be realised that different species of plants vary considerably in their requirements of nutrients. There is also the doubt as to whether results obtained from such glasshouse experiments could be directly translated to field conditions. Nevertheless observations of limited application can be obtained using this technique.

6.4 Sand and water culture experiments

The development of the techniques of sand and water culture experimentation was in fact the forerunner to the discovery of many of the essential micronutrients. The most important feature of this method is that conditions of experimentation can be rigidly

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*Cited by C. Bould in Mineral nutrition of plants in soils, *in* "Plant Physiology" Vol. III, (*ed.* F. C. Steward) P 77 Acad. Press. N.Y, and London.

**T. B. Paltridge and K. Santhirasegaram. Studies on the nutrient status of some coconut soils of Ceylon I. The lateritic Soils of Bandirippuwa Estate. CRI Bull. No. 11 (1957)

**T. B. Paltridge and K. Santhirasegaram. Studies on the nutrient status of some coconut soils of Ceylon II. The cinnamon sand of Horekelly Estate. CRI Bull. No. 12 (1957) controlled. However, as in the case of the bio-assay procedure, practical application of results to field operations is unavoidably limited.

In sand and water culture experiments great care has to be taken in cleaning and rinsing of the sands, posts and other equipment used. This is specially true for studies on micronutrients, where sands and pots may have to be treated with hot mineral acids to remove impurities before experiments could be laid out. The technique of sand and water culture experimentation is authoritatively reviewed by E. J. Hewitt*, and those interested are referred to this publication.

A procedure of special interest in nutrient culture studies is the method of subtractive treatment. In this method potted plants in sand culture are treated with a balanced nutrient solution with one essential element omitted. This procedure enables the experimenter to study the reactions of a plant to an absolute deficiency of a nutrient. In Sri Lanka the technique developed by Nathanael** to study the nutrition of tree crops using culture media in massive concrete pots with an intermitant flow of nutrient solution, aroused considerable interest.

6.5 Soil analysis

Soil analysis as a means of stuaying the fertility of soils dates back to the middle of the last century, when attempts were made to discover simple tests for rapid detection of deficiencies. Later work was devoted to developing procedures for the quantitative extraction of nutrients available to the plant. Among the solvents that have been tested are the following: crtric acid (1 per cent solution), sulphuric acid, constant boiling hydrochloric acid, acetic acid (0.5 *N*) buffered to pH 4.8 with sodium acetate and neutral salt solutions (eg. *N* ammonium acetate solution). Although no single solvent has had universal success, most of these have been found to be useful under certain conditions.

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*E. J. Hewitt. Sand and water culture methods used in the study of plant nutrition. 2nd ed. Commonw. Bur. Hort. Plantation Crops (Gt. Brit.) Tech. Commun. No. 2 (1966)

**W. R. N. Nathaneal. Coconut nutrition and fertilizer requirements - the plant approach. *Ceylon Cocon. Q.* 12, 101 - 120 (1961)

By the beginning of the present century it was evident that views on nutrient availability were crystallizing out in a definite pattern. Thus for example it was recognised that plants may draw their requirements of mineral nutrients from several sources, available in the soil. First of these was evidently the water-soluble fraction. This fraction is normally extracted by shaking a known quantity of soil in a given volume of water and determining the contents of nutrients in the extract. This fraction is very small, and would certainly not be the only source from which the plant would depend for its requirements. In the case of cations, the next significant fraction is called the "exchangeable bases". The solvent used to extract this part is usually *N* ammonium acetate solution adjusted to pH 7.0. The "exchangeable cations" determined by this method has had widespread success in characterizing the fertility of soils. It normally includes the water-soluble fraction plus the cations that could exchange places with the ammonium radicle of the solvent. The next fraction that could be extracted is generally referred to as "total bases", and includes, water-soluble bases, exchangeable bases and contributions from the secondary and primary minerals. The solvent used for this extraction is constant boiling hydrochloric acid. In the final analysis, the minerals are broken down by fusion with sodium carbonate, and the quantities of elements so obtained are the "ultimate" contents.

In the case of anions, a fraction called the "available" nutrient fraction is determined by extraction with dilute mineral acids. Estimation of available phosphorus has been, and continues to be a problem, mainly because of fixation. Therefore in recent years tracer techniques using the radio-active isotope P^{32} have been used with success.

Although several important modifications have been introduced for the chemical methods described above, as pointed out earlier, no one method has had universal success. Thus for example, more than two decades ago coconut palms growing in the South-Western Province of Sri Lanka began to develop characteristic symtptoms magnesium deficiency. Classical methods of soil analysis consistently failed to draw a distinction between soils sustaining healthy and deficient plants. However, when the soils were extracted with a solution of 0.01 molar calcium chloride, a fraction of magnesium was obtained which correlated well with the magnesium content of the plant (See Figures 6.0 and 6.1). The results were even more convincing when the molar Mg/Ca ratio was considered. Accordingly it was suggested that if the molar Mg/Ca ratio in such soil extracts fell below 0.02, a deficiency of magnesium could be expected in coconut plantations*.

6.6 Plant analysis

As in the case of soil analysis studies on plant analysis resulted in the development of two different techniques of investigations. First of these was a simple and rapid tissue test for diagnostic purposes, while the second was a longer procedure for quantative assessment of the nutritional status of plants.

6.6.1 Tissue tests

The technique of tissue test was proposed mainly to provide a means of testing rapidly in a qualitative or semi quantitative manner the nutritional status of a plant. Basically, it involves the extraction of soluble, unelaborated nutrients from a tissue, and spot-testing it for the concentration level. By this means it has been possible to diagnose deficiences in certain plants. The test is however, of limited use, and is not so widely used as total plant analysis.

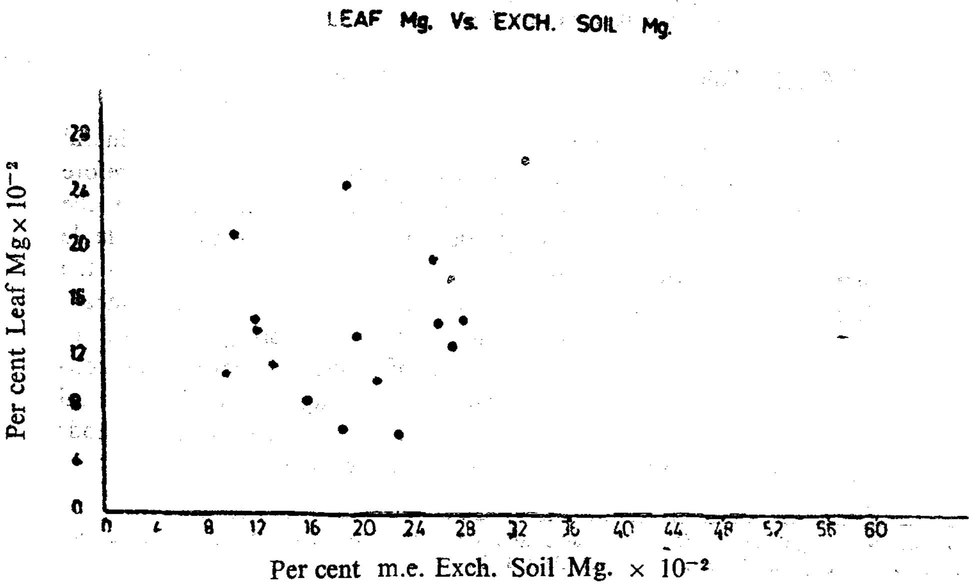

Figure 6.0 : The plot of leaf magnesium content versus exchangeable magnesium of soil (After Nethsinghe *et al**)

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*D. A. Nethsinghe, *et al.* Diagnosis and correction of magnesium deficiency in coconut palms. *Proc. Ceylon Assoc. Adv. Sci. Part I* 16 - 17 (1962)

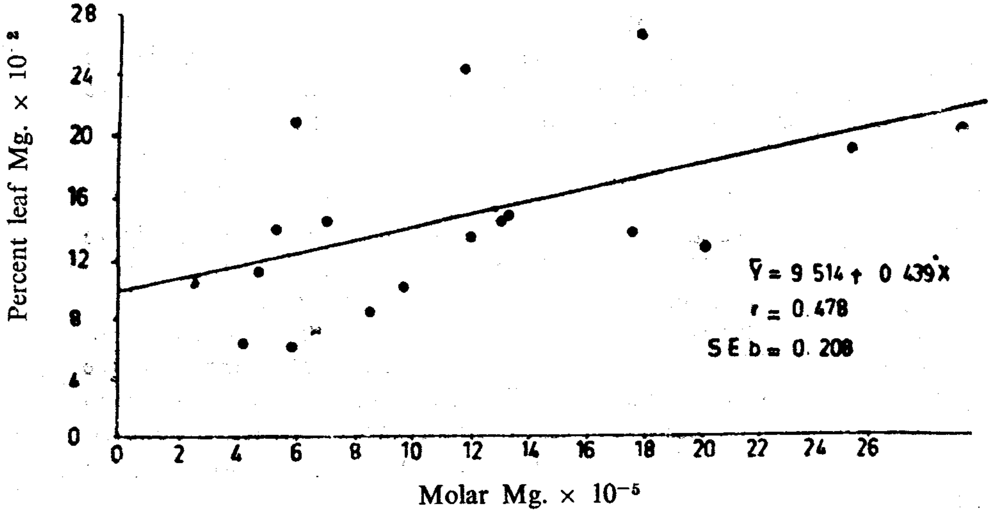

Figure 6.1 The relationship between leaf magnesium and the molar magnesium content of soils extracted with 0.01 molar calcium chloride solution. (After Nethsinghe *et al**)

6.6.2 Foliar analysis

Most land plants obtain their requirements of mineral nutrients through the root system. It would therefore be expected that the concentration of nutrients in the root tissue at any particular time may reflect the available nutrient levels of the soil medium. This was indeed the view of the earlier plant nutritionists when they concentrated their attention on root analysis as a means of characterizing the fertility of soils. However, the consistent failure of root analysis as a diagnostic tool in mineral nutrition, prompted researchers to look for better methods to study the nutritional requirements of plants.

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*D. A. Nethsinghe *et al* Diagnosis add and correction of magnesium dificiency in coconut palms. Proc. Ceylon Associ. Adv. Sci Part I 16-17 1962

Although various plant organs (e.g. grains, seeds, flowers and even pollen grains) have been used with varying success, it is generally recognized today that the leaf is the most suitable material to assess the nutritional status of plants.

The earlier scientists used plant analysis as a means of studying the fertility of soils, and this was indeed the main reason for the doubtful success attained by these workers. The modern concept of plant analysis is to study the nutritional status of plants, which by itself furnishes valuable information on the interactions and availability of nutrients.

P. Macy[*] believed that yield response of a plant could be related to concentrations of nutrients in its leaves by a curve, which would be characteristic of the particular plant species. As shown in Figure 6.2 this curve basically consisted of 3 parts, the first of which probably represented the stage when yield increase was limited by the deficiency of a nutrient. In this stage (minimal percentage) the plant was shown to respond to applications of fertilizer by increasing the yields; but the concentration of nutrients will remain virtually unchanged. The next stage referred to as the "poverty adjustment range" will show an increase in the leaf nutrient content together with a corresponding increase in yield. This stage will be climaxed by a point referred to as the "critical percentage, above which there would be a steep increase in the nutrient concentration, without an increase in yield. This portion of the curve is said to show the phenomenon of "luxury consumption" of the nutrient.

Steenbjerg and Jakobsen[**] came to the conclusion that leaf analysis can be a useful technique for nutritional studies, if the cuve representing the yield versus leaf nutrient concentration takes an S-shaped form, as shown in Fiugure 6.3. According to this curve a deficient nutrient when

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[*] P. Macy. The quantitative mineral nutrient requirements of plants. *Plant Physiol.* 11, 749 - 764 (1936)

[**] F. Steenbjerg and S. T. Jackobson. Plant nutrition and yield curves. *Soil. Sci.,* 95, 69 - 88 (1963)

supplied to a plant, will initially show a slow increase in concentration coupled with a steady increase in yield. Then at a certain point there will be a sharp rise in yield for a relatively smaller increase in concentration. Finally the yield increase will reach a maximum, while nutrient concentration in the leaf continue to increase.

These authors however, cautions that under certain conditions when a deficiency of a nutrient is fairly severe, only the upper half of the curve (C-shaped) would be observed, and this will present a distorted picture of the nutrition of the plant.

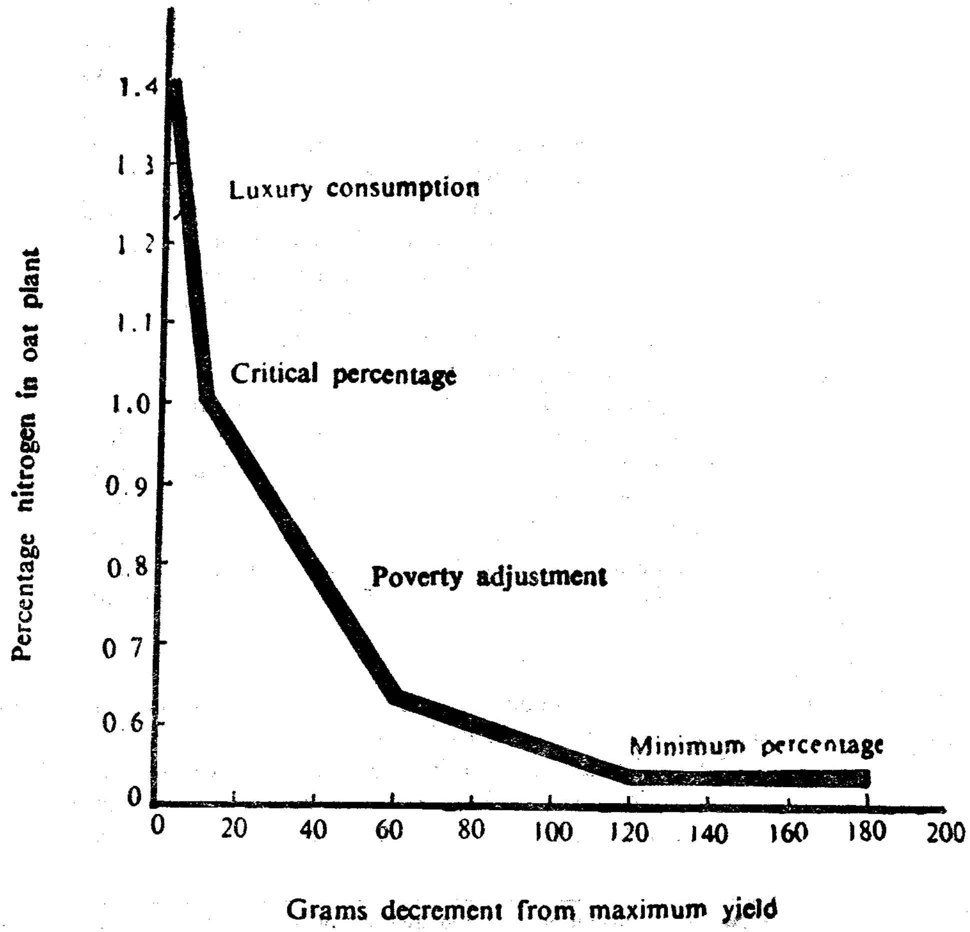

Figure 6.2 Curve described by Macy to show the relationship between yield and the nutrient centent of leaf

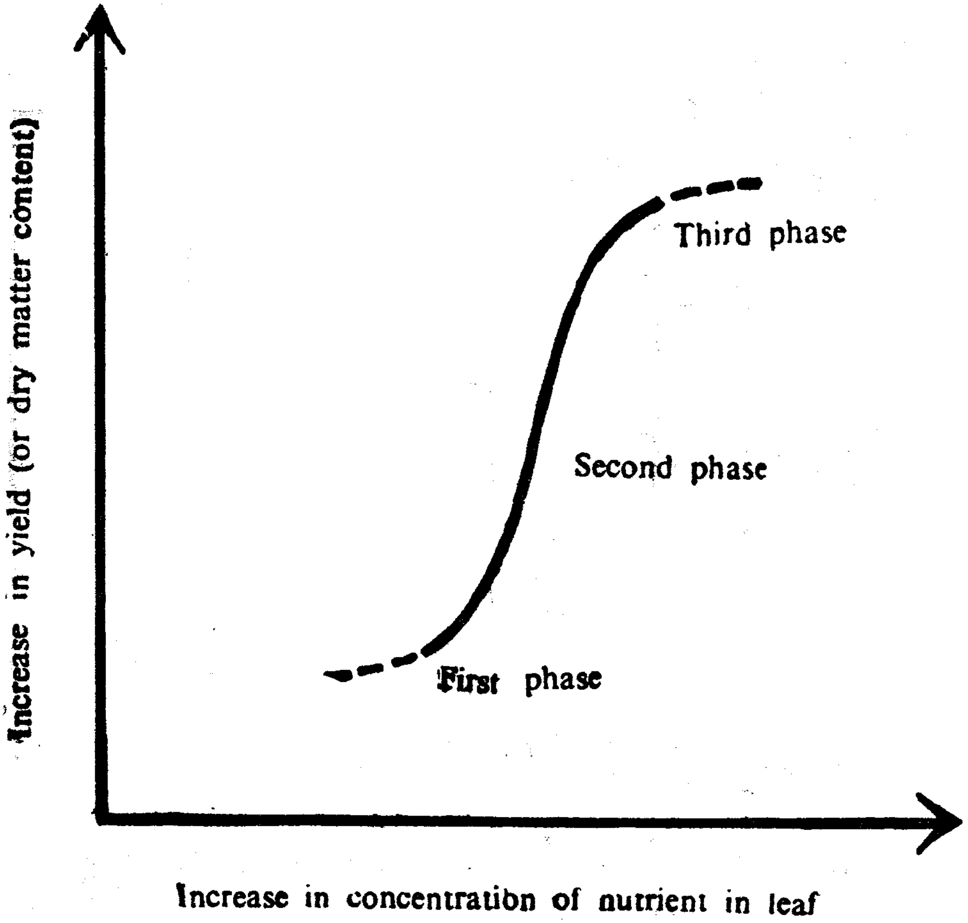

Figure 6.3 The S-shaped curve to show the relationship between yield and nutrient content of leaf.

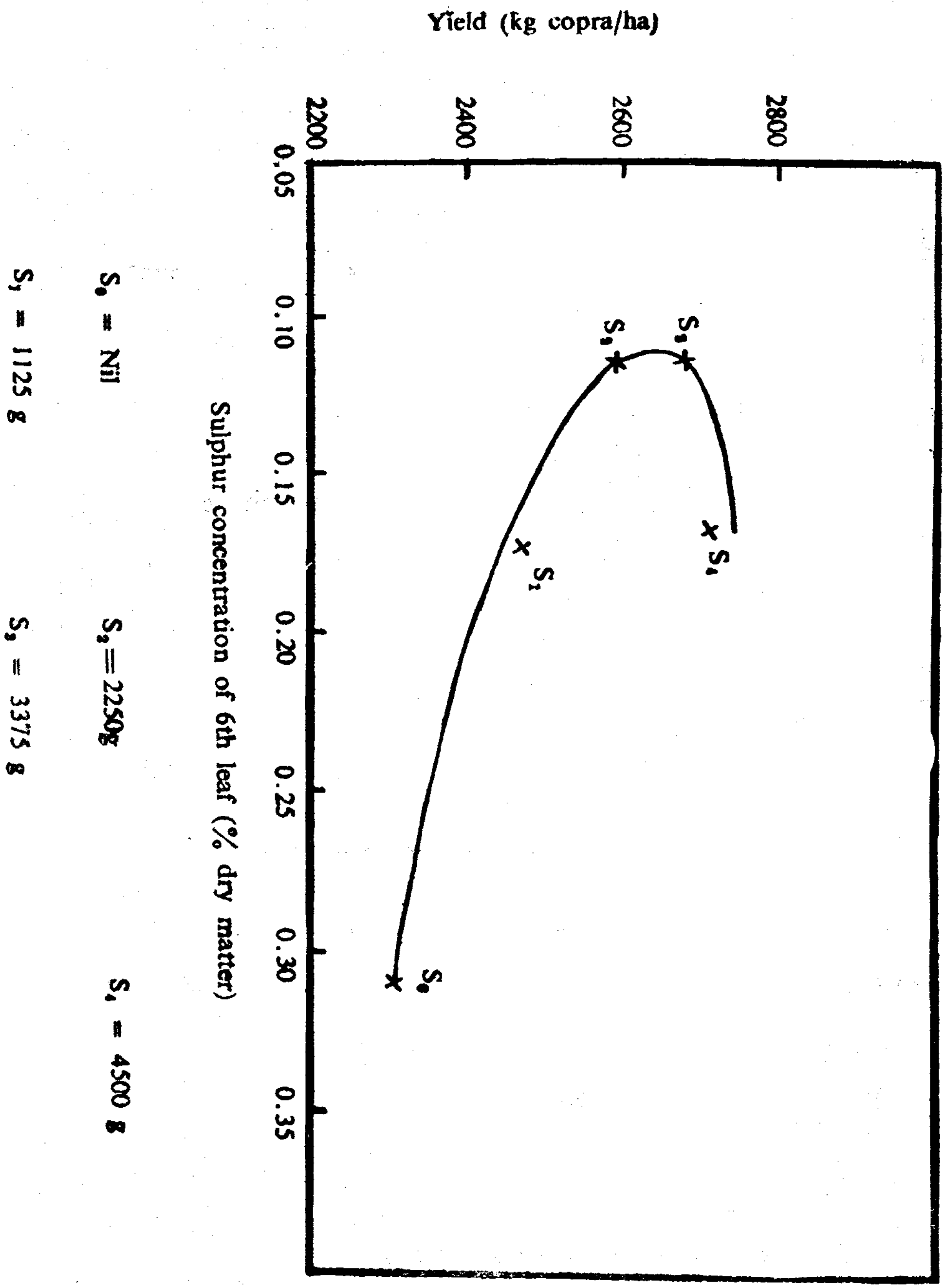

Figure 6.4 The C-shaped curve to show the relationship between yield and sulphur content of leaf in coconut palms

In a recent study on the sulphur nutrition of coconut palms, De Silva *et al** obtained a C-shaped curve resembling the one described by Steenbjerg and Jacobson (See Figure 6.4).

However, these workers were able to make use of this curve to detect a nutritional disorder of particular importance to the coconut industry.

6.7 Diagnosis and correction of nutrient deficiencies

A plant is said to be deficient in a nutrient, if restoration of its supply causes an increase in yield. It should of course be a specific response to the particular element concerned. A deficiency of an essential nutrient generally causes initially a lowering of the yield, without any other visual symptoms. Depending on the type of plant this phase may remain unnoticed for many years before any visual symptoms could occur. It is interesting to note that visual symptoms of deficiency are quite characteristic of the plant species, and when accurately described could be used to detect deficiencies. In general, the appearance of visual sysmptoms normally occur when the magnitude of the disorder is fairly large. It is therefore obvious that a simple and easy method must be devised to detect a deficiency long before the appearance of visual symptoms.

One of the most useful methods of detecting nutrient deficiencies is through leaf analysis (foliar diagnosis). In this procedure initially a study is carried out to determined the effect of various factors on the concentration of nutrients in the leaf. Among the common factors, which could have such effects are the following: (a) leaf maturity and position, (b) season and time of sampling, and (c) nutrient availability.

The effect of factors (a) and (b) are investigated by means of simple observation trials** while the factor (c) is studied by means of

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*M. A. T. de Silva *et al.* The Sulphur nutrition of coconut. *Expl. Agric.* 13, 265 - 27 (1977).

M. A. T. de Silva. Micronutrients in the nutrition of coconut - I Methods and Preliminary investigations. *Ceylon Cocon. Q.* 25, 116-127 (1974) carefully laid out fertilizer experiments combined with investigations involving soil and leaf analysis. By this means average leaf nutrient levels are determined which could be used to detect any deficiencies. A particular advantage in leaf analysis as a diagnostic tool is that not only deficiencies, but also other nutrient disorders such as, interactions could be detected.

Although the leaf has been the most important plant tissue for nutritional studies, it has to be recognised that for certain specific problems, other plant organs have been more useful than the leaf. Thus in the case of coconut plantations again, the liquid endosperm. (coconut water) of the fruit has been used very successfully as a rapid method of diagnosing potassium and phosphorus deficiencies. A concentration of 0.2 per cent K_2O and 100 mg per litre of P_2O_5 are considered critical values for potassium and phosphorus respectively in coconut water*

In this diagnostic procedure it has been possible to estimate potassium and phosphorus contents within a few hours of collection of sample, using simple chemical methods.

Apart from observations of visual symptoms and foliar diagnostic methods, the techniques of foliar sprays have been used successfully to detect and identify nutrient deficiencies. Correction of disorders through regular foliar sprays have been successful with annual and certain perenial plant species, but on tree crops foliar sprays can only be used for diagnostic purposes. This was amply demonstrated in coconut plantations when serious attempts were made to correct magnesium deficiency by application of foliar sprays at fortnightly intervals**. Corrective measures in most cases are effective only through the application of requisite quantities of fertilizers.

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*M. L. M, Salgado *et al.* The phosphate content of coconut water in relation to phosphate availability and phosphate response *Proc. Ceylon Associ, Adv. Sci.* Part 1, (1956)

**D, A, Nethsinghe *et al,* Diagnosis and correction of magnesium deficiency in coconut palms. *Proc. Ceylon Associ. Adv. Sci.* Part I 16-17 (1962)

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