Mirza Hasanuzzaman · Masayuki Fujita
Hirosuke Oku · Kamrun Nahar
Barbara Hawrylak-Nowak *Editors*

Plant Nutrients and Abiotic Stress Tolerance

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Preface

Plant nutrients are the vital elements for plant growth and survival. Among the seventeen essential plant nutrients, only three (C, H and O) are derived from the atmosphere and the rest are supplied either from soil or by fertilizers. Each of the nutrients plays a unique role in plant life cycle and their requirement varies with the plant species and growth stages. Both the deficiency and excess of these nutrients render negative effects on plant growth and development. Besides, to ensure the efficient utilization of the nutrients, the environmental factors should be favourable.

Over the last few decades, abiotic stresses have turned into an important topic of concern for plant biologists. Numerous studies have been conducted and are still under experiment considering this fact that to survive the time-bound environmental changes, plants must possess some tolerance mechanisms within their cellular level. A large number of elements have been experimented among which plant nutrition has been a promising factor of study as it is an integral part of plant life cycle. Of all the plant nutrients, N, P, K, Mg, Mn, Cl and Fe are directly involved in plant photosynthetic activities; Ca, B, Cu, Fe, Mn, Zn and Mo are involved in enzymatic activities; N and S are involved in protein synthesis. These nutrients also play some more specific and crucial roles which are essential for sustaining normal plant biology and physiology. The unavoidable production of ROS during photosynthesis is intensified by the abiotic stress induced limited use of light energy and CO_2 fixation. Nutrients like N, K, Ca, Mg and Zn have been reported to maintain the utilization of light and CO_2 fixation and other photosynthetic activities to a required level. Especially K and Zn are observed to interfere with NADPH-oxidizing enzyme and as a result render protective roles against ROS-induced damages under abiotic stresses.

In the recent decades, some beneficial trace elements (such as Si and Se) at low concentration showed tremendous effect in conferring various abiotic stresses. Due to the advancement of science, intensive research works have been carried out globally to explore the underlying mechanisms of plant nutrient uptake, their metabolism, homeostasis and protection against abiotic stresses. Excellent review articles on the role of plant nutrients on abiotic stress tolerance have been published in journals, annual reviews and as chapters of some books. However, no comprehensive book on this topic has been published so far. Therefore, the objective of the book is to provide the insight into the latest findings on the role of plant nutrients in conferring abiotic stress tolerance to plants. This book will be a time-demanding topic for a large group of audience including plant scientists, agronomists, soil scientists, botanists, molecular biologists and environmental scientists.

We, the editors, would like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. We are highly thankful to Ms. Lee, Mei Hann, Editor (Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. We are also thankful to RaagaiPriya ChandraSekaran, Project Coordinator of this book and all other editorial staffs for precious help in formatting and incorporating editorial changes in the manuscripts. Special thanks to Dr. Md. Mahabub Alam, Noakhali Science and Technology University, Bangladesh, and Ms. Taufika Islam Anee, Sayed Mohammad Mohsin and Khursheda Parvin of Sher-e-Bangla Agricultural University, Bangladesh, for their generous help in formatting the manuscripts. The editors and contributing authors hope that this book will include a practical update on our knowledge for the role of plant nutrients in abiotic stress tolerance.

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Prof. Hasanuzzaman has published over 60 articles in peer-reviewed journals and books. He has edited 2 books and written 35 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to plant species. These books were published by the internationally renowned publishers (Springer, Elsevier, CRC Press, Wiley, etc.). His publications got over 2000 citations with h-index: 23 (according to Scopus). Prof. Mirza Hasanuzzaman is a research supervisor of undergraduate and graduate students and supervised 20 MS students so far. He is Editor and Reviewer of more than 50 peer-reviewed international journals and recipient of "Publons Peer Review Award 2017." He is an active member of about 40 professional societies and acting as Publication Secretary of Bangladesh Society of Agronomy. He has been honored by different authorities due to his outstanding performance in different fields like research and education. He has received the World Academy of Science (TWAS) Young Scientist Award 2014. He has attended and presented 25 papers and posters in national and international conferences in different countries (USA, UK, Germany, Australia, Japan, Austria, Sweden, Russia, etc.).

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Barbara Hawrylak-Nowak is currently Associate Professor at the University of Life Sciences in Lublin, Poland. She earned her Master's degree in Biology (specialization: environmental biology) at the Department of Plant Physiology at Maria Curie-Skłodowska University in 2000. In the same year, she started doctoral studies at the Department of Plant Physiology, University of Life Sciences, Lublin. Barbara joined the team headed by Professor Maria Szymańska, which was focused on the biological activity of trace elements and mitigation of the effects of abiotic stress in crop plants. In 2002, she earned her Master's degree in Biotechnology at the Department of Molecular Biology, Maria Curie-Skłodowska University. She was granted the PhD degree in Agricultural Sciences in the field of Horticulture (specialization: plant physiology) in 2004. In her thesis, she pioneered investigations of the substrate pH-dependent biological activity of three chemical forms of selenium (selenite, selenate and selenomethionine) in three crop plant species. After completion of her Ph.D., Barbara accepted a position of Assistant Professor at the Department of Plant Physiology, University of Life Sciences in Lublin, where she worked for 13 years. During that time, she focused in particular on issues related to the application of trace elements and other phytoprotectants in mitigation of the impact of unfavourable environmental factors on plants, mineral nutrition of plants and ecological investigations. In 2017, Barbara was promoted to an Associate Professor position at the Department of Plant Physiology, University of Life Sciences in Lublin, where she has been working since that time. She also became the head of this department. Her teaching activity includes obligatory and facultative courses (lectures, laboratories) e.g. 'Plant physiology', 'Non-infectious plant diseases', 'Plant under stress conditions', 'Biological adaptations of plants to the environment', and 'Physiology of woody plants'. As part of the didactic work, she conducts seminars and laboratories for graduate students performing engineering and Master's research under her scientific supervision.

Barbara Hawrylak-Nowak has written over 40 refereed publications, including 25 papers published in journals indexed in JCR. Her research results were presented in over 35 conference reports at national and international scientific conferences. Her work has contributed to the knowledge of biological activity of trace elements in plants, especially grown under stressful conditions. She actively collaborates with several researchers/research groups in Poland and abroad.

Chapter 1
Biological Functions, Uptake and Transport of Essential Nutrients in Relation to Plant Growth

K. S. Karthika, I. Rashmi, and M. S. Parvathi

Abstract Plant nutrition takes care of the interrelationship between soil nutrients and plant growth. The role of nutrients in plant growth and physiology is dealt in this chapter in its maximum possible extent including the details on essential nutrients, their physiological roles, uptake and assimilation, nutritional disorders, the availability of nutrients in soil and their movement to plant roots and availability to plants by different modes of absorption. Every nutrient plays an indispensable role in carrying out physiological functions of plants enabling proper plant growth, the deficiency of which leads to particular disorders. Some nutrients are needed in larger quantities and some smaller but still essential for a plant to complete its life cycle. The primary roles of major nutrients in plant growth and physiology are widely studied and well documented. The functions of beneficial elements in plant nutrition may be investigated further. Soil, a complex substrate, acts as a storehouse of nutrients and water for plant growth. Plants have extensive root system for the nutrient uptake from the soil. However, the availability of all these nutrients in soil may fluctuate depending on so many factors. From the soil, nutrients move towards the roots by following certain mechanisms of transport, which include mass flow, diffusion and root interception. The nutrients thus reaching the roots are absorbed by plants either actively by spending energy or passively by no involvement of energy. Hence, a better understanding on plant nutrition would help to enhance crop productivity and nutritional value for the burgeoning world population.

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Keywords Mineral nutrients · Physiological functions · Plant growth · Deficiency · Toxicity · Growth laws

1.1 Introduction

For a healthy crop, adequate supply of nutrients is indispensable from soil. Thus healthy soils result in a healthy crop. Plant nutrition deals with the effect of nutrients present in the soil in plant growth and development. Plants form the basis of several food chains; hence, plant nutrition has impacts both on growth of plants and other living organisms (Maathuis 2009).

Every nutrient has a particular sufficiency range in plant. An imbalance in this range would affect the crop growth, and this imbalance could be either nutrient deficiency or toxicity. This could be a result of inadequate level of nutrient supply from the soil due to improper, inadequate and imbalanced application of fertilizers or nutrient sources. Toxicity occurs when a nutrient is above the sufficiency range than the plant needs, and this results in a decrease in growth of plant or its quality (McCauley et al. 2011). These disorders in plants are expressed as characteristic symptoms. As symptoms in plants arise due to several factors like pests, diseases, nutrient deficiency, toxicity, etc., it becomes important to identify the exact reason.

Deficiencies and toxicities of nutrients adversely affect crop health resulting in the appearance of unusual visual symptoms, thereby decreasing crop productivity. According to McCauley et al. (2011), the role and mobility of each essential nutrient need to be well understood as to determine which nutrient is responsible for a particular symptom, whether deficiency or toxicity. A proper focus on the knowledge on role of nutrients in plant growth is therefore important. Hence, a better understanding on plant nutrition would help to enhance crop productivity and nutritional value for the burgeoning world population. The role of nutrients in plant growth and physiology is dealt in this chapter in its maximum possible extent including the details on essential nutrients, their physiological roles, uptake and assimilation, nutritional disorders, the availability and status of nutrients in soil and their movement to plant roots and availability to plants by different modes of absorption.

1.2 Essential Nutrients

1.2.1 Criteria for Essentiality

An element is considered as essential when the three criteria as proposed by Arnon and Stout (1939) are met. These include:

1. A deficiency of the element makes it impossible for the plant to complete its life cycle.
2. The deficiency is specific to the element and can be prevented or corrected only by supplying the element in question.

Table 1.1 Critical information on nutrients in relation to plants

Nutrient	Essentiality discovered by	Year of discovery	Plant-usable form	Average conc.in plant tissue	Relative number of atoms compared to Mo as one
H	Since time immemorial		H_2O	6%	60,000,000
O	Since time immemorial		H_2O and O_2	45%	30,000,000
C	Priestley et al.	1800	CO_2	45%	30,000,000
N	Theodore de Saussure	1804	NO_3^-, NH_4^+	1.5%	1,000,000
K	C. Sprengel	1839	K^+	1.0%	400,000
Ca	C. Sprengel	1839	Ca^{2+}	0.5%	200,000
Mg	C. Sprengel	1839	Mg^{2+}	0.2%	100,000
P	C. Sprengel	1839	$H_2PO_4^-$, HPO_4^{2-}	0.2%	30,000
S	Sachs and Knop	1860	SO_4^{2-}	0.1%	30,000
Cl	T.C. Broyer, A.B. Carlton, C.M. Johnson and P.R. Stout	1954	Cl^-	100 mg kg^{-1}	3000
Fe	E. Gris	1843	Fe^{2+}	100 mg kg^{-1}	2000
B	K. Warington	1923	H_3BO_3, $H_2BO_3^-$, HBO_3^{2-}, BO_3^{3-}	20 mg kg^{-1}	2000
Mn	J.S. McHargue	1922	Mn^{2+}	20 mg kg^{-1}	2000
Zn	A.L. Sommer and C.P. Lipman	1926	Zn^{2+}	20 mg kg^{-1}	300
Cu	A.L. Sommer, C.P. Lipman and G.McKinney	1931	Cu^{2+}	6 mg kg^{-1}	100
Mo	D.I.Arnon and P.R. Stout	1939	MoO_4^{2-}	0.1 mg kg^{-1}	1
Ni	P.H.Brown, R.M. Welch and E.E.Cary	1987	Ni^{2+}	0.1 mg kg^{-1}	–

Source: Tisdale et al. (1997)

3. The element is directly involved in the nutrition of the plant, for example, as a constituent of an essential metabolite or needed for the action of a particular enzyme system.

Based on these criteria, the following elements are considered essential for higher plants. There are 17 essential nutrients recognized for growth of plants. These are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sulphur (S), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), molybdenum (Mo), chlorine (Cl) and nickel (Ni). Carbon (C), hydrogen (H) and oxygen (O) are obtained primarily from water and carbon dioxide; hence these are not considered mineral nutrients (Taiz and Zeiger 2002). Critical information on these essential nutrients is presented in Table 1.1.

1.3 Classification of Nutrients

1.3.1 Classification Based on Quantity

Essential nutrients are classified into macronutrients or micronutrients on the basis of their relative concentration in plant tissue. This is the quantity-based classification (Rattan 2015).

1.3.1.1 Major or Macronutrients

Those nutrients that are required by plants in large quantities are classified under major or macronutrients. These include C, H, O, N, P, K, Ca, Mg and S. Among these N, P and K are called primary nutrients and Ca, Mg and S form the secondary nutrients.

Primary Nutrients: Nitrogen (N), phosphorus (P) and potassium (K) are the primary nutrients as they are required in larger quantities by plants. Application of fertilizers containing N, P and K would help in correcting these deficiencies once noticed.

Secondary Nutrients: Calcium (Ca), magnesium (Mg) and sulphur (S) are secondary nutrients due to their moderate requirements by plants and localized deficiencies (Rattan 2015).

1.3.1.2 Micronutrients

Those nutrients that are required by plants in relatively lesser quantities but as essential as macronutrients are classified as micronutrients. These include Fe, Mn, Zn Cu, Ni, B, Mo and Cl. Micronutrients can be cationic (Fe, Mn, Zn, Cu, Ni) and anionic (B, Mo and Cl) in nature. Cationic micronutrients are absorbed as the divalent cations and anionic micronutrients are absorbed in anionic forms by the crops. Boron could also be taken up as neutral H_3BO_3 molecule by the plants.

There are certain elements that promote plant growth and essential for some but not for all higher plant species. These are classified as *beneficial elements*. These include silicon (Si), sodium (Na), cobalt (Co) and selenium (Se). These elements promote growth for different species under different environmental conditions. However, for each element and plant species, the roles played by these nutrients and their concentration vary (Pilon-Smits et al. 2009).

1.3.2 Classification Based on Biochemical Behaviour

A classification based on the biochemical properties is arrived at as the classification based on relative concentration in plant tissues does not take into consideration the physiology of higher plants and the role of nutrients in plant physiology on a

Table 1.2 Classification of plant nutrients based on biochemical behaviour

Nutrient	Biochemical functions
Group 1	Nutrients that are part of carbon compounds
N	Constituent of amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes, hexoamines, etc.
S	Component of cysteine, cystine, methionine and proteins. Constituent of lipoic acid, coenzyme A, thiamine pyrophosphate, glutathione, biotin, adenosine-5′-phosphosulphate and 3-phosphoadenosine
Group 2	Nutrients that are important in energy storage or structural integrity
P	Component of sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, phytic acid, etc. Has a key role in reactions that involve ATP
Si	Deposited as amorphous silica in cell walls. Contributes to cell wall mechanical properties, including rigidity and elasticity
B	Complexes with mannitol, mannan, polymannuronic acid and other constituents of cell walls. Involved in cell elongation and nucleic acid metabolism
Group 3	Nutrients that remain in ionic form
K	Required as a cofactor for more than 40 enzymes. Principal cation in establishing cell turgor and maintaining cell electroneutrality
Ca	Constituent of the middle lamella of cell walls. Required as a cofactor by some enzymes involved in the hydrolysis of ATP and phospholipids. Acts as a second messenger in metabolic regulation
Mg	Required by many enzymes involved in phosphate transfer. Constituent of the chlorophyll molecule
Cl	Required for the photosynthetic reactions involved in O_2 evolution
Mn	Required for activity of some dehydrogenases, decarboxylases, kinases, oxidases and peroxidases. Involved with other cation-activated enzymes and photosynthetic O_2 evolution
Na	Involved with the regeneration of phosphoenolpyruvate in C4 and CAM plants. Substitutes for potassium in some functions
Group 4	Nutrients that are involved in redox reactions
Fe	Constituent of cytochromes and non-haem iron proteins involved in photosynthesis,N_2 fixation, and respiration
Zn	Constituent of alcohol dehydrogenase, glutamic dehydrogenase, carbonic anhydrase, etc.
Cu	Component of ascorbic acid oxidase, tyrosinase, monoamine oxidase, uricase, cytochrome oxidase, phenolase, laccase and plastocyanin
Ni	Constituent of urease. In N2-fixing bacteria, constituent of hydrogenases
Mo	Constituent of nitrogenase, nitrate reductase and xanthine dehydrogenase

Source: After Evans and Sorger (1966) and Mengel and Kirkby (1987)

large scale. Hence, this classification is adopted as proposed by Mengel and Kirkby (1987). The classification is presented in Table 1.2 in which nutrients are classified under four basic groups.

1. Firstly, those elements that are involved in the formation of organic compounds in the plant which are assimilated by the plants through biochemical reaction involving oxidation and reduction (redox reactions).

2. Secondly, elements that are present in the reactions with involvement of energy storage and for structure maintenance. Phosphorus, silicon and boron contribute to carry out these functions.
3. Those nutrients present in ionic forms are classified in this third group, such as those that serve the functions of cofactors and in osmoregulation.
4. Nutrients involved in redox reactions are classified in the fourth group.

1.4 Role of Nutrients in Plant Growth and Physiology

The role of nutrients in plant growth including their assimilation, physiological functions, nutrient deficiency symptoms and toxicity symptoms are described individually hereunder.

1.4.1 Nitrogen

Nitrogen is required by plants in greatest amounts. Nitrogen, being a very mobile element, circulates well between the atmosphere, the soil and the living organisms. Nitrogen-sufficient plants contain 1–5% of N (10,000–50,000 ppm or mg kg^{-1} dry matter).

1.4.1.1 Uptake and Assimilation

Nitrogen is absorbed either as nitrate (NO_3^-) ion, the prevalent form of uptake, or as ammonium (NH_4^+) ion depending on plant species and the conditions of soil like pH and redox state. Under reduced conditions, such as in the case of rice, N is taken up in ammoniacal form. Nitrogen, up on reduction, attains its −3 valence state for its assimilation and uptake. Nitrate reductase and nitrite reductase are the two important enzymes that ensure the conversion of nitrate (NO_3^-) to ammonium (NH_4^+). The translocation of nitrogen in higher plants takes place mainly as nitrate and amino acids mainly through the xylem from the roots towards the upper plant parts. High-affinity H^+-coupled symporters belonging to the NRT family mediate NO_3^- uptake. MT transporters or NH_3/H^+ symporters mediate NH_4^+ uptake. Nitrate reduction and assimilation occur mostly in the shoot. The mechanism of N uptake and assimilation is represented in Fig. 1.1.

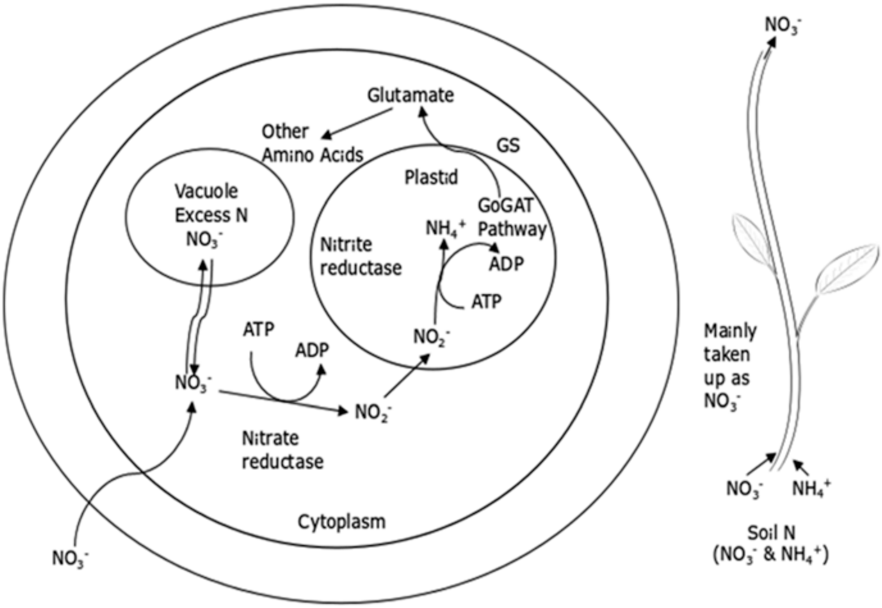

Fig. 1.1 Mechanism of N uptake and assimilation. Enzyme nitrate reductase reduces nitrates to nitrites in the cytoplasm. Reduction of nitrites to ammoniacal form occurs in chloroplasts with the help of enzyme nitrite reductase. Ammoniacal N is assimilated into the amino acid glutamate. The excess nitrogen is stored in vacuoles as nitrates

1.4.1.2 Physiological Functions

- Nitrogen is an important constituent of several plant cell components. It is an essential component of nucleic acids, proteins, amino acids, phospholipids and many other secondary metabolites. The amino groups in amino acids are provided by the element N, which thereby remains its foremost function.
- Nitrogen is present in the ring structure of purine and pyrimidine bases of nucleotides, which form the basis of nucleic acids. As the component of nucleic acid either as deoxyribonucleic acid (DNA) or as ribonucleic acid (RNA), N holds its responsibility in the transfer of genetic code to the offsprings (Rattan 2015)
- Chlorophyll, the pigment which imparts green colour to the leaves, contains N in it. Nitrogen due to its presence in chlorophyll enhances the quality of leaves, especially in leafy vegetables and fodders (Rattan 2015).
- The proportion of amino acids like glutamic acid ($C_5H_9NO_4$), proline ($C_5H_9NO_2$), phenylalanine ($C_9H_{11}NO_2$), cysteine ($C_6H_{12}N_2O_4S_2$), methionine ($C_5H_{11}NO_2S$) and tyrosin ($C_9H_{11}NO_3$) are enhanced, and the amounts of lysine ($C_6H_{14}N_2O_2$), histidine ($C_6H_9N_3O_2$), arginine ($C_6H_{14}N_4O_2$), aspartic acid ($C_4H_7NO_4$), threonine ($C_4H_9NO_3$), glycine ($C_2H_5NO_2$), valine ($C_5H_{11}NO_2$) and leucine ($C_6H_{13}NO_2$) in the grain are decreased with nitrogen fertilization. This improves quality of protein in the food grains (Rattan 2015).

- Nitrogen is found to play an essential role in the biochemistry of coenzymes, photosynthetic pigments which are nonprotein compounds. In ample supply, nitrates get deposited in the vacuole. This plays an important role in turgor generation (Maathuis 2009).

1.4.1.3 Deficiency Symptoms

- Nitrogen deficiency inhibits overall growth of the plant. The symptoms include yellowing or chlorosis of leaves due to a collapse in chloroplasts. Since N is mobile in plants, the deficiency appears in the older leaves near the base of the plant. Later it advances towards the younger leaves under conditions of severe deficiency. This may lead to necrosis of entire leaf or parts of the leaf (Agarwala and Sharma 1976).
- The plants appear small with spindly stems. Nitrogen deficiency results in smaller leaves, and there occurs premature falling of older leaves. Branching of roots gets restricted and this adversely affects the root growth. However an increase in the root/shoot ratio is observed with nitrogen deficiency (Mengel and Kirkby 2006).
- Amino acids especially Gln, proteins and chlorophyll content are found to decrease with a deficiency in N. Nitrogen starvation could also lead to an increase in starch and specific flavonoids (e.g. rutin and ferulic acid) and phenyl propanoids (Amtmann and Armengaud 2009).
- In cereals nitrogen deficiency results in decreased tillering, reduction in the number of ears per unit area and also the number of grains per ear. Though the grains remain small, protein concentration remains relatively higher. This is attributed to the decrease in the import of carbohydrate into the grains which takes place at the later stages of grain filling (Mengel and Kirkby 2006). Nitrogen deficiency characterized by pale green or yellowish leaves of corn is shown in Fig. 1.2.
- In case of nitrogen deficiency, synthesis of anthocyanin results due to the nonusage of carbohydrates in nitrogen metabolism, leading to its accumulation. In tomato and certain varieties of corn, nitrogen deficiency is observed as purple coloured leaves, stems and petioles (Taiz and Zeiger 2002).
- In cocoa, leaves turn pale yellow in colour and are reduced in size in case of nitrogen deficiency. Older leaves exhibit scorching at the tip, and petioles make an acute angle with the stem.

1.4.1.4 Toxicity Symptoms

Excess of nitrogen contributes to darker green colouration of leaves and succulent growth of plants. The plants grow taller with heavier heads succumbing plants to easy lodging. Thick succulent growth attracts insect, pest and disease attacks (Rattan 2015).

Fig. 1.2 N deficiency in corn. (Photo: by K.S. Karthika)

1.4.2 Phosphorus

Phosphorus is the second most abundant mineral in the human body. In the soil, the dominant form in which phosphorus occurs is orthophosphate ion, whereas in plants, it also occurs in pyrophosphate form to a minor extent. Phosphorus is considered to be an immobile element in soils and mobile element in plants. The P concentration in plants with sufficient P varies from 0.1 to 0.4% by weight, which is 1/5 to 1/10 of N or K content (Rattan 2015).

1.4.2.1 Uptake and Assimilation

Phosphate taken up directly as inorganic PO_4^{3-} (Pi) by roots is xylem translocated. It moves to the fast-growing young laminae in its oxidized form. Inorganic P forms occur mainly as soluble Pi (orthophosphate) or as PP (pyrophosphate). Newer leaves receive phosphate both from the roots and from the older leaves. This was observed in a study to understand the transport and assimilation of P on castor bean by Jeschke et al. (1997). Organic P upon hydrolysis is translocated via the phloem. The mechanism of P uptake and assimilation is represented in Fig. 1.3.

1.4.2.2 Physiological Functions

- Phosphorus is an important constituent in the structure of nucleic acids and lipid membranes.

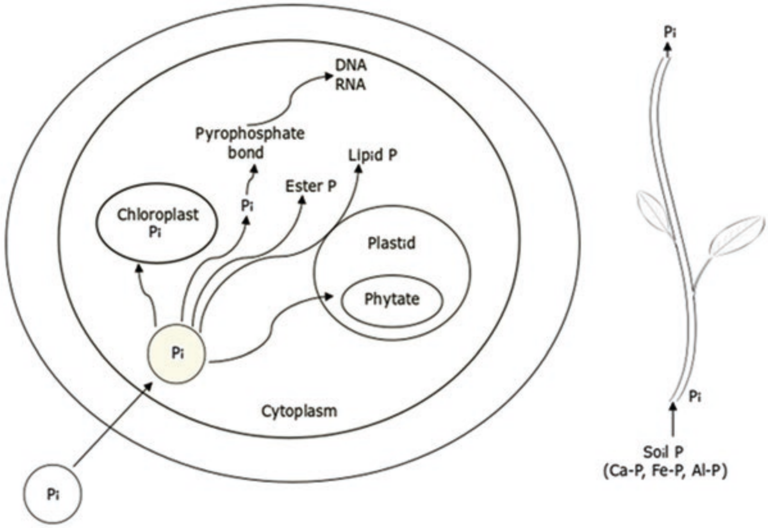

Fig. 1.3 Mechanism of P uptake and assimilation. H^+-coupled high-affinity transporters mediate the direct uptake of P in the form of inorganic PO_4^{3-} (Pi). Inorganic P (Pi) inside the cells forms high-energy pyrophosphate and ester bonds. This Pi is an essential component of lipid membrane in maintaining the integrity of membrane. In chloroplasts, Pi is essential during photosynthesis in the formation of high-energy bonds. Pi enters the chloroplast in exchange for glyceraldehyde-3-phosphate (G3P). Phosphorus is stored as phytate together with minerals in plastids

- Phosphorus is an important component of adenosine triphosphate (ATP). Phosphorus is involved in all energy transfer reactions in the cell, as ATP is known as the energy currency of the cell.
- Phosphorus is involved in photosynthesis, translocation of sugars and starch, movement of nutrients within the plant and transfer of genetic characteristics from one generation to the next as it is a component in DNA and RNA (Taiz and Zeiger 2002).
- It plays an indispensable role in the formation of flower and seeds and in the growth of plant. Root proliferation is enhanced by P, and thus it helps the plant to explore bigger soil volume for water and nutrients. Phosphorus has another essential role in cellular metabolism. Large amounts of P are stored in seeds to enable embryo development, germination and seedling growth (Marschner 1995).
- Rhizobium bacteria which convert atmospheric nitrogen (N_2) into ammoniacal (NH_4^+) form have P as an essential ingredient. Nodule development in nitrogen-fixing legumes is enhanced by the availability of P as it is an energy source.
- It reduces the severity of crop diseases and increases resistance to drought and salinity. Phosphorus enhances water use efficiency of crops under limited soil moisture conditions.