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Molecular mechanism of nutrient uptake in plants

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ABSTRACT

Only the green plants of all living organisms, are able to synthesize the organic food from the relatively raw materials of the inorganic world, although certain bacteria, e.g. nitrifying and sulphur bacteria also have this capability. They obtain their energy by oxidizing ammonia and hydrogen sulphide and obtain carbon from the carbon dioxide of the air without the agency of sunlight, and the organic substances produced are relatively negligible in amount. Each nutrient assists with different plant functions that allow the plants to grow and reproduce. It is useful to know the relative amounts of each nutrient that is needed by a crop in making fertilizer recommendations. Two classes of nutrients are considered essential for plants: macronutrients and micronutrients. Macronutrients are the building blocks of crucial cellular components like proteins and nucleic acids; as the name suggests, they are required in large quantities. Nitrogen, phosphorus, magnesium, and potassium are some of the most important macronutrients. Carbon, hydrogen, and oxygen are also considered macronutrients as they are required in large quantities to build the larger organic molecules of the cell; however, they represent the non-mineral class of macronutrients. Micronutrients, including iron, zinc, manganese, and copper, are required in very small amounts. Micronutrients are often required as cofactors for enzyme activity. A little progress has been made in the molecular aspects of nutrient uptake and transport within plants. Proteins are required to transport protons, inorganic ions, and organic solutes across the plasma membrane and the tonoplast at rates sufficient to meet the needs of the cell. Membranes contain different types of transport proteins: ATPases or ATP-powered pumps, channel proteins, and cotransporters.

Introduction

Cultivated plants almost always have a sufficient supply of carbon dioxide for photosynthesis and oxygen for respiration and light which are likewise usually plentiful. As per research based findings the plants require 17 nutrients, also called ‘essential elements’ (Marschner, 1995).

Each plant nutrient is needed in different amounts by the plant, and varies in how mobile it is within the plant. It is useful to know the relative amounts of each nutrient that is needed by a crop in making fertilizer recommendations. In addition, understanding plant functions and mobility within the plant has been useful in diagnosing nutrient deficiencies. To be classified as essential, an element needs to meet the following criteria: 1) The plant cannot complete its life cycle (seed to new seed) without it, 2) The element's function cannot be replaced by another element, 3) The element is directly involved in the plant growth and reproduction and 4) Most plants need this element to survive.

Primary (Macro) nutrients

Primary nutrients (macro-nutrients) are nitrogen, phosphorus, and potassium. They are the most frequently required in a crop fertilization program. They are needed in the highest quantity by plants as fertilizer. Nitrogen is necessary for formation of amino acids, the building blocks of protein and essential for plant cell division. It is vital for plant growth, directly involved in photosynthesis. It is one of the necessary components of vitamins too. It helps in production and use of carbohydrates and affects energy reactions in the plant.

Phosphorus is involved in photosynthesis, respiration, energy storage and transfer, cell division, and enlargement and promotes early root formation and growth. It improves quality of fruits, vegetables, and grains. It is vital to seed formation, helps plants survive harsh winter conditions, increases water-use efficiency, and hastens maturity.

Potassium is involved in carbohydrate metabolism, and the break down and translocation of starch. It increases photosynthesis and water-use efficiency. It is essential in protein synthesis and important in fruit formation. It activates enzymes and controls their reaction rates. It improves quality of seeds and fruit, and winter hardiness. It also increases disease resistance.

Secondary (Macro) nutrients

The secondary nutrients (macro-nutrients) are calcium, magnesium, and sulphur. For most crops, these three are needed in lesser amounts than the primary nutrients. They are gaining more importance in crop fertilization programs due to more stringent clean air standards and efforts to improve the environment. Calcium is utilized for continuous cell division and formation. It is involved in nitrogen metabolism. It reduces plant respiration, and helps in translocation of photosynthates from leaves to fruiting organs. It increases fruit set. It is essential for nut development in peanuts. It also stimulates microbial activity. Magnesium is one of the key elements in chlorophyll production. It improves utilization and mobility of phosphorus. It is activator and component of many plant enzymes. It increases iron utilization in plants. It influences earliness and uniformity of maturity. Sulphur is the integral part of amino acids. It helps in developing enzymes and vitamins. It promotes nodule formation on legumes. It is involved in seed production. It is also necessary in chlorophyll formation (though it isn't one of the constituents).

Micronutrients

They include boron, chlorine, copper, iron, manganese, molybdenum, and zinc. These plant food elements are used in very small amounts, but they are just as important to plant development and profitable crop production as the major nutrients. Especially, they work "behind the scene" as activators of many plant functions. Boron is essential for germination of pollen grains and growth of pollen tubes. It is also essential for seed and cell wall formation and promotes maturity. It is also necessary for sugar translocation. Affects nitrogen and carbohydrate metabolism too. The role of B in plant metabolism is not well understood. In fact, no specific function of B has been identified. Only information on the physiological consequence of B deficiency is available to us, and this has been reviewed by Jackson and Chapman. Chlorine interferes with P uptake, enhances maturity of small grains in some soils. So far there is not much information about its function. Copper catalyzes several plant processes. Major functions are in photosynthesis, reproductive development. It indirectly plays role in chlorophyll synthesis. It increases sugar content, intensifies color and improves flavor of fruits and vegetables. Copper like most cations, is primarily involved with enzyme activity. Several enzymes that are affected directly by copper deficiency have been identified. The physiological result of copper deficiency is an apparent wilting of leaves. It is suggested that this wilted appearance is the result of structural weakness of the cell wall in copper-deficient plants, and is not related to water stress. However, copper deficiency also reduces root growth more than shoot growth, creating an unfavorable shoot root ratio. This increased shoot root ratio could lead to plant/water stress. These two phenomena may work together to create the wilted appearance. Iron promotes formation of chlorophyll. It acts as an oxygen carrier, and also involved in reactions involving cell division and growth. Iron is readily oxidized and reduced between its two oxidation states Fe 3+ and Fe 2+. Its role in plant metabolism is closely linked to this reversible Fe2+/ Fe 3+ oxidation. Many of the reactions associated with Fe are the redox reaction of chloroplasts, mitochondria, and peroxisome. These reactions include coupled electron-transfer reactions (cytochromes a and b), oxidases (cytochrome oxidase), and peroxidases (catalase and peroxidase) (Fig. 4). Iron also plays a role in the formation of amino levulinic acid, which is a precursor of chlorophyll synthesis. Manganese functions as a part of certain enzyme systems. It helps in chlorophyll synthesis. It also increases the availability of phosphorus and calcium. The role of Mn in plant matabolism is very unclear. Manganese has properties similar to Mg and can substitute for Mg in some enzyme systems. This is probably not a common occurrence in nature since Mg is taken up by crops in much greater quantities than is Mn. Only one system, albeit a very important one, has been shown to require Mn. This is the splitting of water by photolysis in photosystem II. Molebdenum is required in the least amount of all the essential micronutrients. It is required to form the enzyme "nitrate reductase" which reduces nitrates to ammonium in plants, the first step of incorporating inorganic NO into organic N compounds. Nitrate reductase activity is reduced by Mo deficiency. It aids in the formation of legume nodules. It is needed to convert inorganic phosphates to organic forms. Other than nitrate reductase it is also involved in several enzyme systems including nitrogeneous nitrate reductase, xanthine oxidase, aldehyde oxidase and sulfate oxidase. The Mo deficiency results in a disrupted nitrogen metabolism. Zinc helps in plant growth hormones and enzyme system. It is necessary for chlorophyll and carbohydrate synthesis. It also helps in seed formation. Zinc serves both the structural and regulatory roles in enzyme activity in plant tissue. Only a few enzymes have clearly been identified as requiring Zn; however, for several others there is considerable indirect evidence of Zn involvement.

In addition to the 13 nutrients listed above, plants require carbon, hydrogen, and oxygen, which are extracted from air and water to make up the bulk of plant weight.

Carbon, hydrogen and oxygen are the main constituent of carbohydrates, proteins and lipids, and involved in almost all the metabolism. Hydrogen maintains osmotic balance, and oxygen is required in respiration. In this review the factors that control micronutrient uptake, the crop's response to this uptake, and the way in which the tropical climate and crop varieties might affect the amounts of micronutrients needed, are discussed at large. The trends in crop management and yield levels and how these factors affect micronutrient needs, are also touched.

Plant uptake of nutrients

Nutrient uptake by roots is dependent on both the ability of the roots to absorb nutrients and the nutrient concentration at the surface of the root. Roots constitute the main absorbing surface for various nutrients for a plant. Roots are composed of both a mature zone near the shoot, and an 'elongation zone' near the root tip, or cap (Figure 1). Nutrients and water move freely through this elongation zone into the center of the root (the xylem), and then up into the shoot. It is more difficult for nutrients to enter the root through the more mature zone of the root due to a restriction called a 'casparian strip'. Therefore, nutrient levels in deep soil likely become more important later in the growing season, especially for deep-rooted plants. Roots spread out both laterally and vertically as the plant grows to take advantage of areas within the soil that have more water and nutrients.

Root, the main organ in nutrient absorption

In vascular plants, the root is the organ of a plant that typically lies below the surface of the soil. The first root that comes from a plant is called the radicle. The four major functions of roots are 1) absorption of water and inorganic nutrients, 2) anchoring of the plant body to the ground and 3) storage of food and nutrients and 4) to prevent soil erosion. In response to the concentration of nutrients, roots also synthesize cytokinin, which acts as a signal as to how fast the shoots can grow. Roots often function in storage of food and nutrients. Roots do not intentionally grow towards a nutrient source. For nutrient uptake to occur, the individual nutrient ion must be in position adjacent to the root. Positioning of the nutrient ion can occur by one or more of three processes.

Mass flow- It is the process in which the soluble fraction of nutrients present in soil solution (water) and not held on the soil fractions flow to the root as water is taken up. Nutrients such as nitrate-N, calcium and sulfur are normally supplied by mass flow.

Diffusion- This creates a gradient for the nutrient to diffuse through the soil solution from a zone of high concentration to the depleted solution adjacent to the root. Diffusion is responsible for the majority of the P, K and Zn moving to the root for uptake. The roots of plants are the absorbers of water and mineral matter from the soil. These, with the carbon dioxide taken from the air, are the materials out of which not only the food for plants but the world's food supply is manufactured by plants.

Mobility- It is the property of a nutrient which determines its translocation within the plant system. The mobile nutrients like N, P, K, Mg and Fe are translocated from old leaves to new growth regions under all conditions. The variable mobile nutrients like Cu, Zn, S and Mo are translocated from old leaves to new growth regions under some conditions. All nutrients move relatively easily from the root to the growing portion of the plant through the xylem.

Interestingly, some nutrients can also move from older leaves to newer leaves if there is a deficiency of that nutrient. Knowing which nutrients are 'mobile' (i.e., able to move) is very useful in diagnosing plant nutrient deficiencies because if only the lower leaves are affected, then a mobile nutrient is most likely causing the deficiency. Conversely, if only the upper leaves show the deficiency, then the plant is likely deficient in an immobile nutrient, because that nutrient cannot move from older to newer leaves. Sulfur is one element that lies between mobile and immobile elements depending on the degree of deficiency.

Timing of nutrient uptake

Nutrient uptake does not necessarily match plant growth. For example, when corn biomass represents 50% of its total mature biomass, it has accumulated approximately 100% of its mature K, 70% of its N, and 55% of its P. Therefore, supplying sufficient K and N early in a crop's growing season is likely more important than during the middle of the growing season. However, late in the growing season, nutrients accumulate in the grain rather than in the leaves or stalk. Therefore, late season nutrient application may increase both quality and grain yield if other plant requirements are met, such as water. For example, nitrogen top dressed at tillering has been found to increase bothyield and protein of winter wheat grown inMontana, especially at low soil N levels (Lorbeer *et al*., 2000).

Cell membrane as the site of nutrient transport

An appreciation of the structure of the cell membrane is essential for understanding the mechanism of nutrient uptake by plant roots. This structural design of the membrane offers scope for the transport of nutrient elements only through integral proteins of the membranes. These transport proteins are very similar to enzymes in their specificity in recognising the molecules and ions for transport. The driving force for the transport process is provided by the membrane-bound ATP hydrolysing enzyme, H+-ATPase. The above mechanism has already been developed (Fig. 3).

Foliar spray applied for nutrient uptake

Foliar sprays are widely used to apply micronutrients, especially iron and manganese, for many crops. Soluble inorganic salts generally are as effective as synthetic chelates in foliar sprays, so the inorganic salts are usually chosen because of lower costs. Suspected micronutrient deficiencies may be diagnosed with foliar spray trials with one or more micronutrients. Correction of deficiency symptoms usually occurs within the first several days and then the entire field could be sprayed with the appropriate micronutrient source. Inclusion of sticker-spreader agents in the spray is suggested to improve adherence of the micronutrient source to the foliage. Caution should be used because of leaf burn due tohigh salt concentrations or inclusion of certain compounds in foliar sprays. Advantages of foliar sprays are: (1) application rates are much lower than for soil application; (2) a uniform and (3) response to the applied nutrient is almost immediate so deficiencies can be corrected during the growing season. Low residue foliar sprays of manganese and zinc have been used to correct deficiencies of citrus and other fruit crops, but sprays which will discolor the fruit should be avoided. Disadvantages of foliar sprays are: (1) leaf burn may result if salt concentrations of the spray are too high; (2) nutrient demand often is high when the plants are small and leaf surface is insufficient for foliar absorption;

(3) maximum yields may not be possible if spraying is delayed until deficiency symptoms appear; and (4) there is little residual effect from foliar sprays. Application costs will be higher if more than one spray is needed, unless they can be combined with pesticide spray applications.

Nutrient transporters

The uptake and transport of water and mineral ions are among the oldest subjects in plant physiology, and numerous studies have described these processes at the whole-plant level and at the organ level (e.g., with excised roots). Subsequent work was based on isolated membrane vesicles and electrophysiology to characterize transport processes at the level of the membrane. The selectively permeability feature of plasma membrane makes it impermeable to certain units. Therefore, certain specific proteins are there to facilitate their entry through plasma membrane, which are called as transporters. The recent cloning of the genes for a large number of transport proteins and the availability of knockout mutants make it possible to dissect transport processes in greater detail and to begin to understand the interactions between ion uptake processes that had often been observed at the organ level. The plasma membrane of the plant cell is a selectively permeable barrier that ensures the entry of essential ions and metabolites into the cell (Fig.2). Together with the vacuolar membrane (tonoplast), it permits the cytoplasm to maintain intracellular homeostasis. These membranes consist primarily of phospholipid bilayers with transmembrane proteins that permit the traversing of water, ions, and metabolites and the maintenance of a cytosolic pH that is one to three units higher than that of the cell exterior or the vacuole. Pure phospholipid bilayers are permeable to gases, such as O_2 and CO_2, but they are barely permeable to water and nearly impermeable to inorganic ions and other hydrophilic solutes, such as sucrose and amino acids. Proteins are required to transport protons, inorganic ions, and organic solutes across the plasma membrane and the tonoplast at rates sufficient to meet the needs of the cell. Membranes contain different types of transport proteins: ATPases or ATP-powered pumps, channel proteins, and cotransporters (Lalonde *et al.*, 1999; Sze *et al.*, 1999).

The physiological analysis of ion uptake by plant roots has revealed several distinct classes of regulated transport activities. The original work of Epstein (1966) classified these activities into two mechanisms. In plant cells, H^+-ATPases pump protons across the plasma membrane or tonoplast to acidify the extracellular matrix or the vacuole, respectively (Sze *et al.*, 1999). Channel proteins facilitate the diffusion of water and ions down energetically favorable gradients.

Iron is an essential nutrient for virtually all organisms. The IRT1 (iron-regulated transporter) gene of the plant *Arabidopsis thaliana*, encoding a probable Fe(II) transporter, was cloned by functional expression in a yeast strain defective for iron uptake. Yeast expressing IRT1 possess a novel Fe(II) uptake activity that is strongly inhibited by Cd. Rice is unique in the sense that it utilizes both strategies. Besides secreting DMA, it also absorbs Fe2+, which is more abundant than Fe3+ under the submerged conditions to which rice is well adapted (Ishimaru et al., 2009). Although two homologs of ferric-chelate reductase are present in rice, the expression of these genes is not observed under Fe-deficient or Fe-sufficient conditions, and the level of Fe3+ chelate reductase activity is very low compared to that in other plants. The importance of zinc in organisms is clearly established, and mechanisms involved in zinc acquisition by plants have recently received increased interest. In this report, the identification, characterization and location of GmZIP1, the first soybean member of the ZIP family of metal transporters, are described. GmZIP1 was found to possess eight putative transmembrane domains together with a histidine-rich extra-membrane loop. Transgenic *Arabidopsis* that over-expressed a ZAT gene exhibited enhanced zinc resistance and increased zinc content in the roots of plants grown in a high external zinc environment. Measurable phenotypic changes have also been observed in tests that over expressed a few other types of plant membrane transporters (Mitsukawa et al., 1997; Curie et al., 2000). Much progress has recently been made towards identifying the molecular mechanisms of zinc transport in plants (Gaither and Eide, 2001). As a result, several possible targets are now available for engineering zinc efficiency in plants and for increasing the zinc content of edible parts. Among these targets are divalent cation transporters from the plasma membrane and the vacuole. The plasma membrane cation transporters include the ZIP family of zinc and iron transporters (Guerinot, 2000). Another class of transporters located in the vacuolar membrane includes ZAT and MHX (Shaul et al., 1999; van der Zaal et al., 1999; Assuncao et al., 2001; Shaul, 2002). Testing the over-expression and engineering of these transporters in plants will determine if this approach will lead to solutions for increasing zinc uptake when this micronutrient is available for uptake.

Although generally low, soil nitrogen availability can fluctuate greatly in both space and time due to factors such as precipitation, temperature, wind, soil type and pH. Therefore, the preferred form in which N is taken up depends on plant adaptation to soil conditions. Nitrate uptake occurs at the root level and two nitrate transport systems have been shown to coexist in plants and to act co-ordinately to take up nitrate from the soil solution and distribute it within the whole plant (Daniel-Vedele et al., 1998; Tsay et al., 2007). It is generally assumed that the NRT1 gene family mediates the root low-affinity transport system (LATS), with the exception of the AtNRT1.1, which is both a dual affinity transporter (Wang et al., 1998; Liu et al., 1999) and a nitrate sensor (Ho et al., 2009). In *Arabidopsis*, 53 genes belong to the NRT1 family. Among them 51 genes are expressed and exhibit different tissue expression patterns in the whole plant (Tsay et al., 2007), suggesting a specialized and unique function for at least some of them.

Positively charged macronutrients such as potassium (K^+), ammonium (NH_4^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}) are required in relatively large amounts for plant growth and development. Additional cationic micronutrients (iron, manganese, zinc, copper, and nickel) play essential roles as cofactors and activators of enzymes. Magnesium (Mg^{2+}) is the most abundant divalent cation in plant cells and plays a critical role in many physiological processes. Ten members of *Arabidopsis* gene family (*AtMGT*) encoding putative Mg^{2+} transport proteins have already been identified. Most members of the *AtMGT* family are expressed in a range of *Arabidopsis* tissues. One member of this family, *AtMGT1*, functionally complemented a bacterial mutant lacking Mg^{2+} transport capability. A second member, *AtMGT10*, complemented a yeast mutant defective in Mg^{2+} uptake and increased the cellular Mg^{2+} content of starved cells threefold during a 60-min uptake period. Because no convenient radioactive isotope of K^+ exists, transport of K^+ is measured with radioactive Rb^+. Classical studies of K^+ (Rb^+) uptake into roots showed two main transport components, described as high-affinity (mechanism I) and low-affinity (mechanism II) transport, respectively (reviewed in Epstein, 1972). One of the high-affinity K^+ uptake components is induced by removing K^+ from the nutrient medium.

Work of modern biotechnology

All organisms are made up of a cell which is having a same genetic material called DNA (deoxyribonucleic acid). Each unit of DNA is made up of a combination of the following nucleotides – adenine (A), guanine (G), thymine (T), and cytosine (D) -- as well as a sugar and a phosphate. These nucleotides pair up into strands that twist together into a spiral structure call a "double helix." This double helix is DNA. Segments of the DNA tell individual cells how to produce specific proteins. These segments are genes. It is the presence or absence of the specific protein that gives an organism a trait or characteristic. More than 10,000 different genes are found in most plant and animal species. This total set of genes for an organism is organized into chromosomes within the cell nucleus. The process by which a multicellular organism develops from a single cell through an embryo stage into an adult is ultimately controlled by the genetic information of the cell, as well as interaction of genes and gene products with environmental factors.

Genetic engineering

Genetically Modified Organisms (GMO) are organisms whose genetic material has been altered by genetic engineering techniques generally known as recombinant DNA technology. Genetic engineering has expanded the genes available to breeders to utilize in creating desired germlines for new crops. After mechanical tomato-harvesters were developed in the early 1960s, agricultural scientists genetically modified tomatoes to be more resistant to mechanical handling. More recently, genetic engineering is being employed in various parts of the world, to create crops with other beneficial traits. New research on woodland strawberry genome was found to be short and easy to manipulate. Researchers now have tools to improve strawberry flavors and aromas of cultivated strawberries as stated in a publication by Nature Genetics.

Herbicide-tolerant GMO crops

Roundup Ready seed has a herbicide resistant gene implanted into its genome that allows the plants to tolerate exposure to glyphosate. *Roundup* is a trade name for a glyphosate-based product, which is a systemic, nonselective herbicide used to kill weeds. *Roundup Ready* seeds allow the farmer to grow a crop that can be sprayed with glyphosate to control weeds without harming the resistant crop. Herbicide-tolerant crops are used by farmers worldwide. Today, 92% of soybean acreage in the US is planted with genetically modified herbicide-tolerant plants (IBS News report, 2006).

With the increasing use of herbicide-tolerant crops, comes an increase in the use of glyphosate-based herbicide sprays. In some areas glyphosate resistant weeds have developed, causing farmers to switch to other herbicides.(Farmers guide to GMO Some studies also link widespread glyphosate usage to iron deficiencies in some crops, which is both a crop production and a nutritional quality concern, with potential economic and health implications (Ozturk, et al. 2008).

Insect-resistant GMO crops

Other GMO crops used by growers include insect-resistant crops, which have a gene from the soil bacterium *Bacillus thuringiensis* (Bt), which produces a toxin specific to insects. These crops protect plants from damage by insects; one such crop is Starlink. Another is cotton, which accounts for 63% of US cotton acreage (Cornezo, 2006).

Some believe that similar or better pest-resistance traits can be acquired through traditional breeding practices, and resistance to various pests can be gained through hybridization or cross-pollination with wild species. In some cases, wild species are the primary source of resistance traits; some tomato cultivars that have gained resistance to at least 19 diseases did so through crossing with wild populations of tomatoes (Kimbrell, 2002).

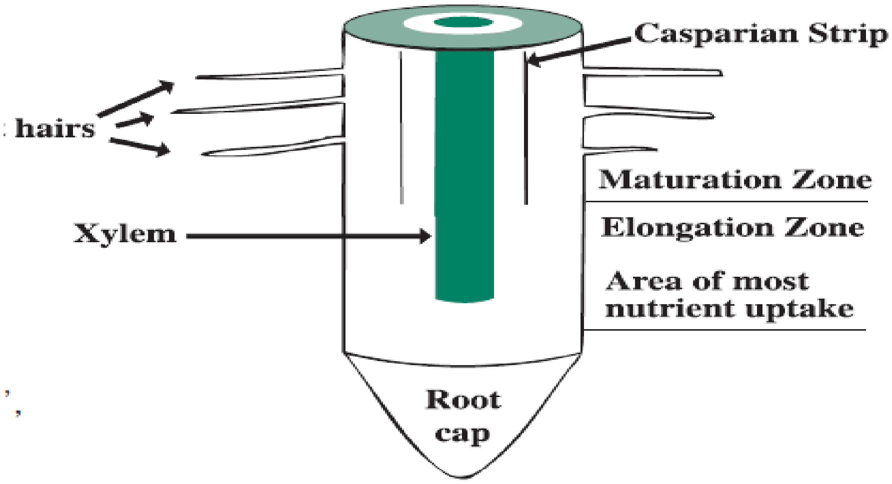
Costs and benefits of GMOs

Genetic engineers may someday develop transgenic plants which would allow for irrigation, drainage, conservation, sanitary engineering, and maintaining or increasing yields while requiring fewer fossil fuel derived inputs than conventional crops. Such developments would be particularly important in areas which are normally arid and rely upon constant irrigation, and on large scale farms. However, genetic engineering of plants has proven to be controversial. Many issues surrounding food security and environmental impacts have risen regarding GMO practices. For example, GMOs are questioned by some ecologists and economists concerned with GMO practices such as terminator seeds (Conway, 2000; Pillarisetti and Radel 2004), which is a genetic modification that creates sterile seeds.

Farmers using patented seed are restricted from saving seed for subsequent plantings, which forces farmers to buy new seed every year. Since seed saving is a traditional practice for many farmers in both developing and developed countries, GMO seeds legally bind farmers to change their seed saving practices to buying new seed every year (Farmers Guide to GMO, 2008). Locally adapted seeds are an essential heritage that has the potential to be lost with current hybridized crops and GMOs. Locally adapted seeds, also called land races or crop eco-types, are important because they have adapted over time to the specific micro-climates, soils, other environmental conditions, field designs, and ethnic preference indigenous to the exact area of cultivation (Gary Paul, 1989). Introducing GMOs and hybridized commercial seed to an area brings the risk of cross-pollination with local land races. Therefore, GMOs pose a threat to the sustainability of land races and the ethnic heritage of cultures. Once seed contains transgenic material, it becomes subject to the conditions of the seed company that owns the patent of the transgenic material (Vandana, 2000).

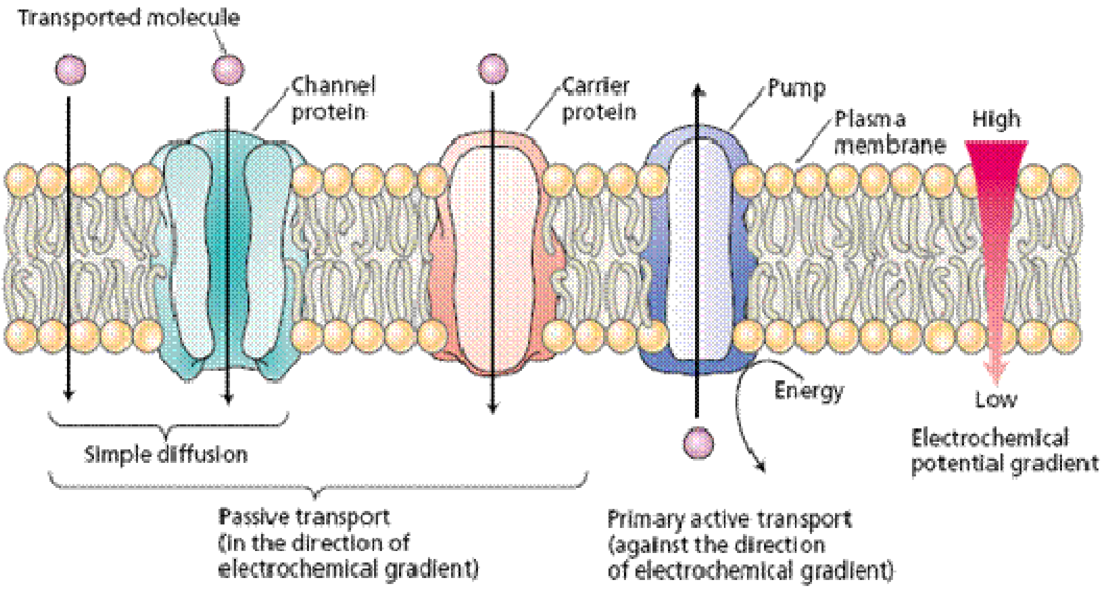
In a world where population growth is outstripping food supply agricultural -and especially plant-biotechnology, needs to be swiftly implemented in all walks of life.

Fig.1 Cross section of lower root tip



Source: Nutrient Management Module No.2

Fig.2 Plasma membrane as the site of nutrient transport



Source: plant physiology by Taiz and Zeiger,2010

Fig.3 Cross sectional view of the cell membrane: The fluid mosaic structure. Lipid bilayer and proteins form the central non-polar and the peripheral polar regions. H+-ATPase (proton pump) pumping protons is also shown in the figure.The + and - signs inside the small circles represent the positive and negative transmembrane potentials outside and inside the cell respectively.

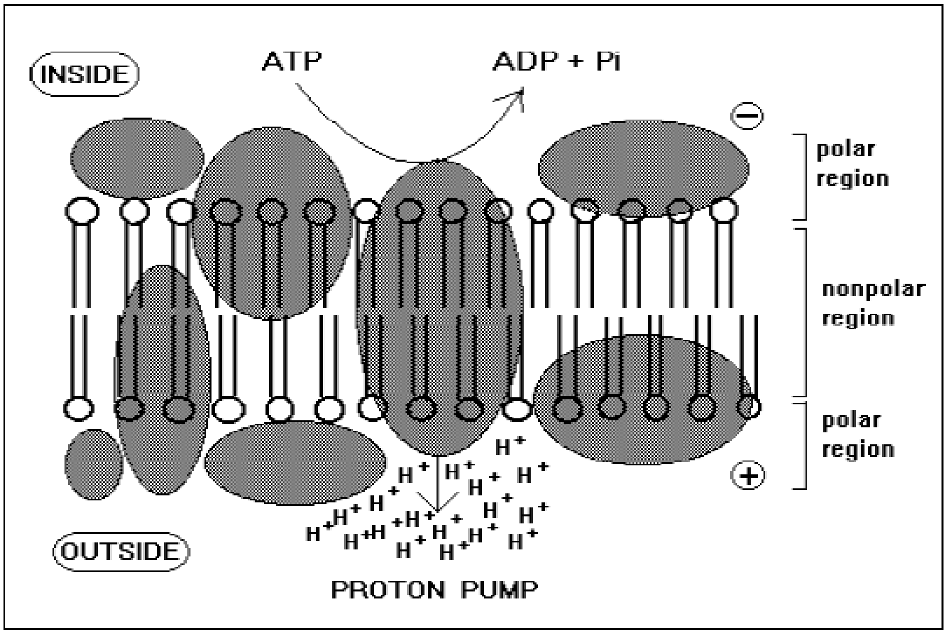
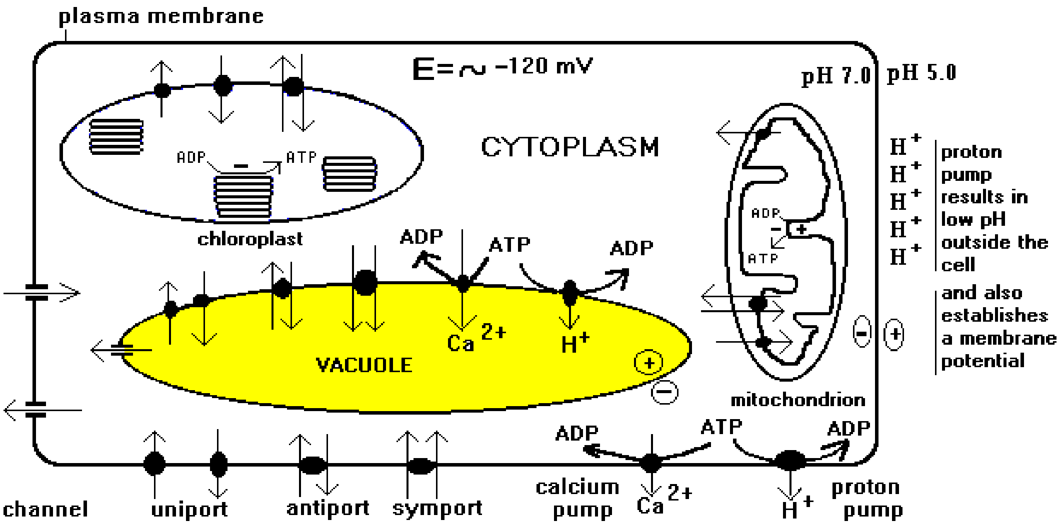


Fig.4 Diagram of a typical plant cell (cell wall not shown) showing the transport of ions and moleculesacross the membranes. ATP synthesis is driven by the proton motive force generated by electrontransport in mitochondrion and chloroplast. On the other hand, hydrolysis of ATP mediated by H+-ATPase generates proton motive forces across plasma and vacuolar membranes resulting in the generation of transmembrane potential (shown as + and - signs within small circles). Ca2+ pumping by Ca2+- ATPase is also shown. Transport processes by uniport, symport, and antiport.



Source: study of general article by shiv kumar swamy

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