Tree Growth and Essential Nutrient Elements

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Abstract - There are 16 elements known to be essential for tree growth. Of these, 4 originate in the atmosphere and 12 in the soil. This paper describes the function of each element in the tree and the consequences of an inadequate supply.

There are 16 elements known to be essential for tree growth. These can be conveniently divided into two groups which we can call macronutrients and micronutrients. This division is based upon their relative needs in the tree. There are nine macronutrients that are required in tree foliage in concentrations generally of 1,000 parts per million (ppm) or more and seven micronutrients that are generally required at a concentration of 100 ppm or less. The macronutrients, in decreasing amounts found, include: carbon (C), oxygen (O), hydrogen (H), nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), and sulfur (S). The micronutrients, in decreasing amounts found, include: chlorine (Cl), iron (Fe), boron (B), manganese (Mn), zinc (Zn), copper (Cu), and molybdenum (Mo). When expressed in terms of the relative number of atoms of each element, the range includes 60,000,000 atoms of H for each 1 atom of Mo.

Most nutrient uptake by trees occurs against a concentration gradient. That is, the concentration in the root is generally higher than it is in the soil during uptake. Thus energy must be expended for nutrient uptake to occur and any factor which affects root or shoot metabolism will affect the rate of nutrient uptake. The nutrient concentration in the tree as well as in the soil affect uptake. A high internal level requires excessive amounts of energy in order to move a nutrient element into the tree against a high concentration gradient.

The energy used in nutrient uptake is derived from carbohydrates which are stored in the roots. Since shoots have first access to carbohydrates formed during photosynthesis, trees must have enough light to conduct ample photosynthesis or nutrient uptake from the soil will be impaired by small, poorly fed root systems with low levels of available carbohydrates.

The rate of movement of nutrients within the tree is greatly influenced by the rate of water movement and eventually to the rate of transpiration. Some elements, once fixed in position in the tree, become quite immobile. These include Ca, Fe, B, Mn, Cu, and Zn. Others are fairly easily redistributed within the tree from older to younger tissues. These elements include N, P, K, and Mg. This redistribution, or internal cycling, may help satisfy some of the annual growth requirements, especially in the spring before leaf-out.

Nutrient balance is considered as important for efficient tree growth as nutrient concentration. Ignoring C, O, and H (all of which come from carbon dioxide and water), more N is used than any of the other elements, and using N as 100, the relative concentrations of the other nutrient elements can be determined. The relative optimum concentration for other macronutrients for seven species of temperate conifers has been determined. They were: K, 54.2; P, 18.9; Mg, 5.4; and Ca, 5.3. Similar values have not been reported for tropical conifers except *Pinus caribaea*.

A high concentration of one element in the soil often depresses the uptake of other similar elements. For example, in serpentine soil, the naturally high level of Mg will depress the uptake of Ca. Likewise, in low K soils, the application of fertilizer with N present in the ammonium (NH_4^+) form, will depress the uptake of K^+ and increase the severity of the K deficiency.

A tree will take up some of almost any element that is in the soil. A single sample of hardwood tree leaves was found to contain more than 60 elements, including gold, lead, mercury, arsenic, and uranium. Some elements such as silicon are not considered as essential for growth but are accumulated in fairly large quantities by certain species of trees. Several hardwoods in the tropics cannot be used for either lumber or pulp because their high silicon content destroys saws and other machines by its abrasive properties.

Roots do have some selectivity in which elements they will take up. This is demonstrated by the fact that the high silicon species occur in mixtures with many other species that do not accumulate silicon, all with their roots intermixed in the same soil.

Nutrient elements are divided not only on the basis of the amount needed (macronutrients and micronutrients), but also on the basis of their function. Some are structural elements and others regulate chemical reactions within the tree. Some elements perform both functions. Thus, this distinction is not as clear as the macronutrient- micronutrient separation. Symptoms indicating a deficiency of any of the nutrient elements are affected by two factors. These are (1) the function or functions performed within the tree and (2) whether or not the nutrient is easily moved (translocated) from old to new parts of the tree.

A typical tree (not a seedling or sapling) contains principally three nutrient elements that we seldom think of as nutrients. They are C, O, and H. Collectively, they constitute more than 94% of the weight of the tree. They constitute most of our seedlings, too. Just not quite that high. Despite the fact that they are often overlooked in discussions of tree nutrition, their roles and functions are discussed in the following section concerning macronutrients.

MACRONUTRIENTS

Carbon - The C forms the skeletons of all the organic molecules in the tree, including both the cellulose and the lignin. It enters the tree as CO_2 through the stomates on the leaves or needles and during photosynthesis the C is reduced. That means that it gains much H from water. Since C represents about 45% of the weight of the tree, a deficiency is shown simply as reduced growth of the tree. Except in enclosed environments, such as in greenhouses, a shortage of CO_2 almost never occurs, yet trees are often not able to obtain CO_2 from the atmosphere at optimum rates. The cause of the apparent deficiency is indirect. Since the CO_2 must enter the stomates, any condition that results in the closing of the stomates will interrupt the supply of CO_2 for photosynthesis and thus reduce growth. The most common cause of closed stomates is drought. Thus the tree has a dilemma. By closing the stomates in order to conserve water it also restricts photosynthesis which provides carbohydrates for both growth and energy. A potassium deficiency will also stimulate stomate closure and produce a similar growth reduction.

Oxygen - There are two major and one minor sources of oxygen for the tree. First, much of the oxygen enters the tree as part of the CO_2 used in photosynthesis. Second, oxygen is used directly from the atmosphere in respiration, as O_2. Third, a small amount of oxygen is acquired from water through hydrolysis reactions. Thus, any oxygen deficiency to the leaves or needles results primarily from drought through its effect on the stomates and on the water status of the tree. Conversely, in the soil, the roots may suffer a deficiency of O_2 needed for respiration, caused by excess water. Like carbon, oxygen provides about 45% of the weight of the tree.

Hydrogen - Perhaps surprisingly, the greatest number of atoms of any element in the tree is hydrogen. This can be seen from the general formula for carbohydrates (CH_2O). However, because of its very low atomic weight, hydrogen is the third element as far as percent composition goes. It represents about 6% of the weight of the tree. The source of the hydrogen is the water used in photosynthesis. Thus, any hydrogen deficiency is the result of drought since it both impairs the water status of the tree and causes the stomates to close, thus excluding CO_2 and preventing photosynthesis from occurring.

Nitrogen - There are two principal forms of nitrogen in the soil that the tree can utilize. These are ammonium (NH_4^+) and nitrate (NO_3^-). Most species of trees appear to make more efficient use of NH_4^+ than they do of NO_3^-. This has been found to be true of all pines and most hardwoods that have been studied. The ultimate source of the nitrogen is the N_2 gas in the atmosphere. It can be fixed into organic forms by only a small group of microorganisms, including some bacteria, actinomycetes, and blue-green algae. When these organisms die, the organic N is mineralized into NH_4^+ (mineralization) and then some of that is transformed into NO_3^- (nitrification) by other specialized bacteria. Poor soil drainage and low soil temperature slow both mineralization and nitrification and can thus induce a nitrogen deficiency despite the presence of plentiful total nitrogen in the soil.

In the tree, the nitrogen is an essential part of all amino acids, proteins, enzymes, coenzymes, chlorophyll, nucleotides, nucleic acids, and many other plant components. Thus, it is an extremely important element.

Worldwide, nitrogen is the most commonly deficient nutrient in forest soils. The deficiency symptoms on most trees are chlorosis (yellowish-green color of entire needles and leaves) and reduced growth. Even where deficiency symptoms don't appear, substantial responses to nitrogen fertilization have occurred. Deficiency of nitrogen is most common in highly leached soils and in peats. In the first case, the deficiency results from a lack of nitrogen in the soil and in the second, from poor mineralization from a large supply.

<u>Potassium</u> - The only macronutrient that does not have a structural role in the tree, potassium is however needed in relatively large quantities to serve its various regulatory functions. Both in the soil and in the tree, the potassium is found as the K^+ ion. Consequently it is highly mobile in the tree and may even be leached from the foliage by heavy rain, especially where the rain is highly acidic. As noted in the discussion of carbon, potassium is important in the regulation of stomate opening and closing. It activates many enzymes and activates starch and protein synthesis. It also is involved in maintaining charge balance in the tree and is transported with anions such as nitrate (NO_3^-), sulfate (SO_4^{-2}), phosphates (HPO_4^{-2} or $H_2PO_4^-$), and organic acids ($RCOO^-$). Considerable potassium is required for this function, for maintaining plant turgor, and for activating enzymes. Evidence also exists that a good K supply increases the tree's resistance to various pathogens, and that it increases the tree's ability to withstand low temperatures.

On most soils, trees are able to obtain sufficient potassium for reasonable growth. Soils most likely to be K deficient are highly leached and acidic. A strong potassium deficiency has been confirmed for some of the glacial outwash soils in the Adirondack Mountains in New York. The symptoms of potassium deficiency are general needle tip or leaf edge chlorosis. Some needle death will occur in extreme cases. However, other symptoms occur in some species. These range from dull blue-green of some needles to a bright red of some hardwoods. Thus, it is necessary to confirm potassium deficiency through detailed knowledge of the various species, through soil or plant analysis, or through potassium fertilization tests.

Calcium - The element is absorbed from the soil as Ca^{+2} but unlike magnesium (see below), it is almost immobile in the tree. The largest amount of calcium is used as part of the Ca-pectates which are in the middle lamella and serve as the glue that holds cells together. In woody tissue, this function is eventually taken over by lignin but in foliage and young tissues, especially in meristems, the Ca is very important. It is also required for normal cell division. A deficiency results in a discoloration of the roots (difficult to see), twisted and deformed tissues, and in pines there may be resin exudation around buds and some leader die-back.

A deficiency of calcium is most likely to occur in acidic, highly leached, eroded soils. It is frequently suspected in phosphorus deficient soils. However, most of the common phosphorus sources (see below) contain more calcium than phosphorus. Consequently, there has been relatively little information gathered on calcium except in laboratory or greenhouse studies. In nurseries, when soil acidity increases, either calcitic or dolomitic lime ($CaCO_3$ or a mixture of $CaCO_3$ and $MgCO_3$, respectively) is added to the soil for pH value adjustment. This practice also provides calcium or calcium plus magnesium fortuitously. Very few examples of calcium deficient forest or nursery soils have been substantiated.

Magnesium - Magnesium is the only mineral element in the chlorophyll molecule. It is essential for photosynthesis to occur. It is also required for many enzymatic reactions in the tree involving ATP and enhances respiratory enzymes and is crucial to protein synthesis. It is more mobile in the tree than calcium. Deficiency symptoms are usually a strong golden or dark yellow. The chlorosis starts at the tips of needles or the edge of leaves and works inward. In hardwood leaves, it often referred to as an interveinal chlorosis. A deficiency of magnesium is most likely in acidic sandy soils that are low in organic matter. Exceedingly high levels of Mg are found in soils that are derived from serpentine rock.

Phosphorus - Trees take up phosphorus from the soil in either of two inorganic forms. They are $H_2PO_4^-$ or $H\ PO_4^{-2}$. Soil acidity is the principal determinant of the form with $H_2PO_4^-$ dominant below pH 7. Much of the phosphorus in the soil is present as organic compounds (sometimes as much as 80%) but these must be mineralized by microorganisms to an inorganic form for use by the tree. Phosphorus is second only to N as the most common limiting element in forest soils.

The most widely recognized role of phosphorus in the plant is in the energy providing (ATP-ADP) system. It is also found in nucleic acids, nucleotides, some proteins, several coenzymes, membrane phospholipids, and attached to many different sugars that are important in photosynthesis and respiration. Also both organic and inorganic phosphates act as buffers in the cell to maintain a constant pH value.

A deficiency of phosphorus results in slow growth of most tree species. In some pines, the only symptom is short primary needles. However in other pines and many hardwoods, the production of anthocyanin pigments becomes very evident and the mature leaves or needles become quite purple. Trees that lack well-developed mycorrhizae often display the purple foliage because of the inability of the non-mycorrhizal roots to take up phosphorus even when an adequate supply is present in the soil.

Sources of phosphorus for use in tree culture include ordinary superphosphate, triple superphosphate, diammonium phosphate, and rock phosphate. The rock phosphate is usually the least expensive but it is only useful where the soil is very acid (<pH 4.5). In such soils, however, it does prevent the phosphorus from being fixed as iron or aluminum phosphates but its rate of release is so slow that it is not useful for recently planted trees that are under a phosphorus stress. It will, however provide a constant source of phosphorus for several years for established trees. The advantage of ordinary superphosphate is that it contains sulfur as well as phosphorus and calcium. Triple superphosphate does not contain any sulfur but it has a high phosphorus content. Thus, where transportation costs are important, it is the most economical to use. The diammonium phosphate is the most soluble of the phosphorus sources and its content of phosphorus is the same as triple superphosphate. It contains a little nitrogen but no sulfur or calcium. It is very useful where a quick response to phosphorus is needed.

<u>Sulfur</u> - The SO_4^{-2} ion is the form of sulfur used by all plants. It is highly mobile in the soil but once metabolized in the tree it becomes quite immobile. Thus deficiency symptoms appear in newly formed tissues. Two vitamins, one coenzyme, and three amino acids contain sulfur. It is important in protein synthesis. These organic forms of sulfur return to the soil during leaf and needle fall. The principal reservoir of sulfur in the soil is the organic compounds but before the tree can take up any of this sulfur it must be mineralized to the inorganic form by microbes. Very dry conditions or low soil temperature will impede this mineralization process. Despite the fact that the

SO_4^{-2} ion is easily leached from the soil, the fact that it is slowly released into the soil solution be microbial mineralization, the tree takes it up and very little is actually lost.

The sulfur in very soluble fertilizer materials such as gypsum ($CaSO_4$) can be leached from the soil because it is all available at once and roots cannot take it up rapidly.

Pines deficient in sulfur have been reported in Australia and in both the southeastern and northwestern United States. Also, sulfur deficiency has become quite common in sandy nursery soils. This has happened since the introduction of triple superphosphate fertilizer which lacks the sulfur contained in ordinary superphosphate. This condition has been corrected through the use of such fertilizer materials a ammonium sulfate (as a nitrogen source), gypsum (as a calcium source) or Epsom Salts (as a magnesium source). All such fertilizers must be applied in small doses since the SO_4^{-2} ion is easily leached from the rooting zone of the soil.

MICRONUTRIENTS

Chlorine - Clearly essential for tree growth, only one function for chlorine has been confirmed. It enhances electron transfer from water to chlorophyll during photosynthesis. The formation of club-shaped root tips in chlorine deficient trees suggests that other roles for this element remain to be discovered. It is absorbed from the soil as the Cl^- ion and despite the fact that it is usually the most abundant of the micronutrients in the tree, the absolute requirement for it is very small. No confirmed chlorine deficiencies in trees in normal soils has ever been reported.

Iron - Iron (Fe) deficient trees are fairly common but the deficiency is usually more strongly related to species or age than to a lack of the element in the soil. The acidity of the soil also strongly affects the availability of the iron. An extreme case of iron deficiency occurred in a pine nursery that was growing seedlings in soil at pH 8.2. The situation was completely cured when the soil was changed to pH 5.3. The seed source remained the same and no iron had been added to the soil. Because iron is a micronutrient, it is possible to apply it to foliage as a complex organic compound called a chelate. This can quickly and inexpensively correct a deficiency. Iron is very immobile in the tree. Thus, it is the newest foliage that exhibits the deficiency symptoms of chlorosis. Iron is essential in photosynthesis, respiration, and nitrogen metabolism.

Fortunately, except for those species that are genetically predisposed to iron deficiency (e.g., oaks and hickories), very little deficiency has been reported in trees beyond the seedling stage or where trees have been improperly transplanted into calcareous soils with high pH values.

<u>Boron</u> - Boron is the most commonly deficient microelements in forest soils. It is especially likely to be deficient in sandy soils that are low in organic matter and in soils of volcanic origin.

One of the first results of boron deficiency is the cessation of the growth of root tips. This is followed by impairment and often death of all apical meristems and the turning brown of the pith near the meristems. This leads to formation of many new buds and the growth of many new branches. These may, in turn, die and the process repeat. Most of the boron in the soil is present in the organic matter and it becomes available as it is mineralized by microorganisms. Thus, drought decreases its availability and rain increases it availability. This pattern of alternating growth is shown by many trees in areas where droughts are common. The trees will grow quite normally during the moist period and then become very crooked. Such growth can be prevented but it cannot be corrected. Thus, in situations where boron deficiency is likely, it is important that sufficient boron be applied to the soil as close to the planting date as possible. Boron availability is directly related to soil organic matter content and negatively related to soil pH value, especially above pH 6. Boron is apparently the only nutrient element taken up in the non-dissociated form. It is taken up directly as boric acid (H_3BO_3).

In general grasses are more tolerant of a low boron status in the soil than pines. Thus, the grass can become a severe competitor with newly planted pines in low boron soils. Application of B near the tree can completely reverse the situation.

In addition to its necessity for growth of new cells in the meristematic regions, boron is needed for protein synthesis, pollination, and carbohydrate movement and metabolism. Because of this latter role, leaves of boron deficient hardwoods often become thickened and curled as carbohydrates accumulate in them.

There is difficulty in determining the optimum concentration of boron in tree foliage because the amount needed is related to the uptake of both calcium and potassium. Thus the application of needed phosphorus (nearly all sources of which contain considerable calcium, as noted above in the discussion of calcium) or potassium can aggravate a marginal boron status in the tree. The correction of one deficiency can easily intensify the other.

<u>Manganese</u> - Most trees tolerate wide ranges in the level of manganese in their tissues. However, both deficiencies and toxicities have been reported. The rate of accumulation is highly dependent on species and two trees of different species, on the

same soil, may vary 10-fold in the amount of manganese accumulated. Deficiency of manganese causes a chlorosis that is between the pale yellow of iron deficiency and the golden yellow of magnesium deficiency. On hardwood leaves, there are often green stripes remaining. Photosynthesis, respiration, fatty acid synthesis, and nucleotide synthesis are all affected by manganese. Its availability is directly related to soil acidity. That is, it is inversely related to the pH value. Thus, the application of lime may induce a manganese deficiency. In natural soil, manganese deficiency rarely occurs.

Zinc - In tree seedlings, zinc deficiency resembles boron deficiency. In older trees it results in a bronzing of new leaves of hardwoods and a chlorosis and stunting of pines. In the tree, zinc activates several enzymes. A deficiency of zinc in native forests is almost unknown but exotics and natives planted off-site have been shown to suffer considerably. Hickories are particularly sensitive.

Copper - In seedlings, copper deficiency is seen as drooping foliage. In larger trees branches twist and droop. In conifers the leader may become a "shepherd's crook." Copper is essential in photosynthesis, respiration, and the formation of at least one hormone. Copper deficiency is most common on organic soils such as peats. It also occurs on coarse sands. Except in a few specific locations, copper deficiency is not usually a problem in tree nutrition.

Molybdenum - Molybdenum is required in the smallest quantities of any nutrient by trees. Its only known function is in nitrate reduction. Somewhat larger amounts are required by the nitrogen-fixing microbes in and on the soil and especially in the nodules of nitrogen-fixing leguminous and actinorhizal trees, shrubs, and herbs. It should also be noted that all nitrogen-fixing organisms also require cobalt. Thus, since their activity is essential for providing most of the nitrogen used by trees, it could be argued that cobalt is at least indirectly required for tree growth. However, there is no evidence at this time to suggest that the trees themselves require any cobalt.

SUMMARY AND CONCLUSIONS

In this summary of the roles of the 16 elements that are known to be essential for the growth and vigor of trees, we have attempted to accomplish three things. First, we have attempted to review the factors of climate and soil that are important to the supply of the various elements. Second, we have described the elements' functions, both as structural components and as metabolic regulators in trees, and symptoms produced by deficiencies. Finally, and perhaps most importantly, we have attempted to call attention to those elements and those soils that are most likely to present problems to the professional arborist or forester.