MINERAL NUTRITION: WHAT ARE THE GUIDING PRINCIPLES?

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As early scientists developed the ability to analyze plants, they found that most of the plant was composed of water and organic compounds, and that in most plants the mineral fraction accounted for less than 10% of the dry mass. At that time, the presence of an element in the plant was accepted as proof that the element was essential to the plant. However, it was found that plants often take up and incorporate any element present in the growing medium, sometimes accumulating an element to toxic levels. By the turn of the century, water and sand cultures were being used to study the mineral needs of plants under controlled conditions. In 1939, Arnon and Stout published the criteria for essentiality of a nutrient element:

- The element must be present in the plant for normal growth and completion of the life cycle.
- The element is required specifically and cannot be replaced by another element.
- The element must be directly involved in growth or metabolism.

By the turn of the century the major or macronutrients necessary for plant growth had been identified. In addition to carbon (C), hydrogen (H), and oxygen (O), nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg), and iron (Fe) had been shown to be essential. In the first half of the 1900s the minor or micronutrients manganese (Mn), copper (Cu), zinc (Zn), molybdenum (MO), boron (B), and chlorine (Cl) were identified. The terms macro- and micronutrients are used to distinguish elements needed in relatively large amounts from those required in only tiny amounts. In no way do these designations mean that any of these elements is less ‘essential’ than any other.

Once it was known that certain mineral elements were needed for plant growth, plant response to the addition of an element that had been lacking was thought to follow a certain pattern of diminishing returns. As one added the deficient element, plant response would be great and then as the deficiency was overcome, response to additional provision would be less and less as the growth rate approached its maximum. However, what we find is that the pattern is more likely to be one with an ‘inversion point’, where growth increases until the element is present in sufficient amounts but declines again when supply of the element becomes excessive (the toxic range). Put simply, if some is good, more is not necessarily better.

We can study the response of cranberry plants to the absence of each mineral element and what happens as we reintroduce it into the medium. But in a field situation, we are more interested in finding out what factor(s) is limiting growth and production. In addition to the mineral elements, other factors may be limiting to production or may interact with mineral nutrition. We can think of all the essential mineral and other factors as different length staves in a barrel. The shortest stave will determine how much the barrel can hold. If that stave is lengthened (the element is added), the barrel will hold more (plant growth and productivity will improve) until a new limiting factor or short stave is reached. In cranberry production, the limiting factor may not always be nutritional. Mineral elements interact with one another, with management, and with cultivar.

Interactions among the responses to the additions of mineral elements may be due to interaction in the soil or during uptake, or may be due to the limiting element rule. For example, if N was lacking, the plants might not respond to the addition of K but if N is added as well, then there might be a K rate response. Often management factors are limiting plant productivity and response to nutrient addition. For example, if a cranberry planting was suffering from upright dieback disease, adding fertilizer might not increase growth and yield. Conversely, in a nutrient poor bed, recovery from tipworm damage might be limited. Response to nutrition also varies by cultivar. An example from research in Oregon by Hart, Poole, and Strik is shown in the table below.

Yield (bbl/A) at various N rates, third year of treatment. Values followed by the same letter are statistically similar.

Cultivar	0 lb/A N	20 lb/A N	40 lb/A N	60 lb/A N
Crowley	85	110b	152a	141 a
Stevens	115	201 c	314b	485 a

Yield response in 'Crowley' was maximized at 40 lb/A nitrogen while 'Stevens' yield continued to increase at the 60 lb/A rate.

Roles of the mineral elements.

The essential elements all have specific roles in plant structure and metabolism. We can group elements according to their functions in the plant:

1. Structural elements make up the physical body of the plants. In addition to C, H, and O that are components of all organic matter, mineral elements play structural roles,
    N and S are components of structural and enzymatic proteins.
    N and P are structural components of DNA.
    P is part of the phospholipids that make up the cell membranes.
    Mg forms the center of chlorophyll molecules.
    Cu and Fe are part of the structure of important energy transferring proteins.
    Ca strengthens cell walls.
2. Mineral elements are involved in enzyme functions.
    K, Mg, and Mn are enzyme activators, acting as catalysts.
    Fe, Cu, Zn, and Mo are part of the active structural part of enzyme cofactors, molecules attached to enzymes that facilitate reactions.
3. Mineral elements are critical in photosynthesis
    Mn and Cl are involved in splitting water to release oxygen in light reactions.
    Fe is involved in energy transfer and in chloroplast development.
    Mg is part of the chlorophyll molecule.
    K is involved in cross-membrane energy harvesting reactions.

In addition to these general roles, some elements play other specific roles in the plant:

1. Nitrogen

As a critical constituent of protein, nitrogen is a controlling element in plant nutrition. The production of chlorophyll, the predominant functional protein in plants, is regulated in part by the availability of N.

2. Phosphorus

Phosphorus plays many roles in plant metabolism. P is involved in energy transfer as part of the ATP molecule. P plays a regulatory role in starch synthesis, active transport of materials across membranes, root growth and function, and hormonal balance. This last is critical to floral induction.

3. Potassium

Potassium is the only major element with no structural role in the plant. K is involved in sugar transport in the phloem tissue (transport among plant organs). K also has a major role in preserving plant turgor (water relations) and in osmoregulation (regulating water movement across plant membranes). This last role accounts for the involvement of K in opening and closing of stomata and extension growth. K is also involved in cold tolerance of plants.

4. Calcium

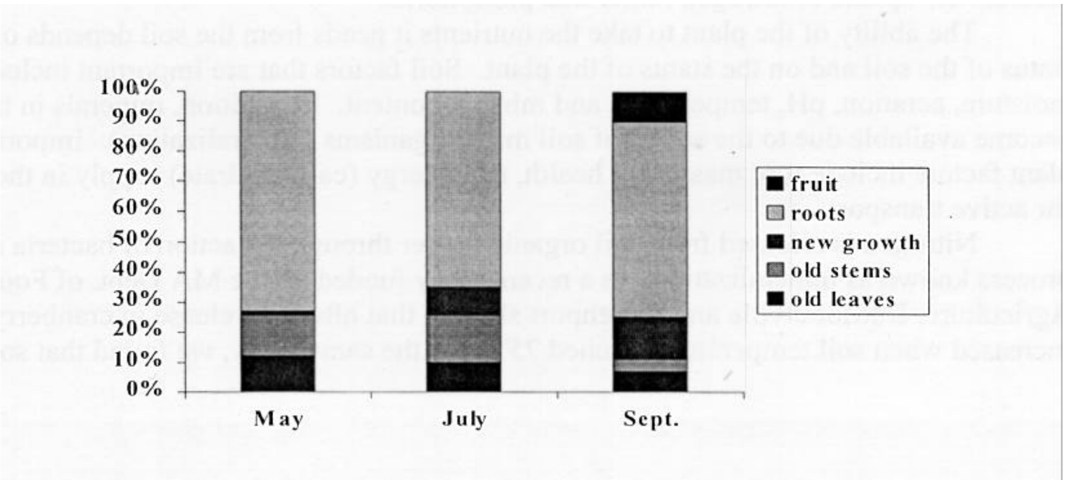
Calcium is involved in determining membrane structural integrity that determines the selectivity of membranes in taking in or excluding materials. This is the basis for the plant's ability to actively take up needed minerals and exclude those that might be harmful.

5. Boron

Boron is essential for pollen tube growth, if B is deficient, pollination may occur but fertilization and fruit set will not be successful. B is also involved in cell elongation and must be present in sufficient amounts for bud and flower retention on the plant.

Periods of peak nutrient demand.

Nutrient demand tends to be driven by production of plant biomass. In cranberry this would correspond to extension of new growth in the spring, fruit formation and filling, initiation of floral buds, and root turnover. Root production occurs after the first flush of new vegetative growth and late in August after vegetative growth has ceased for the season. Patterns of biomass production in cranberries are shown in the figure below (DeMoranville, 1992).



Fruit filling and floral bud initiation occur during the same time period during the summer and so may represent a period of competition among plant parts for resources. Birrenkott and Stang (1990) showed that cranberry fruit on an upright are in competition for resources. Patten and Wang (1994) showed that when numbers of berries on an upright was high, buds produced tended to be small. While it is likely that competition for carbohydrates is mainly responsible for these observations, competition for mineral elements may also play a part. It is known that nutrients are drawn from source areas (roots and storage tissues) to 'sinks', rapidly growing tissues and plant parts with high levels of plant growth regulators (hormones) such as fruit.

Ways to evaluate plant nutrient status.

Tissue testing is used to determine the content of the various nutrients in the plant. This can be informative for crops such as cranberry where standard ranges have been established. Soil testing can also be useful in determining what is available for the plant to acquire from the soil. However, one of the best ways to determine nutritional status is to look at the plant. Stunting or off colors in the foliage may be symptoms of mineral deficiency.

Short or pale uprights in cranberry are often an indication that N is lacking. Because leaf greenness (chlorophyll content) is often related to N status, this parameter can be measured and calibrated to nitrogen status. Minolta markets the SPAD meter, a device that measures leaf greenness in dimensionless units (SPADs) that correlate with chlorophyll content. Tentative ranges for cranberry have been established based on the positive correlation between tissue %N and SPAD reading in an extensive cranberry survey. This allows the use of the SPAD meter to substitute for a mid-season tissue test. This may be useful as tissue test values are only stable and subject to useful interpretation late in the season and thus, mainly serve as a 'report card' for this seasons management and for planning for next season.

Where and how do plants get the nutrients they need?

For the most part, plants take their nutrients from the soil via the roots. This is an active process (requiring the expenditure of energy), allowing the plants to accumulate the nutrients they need. In this way, nutrient concentration in the plant may be greater than that in the soil. In many plants, this uptake is mediated by *mycorrhizae*, fungal organisms that live within the roots. Cranberry plants from associations with Ericaceous mycorrhizae that differ from the more common types in that they are more likely to mediate the uptake of nitrogen rather that phosphorus.

The ability of the plant to take the nutrients it needs from the soil depends on the status of the soil and on the status of the plant. Soil factors that are important include moisture, aeration, pH, temperature, and mineral content. In addition, minerals in the soil become available due to the action of soil microorganisms (mineralization). Important plant factors include root mass, root health, and energy (carbohydrate) supply in the roots for active transport.

Nitrogen is released from soil organic matter through the action of bacteria in a process known as mineralization. In a recent study funded by the MA Dept. of Food and Agriculture, DeMoranville and Davenport showed that nitrogen release in cranberry soils increased when soil temperature reached 75°F. In the same study, we found that soil pH was important in determining the form of the nitrogen after it was released by mineralization. The initial product of mineralization is ammonium, a form preferred by cranberry plants. At low pH, the N remained in this form because the bacteria that convert ammonium to nitrate are suppressed at low pH. This confirms the recent study by T. Roper and A. Krueger. Study results are compiled in the table below.

Effect of temperature on total N release.

Soil temperature	Total N (ppm)
55°F	77.77 b
60°F	65.60 b
65°F	61.55 b
70°F	77.94 b
75°F	183.34a

Effect of pH on conversion to nitrate

Soil pH	Nitrate N (ppm)
High (6.0)	50.22 a
Medium (4.5)	6.45 b
Low (3.0)	8.51 b

Soil pH also has effects on the availability of nutrients in the soil and on the ability of most plants to take up those nutrients. This is due to the change in chemical state of the elements as the soil pH changes. As the chemical state changes, the interaction between the mineral and soil particles changes so that the element becomes more tightly of loosely held in the soil. In fact, at pH 4, all nutrients except the minor element metals are quite tightly bound in the soil (poorly available). Plants often exhibit a preference regarding which chemical form of an element is taken up as well. For example, at pH below 4, nitrate may be taken up preferentially compared to ammonium and K uptake may be depressed. This is due to the need for the roots to exchange acid (H^+) equivalents for the cations (K, ammonium). As soil pH drops, H^+ builds up in the soil and moving more out of the plant becomes more difficult as the gradient increases. Because cranberries evolved in acid soils, they are adapted to life in a nutrient poor environment. To a large extent, pH effects that would be negative for other plants are not a problem for cranberries. This may be an advantage in suppressing pH sensitive weeds.

Moisture and aeration in the soil can determine nutrient availability. Plants take up nutrients dissolved in the soil water. If soil is too dry, minerals cannot dissolve and move to the roots and uptake cannot take place. Conversely, if soil is waterlogged, the oxygen the plant needs for root respiration to drive active uptake will be limited. Hydric status of the soil also determines availability of iron, manganese, and phosphorus that is bound to or released from iron compounds. In flooded soils, availability of these elements is high enough to present a danger of toxicity (especially of Fe and Mn) in species not adapted to flooded conditions. In fact, the ability of cranberries to tolerate high Fe and Mn is indicative of their status as wetland species. The change in P availability during flooding cycles on cranberry soils was shown in laboratory studies (Davenport et al., 1997). In peat and layered, sanded cranberry soils P is released from the soil during flooding. However, as the soil dries, P once again becomes bound on the soil. Moisture availability in the soil may also affect the ability of the plant to take up elements indirectly. If moisture is lacking, the movement of water up through the plant and out through the leaves (transpiration) will be limited and so will the uptake of elements that move in that water stream.

Plants have the ability to exert control over nutrient availability and uptake by releasing chemical compounds into the rhizosphere. Some compounds release needed elements from their attachment to the soil. Other compounds are released onto the root surface and bind elements that are present in excessive levels so that they are prevented from entering the roots. X-ray microanalysis of cranberry roots (Rosen et al., 1990) showed particles on the root surface containing Fe and Mn as well as P bound to the Fe. Both Fe and Mn are present at high levels in acid cranberry soils. While levels in the plants are higher than those in dryland species, they are not extreme, perhaps due to sequestering at the root surface.

Root anatomy may be affected by pH in the rhizosphere. Cranberries grown in solution culture had more branch roots at pH 6.5 than at 4.5 (Finn et al., 1990). This may have an effect on nutrient uptake.

In commercial production systems, some of the nutrition requirement is supplied in fertilizers added to the soil or applied to the foliage. Soil applied fertilizer dissolves in the soil water and is bound to the soil, fixed on the soil, or lost to leaching below the root zone. Bound and fixed fertilizer elements behave as native soil elements as discussed above. Foliar applied fertilizer generally cannot replace soil fertility. However, it can be useful during periods when soil uptake is limited and for elements that become tightly bound in the soil. Foliar uptake of nutrients is limited by the thickness of the leaf cuticle. In cranberry, the cuticle is less thick on the lower surface and some uptake can occur via that route. In addition, urea has been shown to be able to pass through the cuticle. Foliar uptake may also be limited by the amount of nutrient that can be delivered in the spray, washoff by rain, and length of the wet period after application. Uptake generally requires moisture on the leaf surface.

Seasonal nutrient carryover and recycling.

In perennial crops such a cranberry, nutrients can be stored in roots and mature stems. Further, floral buds are formed in the year prior to the crop. These factors make it likely that nutrients acquired in a given season may be more important in determining crop for the following season than for determining current season crop. Davenport and DeMoranville (unpublished) conducted a survey of 30 cranberry plantings in MA including the collection of grower records of N applications and yield. Regression and correlation analyses of surveyed variables showed that N applied in the year *prior* to the crop was an important determinant of yield while N application in the crop year was of little significance.

When labeled N was applied to cranberries in Oregon (Hart et al., 1994) prior to fruit set, at least one half of the label was found in old stems and roots. Nutrients that are incorporated into the fruit are lost when the crop is harvested and removed from the system. Smith (1994) showed that one third of ^{15}N taken into the plant from soil application moved into new growth and fruit in the year of application. The following year, 70% of the label was in mature tissue but 30% had been remobilized into that seasons new leaves and fruit. This illustrates the ability of cranberry plants to both store nutrients and to remobilize them for growth and fruiting.

Nutrition decision making in cranberry production

As we have seen, many factors, including temperature, moisture, pH, and soil type can play a part in the availability of nutrients and the ability of the plant to acquire them. How then can we decide what to supply to cranberries in the form of fertilizer?

1. Observe growth and flowering. Adjust fertilizer based on the appearance of the plants and the potential for cropping. Pay particular attention to upright length and growth above the fruit.
2. SPAD meters may be used to predict if N is sufficient. However, practiced observation of leaf greenness is just as good.
3. Test the soil to determine the organic matter content. This will supply information regarding the potential for mineralization. Soil pH information can be gathered at the same time. Soil testing every three years should be sufficient.
4. Adjust spring fertilizer applications based on soil temperature. Apply only after soil has warmed and decrease N applications if spring has been warm and dry.
5. Do not apply P to wet soils — P is being released under these conditions.
6. Adjust N rate based on cultivar and crop potential. Cultivars that crop heavily generally require more N compared to native selections.
7. Finally, keep good records of your management and observations, look for patterns, and learn how each bed responds to the addition of fertilizer.

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