Uptake processes of nutrients applied in Viticulture

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INTRODUCTION: There are 16 elements essential for thriving vine growth. These can be grouped in terms of the relative amount of each that are utilised during plant growth, i.e. the primary nutrients, secondary nutrients and the micro-nutrients. In Table 1 their sources and chemical form in which they are absorbed is given. Plants obtain their carbon (C) from CO_2 in the air, their O_2 from atmospheric and soil air and their hydrogen from soil water. The other 13 nutrients are normally absorbed in ionic form from the soil by the roots. In vineyard fertilisation the aspects that impact the utilisation of nutrients and influence their availability, must be borne in mind. Various factors affecting the efficiency of nutrient uptake by vine roots are discussed below.

MOVEMENT OF NUTRIENTS TO ROOTS: A small percentage of nutrient ions are absorbed when they come in contact with the roots pushing their way through the soil. This is called interception.

Obviously, the larger the volume of soil that is occupied by roots and the denser the root growth, the larger the amount of nutrients that can be utilised through interception. Organic acids secreted into the soil by root tips may change the chemical state of nutrients (like N, P, K, Ca, Mg) and bring them into solution, thereby improving their uptake into the root tissues. This process is closely related to interception since the root needs to be close to the nutrients for the excreted acids to have an effect. Uptake, however, also depends on nutrient distribution in the soil (Mengel & Kirkby, 1982), illustrated by the fact that it is often observed that root growth is concentrated in areas directly under drippers.

The most important process, however, by which the vine's roots receive their nutrients is through transport to the roots. The entrance of dissolved ions from the soil solution into the vine root is made possible through different mechanisms that bring the ions in contact with the root, i.e. mechanisms that transport nutrients to the root surfaces.

Group of nutrients	Nutrient	Chemical form in which the nutrient is taken up	Source
Primary	Hydrogen	H^+ and H_2O	Air & water
	Oxygen	O_2, OH^-, CO_3^{2-}, SO_4^{2-}	
	Carbon	CO_2	
	Nitrogen	NH_4^+ and NO_3^-	Soils and fertilisers
	Phosphorus	$H_2PO_4^-$ and HPO_4^{2-}	
	Potassium	K^+	
Secondary	Calcium	Ca^{2+}	
	Magnesium	Mg^{2+}	
	Sulfur	SO_4^{2-}	
Micro	Chlorine	Cl^-	
	Copper	Cu^{2+}	
	Boron	$H_2BO_3^-$ and $B(OH)_3^-$	
	Iron	Fe^{2+} and Fe^{3+}	
	Manganese	Mn^{2+}	
	Molybdenum	MoO_4^{2-}	
	Zinc	Zn_2^+	

Table 1. *The essential nutrients for vine growth, their sources and forms in which they are absorbed by the vine (adapted from Follet* et al., *1981).*

Mass flow: As water is lost from the leaf surface by transpiration, water in the soil moves via convective flow transporting solutes and ions, towards the root. This is called mass flow. Nutrients such as nitrate-N (NO_3^-), Ca^{2+} and sulphur (SO_4^{2-}) are normally supplied by mass flow. However, it is not only the nutrient concentration that determines the amount of nutrients reaching the root, but also the rate of water flow, i.e. the water consumption of the vine. Mass flow therefore plays an important role for nutrients present in soil solution in high concentration and when transpiration rates are high. Under such conditions considerable amounts of water are moved to the roots carrying various solutes (Ca^{2+}, Mg^{2+}, NO_3^-). Furthermore, since only newly expanding unsuberised root caps can absorb Ca, any environmental factor that limits active root expansion limits Ca uptake.

Diffusion: This is the process by which an ion is transported from a higher to a lower concentration through thermal motion. As uptake of nutrients occur, the concentration in the soil solution close to the root decreases. This creates a gradient for the nutrient to diffuse through the soil solution from a zone of high concentration into the depleted solution adjacent to the root. Nutrients such as P, NH_4^+ and K^+, that are adsorbed by clay particles and generally exist only in small quantities in the soil solution, tend to move to the root by diffusion. They are also taken up rapidly by plant roots (Mengel & Kirkby, 1982).

In Table 2 a rough estimate of the percentage of uptake facilitated by root interception/solubilisation, mass flow and diffusion of some important nutrients is given.

PREREQUISITES FOR OPTIMAL NUTRIENT UPTAKE:

Sufficient soil moisture: The rate of ion movement in the soil, whether by mass flow or diffusion, depends highly on soil moisture. Sufficient moisture, but not saturated conditions, is therefore

Nutrient	Mechanism of nutrient supply (% of total absorbed)		
	Root interception	Mass Flow	Diffusion
Nitrogen	< 1	80 (NO_3^-)	19 (NH_4^+)
Phosphorus	2	5	93
Potassium	2	18	80
Calcium	150*	375*	0
Magnesium	33	600*	0
Sulphur	5	300*	0
Zn	10	60	30
Mn	10	133*	10
Fe	5	50	45
B	<1	200	20

* Where the number exceeds 100%, the nutrient has the potential of being over-supplied to the vine through this method.

Table 2. *Percentage uptake made possible through root interception/ solubilisation, mass flow and diffusion (Mengel, 1995).*

required for optimal nutrition. Nutrient mobility also depends on nutrient concentration in the soil solution. The higher the concentration of the nutrients in the soil solution, the more is transported to the roots through mass flow. Furthermore, diffusion is generally faster when the concentration of the nutrient in the soil solution is higher. The characteristics of the soil, expressed in terms of its ability to replenish ions absorbed by the roots in order to maintain the concentration within the soil solution will also affect the rate of diffusion towards the roots. Especially the P and K^+ availability is affected.

Sufficient root development: The capability of the vine to exploit the soil for nutrients depends largely on the root depth, root branching as well as the number of root hairs and root tips, i.e. the volume of soil utilised by the vine roots and their rate of proliferation. For example, nutrients like Ca^{2+}, Mg^{2+} and Fe^{2+} are mainly absorbed by young roots in which the cell walls of the endodermis are not yet suberised. The ability of vines to utilise these nutrients strongly depends on the number of active root tips present in the soil.

Sufficient metabolically derived energy: Ions are often taken up metabolically (discussed below), which requires energy. High root carbohydrate content (which act as an energy source) will therefore increase ion uptake. Sufficient oxygen (O_2) is also beneficial because root respiration is the main source of adenosine tri-phosphate (ATP), which is the provider of energy for ion uptake. Some ATP is also provided through photophosphorylation. Sufficient light exposure to aboveground parts (leaves) thus enhances the uptake of ions.

DIFFERENT NUTRIENT UPTAKE PROCESSES: It has been found that there generally is a great discrepancy between the mineral nutrient concentration in the soil and the mineral nutrient requirement of plants. Often the concentrations of mineral nutrients in the soil are higher than what is needed for plant growth. Likewise, vines can often accumulate mineral elements in their cell sap at concentrations much higher than that in the external solution. This is typical of N, P and K. Certain mineral nutrients can also be taken up preferentially, while others are discriminated against or excluded. Selectivity of ion uptake is therefore a typical feature of vines.

During the uptake process, ions in the soil solution are subjected to two forces, namely a concentration gradient and an electrical gradient. Ions move from a higher (outside solution) to a lower concentration (inside the root cells). Furthermore, cations are attracted to a negative electropotential whereas anions to a positive electropotential. The stronger the electropotential, the faster ion movement will be. Both the movement of ions from higher to lower concentration or along the electrochemical gradient will terminate as soon as equilibrium between the outside- and the inside solution has been attained. This is passive uptake. Because the concentration of Na^+, Ca^{2+} and Mg^{2+} in plant cells do not exceed the physical equilibrium (both concentration and electrochemical gradient), it has been concluded that they are passively absorbed (Mengel & Kirkby, 1982). This type of absorption of cations is more or less non-specific. It is mainly determined by the concentration of the different cations in the soil solution. An increased concentration of one cation in the soil solution will thus repress the uptake of other cations. For example, increased Mg^{2+} content in the soil will repress the uptake of Ca2+ and Na+, but not K+ (because it is also taken up actively, as discussed below). As a general rule, when one cation's supply is increased, the concentration of the other cation species in the plant is decreased. This is called *cation antagonism.*

Furthermore, the cation which is taken up the fastest will neutralise the negative charge and therefore reduce the electrostatic attraction for the other cations. Potassium (K^+), for example, which is taken up rapidly by the root cells competes strongly with other cations at high concentrations in the soil solution.

During uptake, solutes generally move by diffusion from the soil solution into the wet cell walls of the root cells. Here some of the cations may be substituted for cations associated with the negatively charged sites on the cell wall. Although water and some solutes may move relatively freely through the cell wall, charged ions cannot readily permeate the plasmalemma or cell membrane. Nevertheless, cells do absorb ions and actually accumulate them in concentrations many times higher than their concentration in the external medium. Where a concentration within the root cells is obtained which is higher than that of the equilibrium condition, transport has taken place against the electrochemical gradient - this happens through active uptake and requires additional energy to that supplied by kinetic and electrical forces. A cation that is often at higher concentrations inside the root cells than in the soil solution is K^+. This implicates active uptake. However, at high concentrations in the soil, K^+ is mainly taken up passively (Marschner, 1995).

Metabolically driven uptake (active uptake) is believed to take place via different mechanisms. The first is by means of a so-called "carrier", which is a molecule with the ability to selectively bind different ions and transport them across the membrane. The second proposed mechanism is the "ion pump". This process of uptake is explained as follows. Cell membranes contain ATPase (the enzyme responsible for controlling ionic permeability) which induces a pH gradient across the membrane by pumping H^+ out of the cell. The result is that the cell becomes more negatively charged and more alkaline compared to the outside solution (soil solution). Because of the negative charge that is formed in this way, cations at the outer side of the membrane are attracted into the cell to neutralise the negative charge. Anions, however, being negatively charged cannot be taken up in this way. It is thus suggested that anions are taken up in exchange for OH^- and HCO_3^-. Furthermore, because plant cells are negatively charged, anions will mostly be subjected to active transport. This is especially true when the anion concentration inside the root cells is higher than that of the outer medium. Nitrate and $H_2PO_4^-$ are thus accumulated actively.

ION COMPETITION, ANTAGONISM AND SYNERGISM: As mentioned before the negative charge of the cell attracts cations and leads to their passive absorption. This absorption is a non-specific process which mainly depends on the concentration of the cation species in the soil solution and the permeability of the cell membranes to that specific cation. If the supply of one cation is increased in the outer solution, the uptake (i.e. levels in the plant) of the other cations will be repressed. This is called *cation antagonism* and can typically occur (1) when one nutrient is supplied in excessive amounts while another is at a level considered marginally sufficient, but also (2) when the levels of two nutrients are both near the deficiency range.

The cations that are taken up the fastest will neutralise the anion equivalents or negative charge and therefore reduce the electrostatic attraction for the other species. Potassium (K^+), for example, which is taken up very fast due to active uptake in addition to diffusion, always competes very strongly with other cations. Likewise NH_4^+ typically competes with Ca^{2+} making the use of large amounts of urea a practice that can potentially suppress Ca2+ uptake. In anion uptake it is presumed that antagonism also occurs due to concentration differences which affect diffusion as well as distinctions in membrane permeability. In this case the most relevant interaction is $H_2PO_4^-$ uptake, which is stimulated in the absence of NO_3^-. *Synergism*, which occurs when the uptake of one ion is stimulated by the presence of another one, is the opposite of antagonism. An example of this is the fact that applications of NO_3^-, an anion that is taken up very rapidly, stimulates the uptake of cations. This occurs due to the formation of negatively charged organic molecules inside the root cells during the process of NO_3^--assimilation (when NO_3^- is converted to amino acids and utilised by the plant). Plants fed on NO_3^--N will therefore contain higher levels of cations than those supplied with NH_4^+ (Mengel & Kirkby, 1982).

Conclusion: Each mineral nutrient, including the micro elements that are not discussed in this article, has a dominant mechanism by which it is transported to the plant roots and is taken up by the vine. By taking note of the differences regarding these aspects between nutrients, as discussed above, table grape producers will develop more insight into the dynamics that needs to be taken into account when compiling a successful fertilisation programme.

GLOSSARY

Active or metabolically driven uptake: Uptake that takes place against an electrochemical or concentration gradient by means of energy supplied by ATP.

Antagonism: The repression of uptake of a nutrient by the presence of another.

Diffusion: The process by which an ion is transported from a higher to a lower concentration through thermal motion.

Interception: The process whereby nutrient ions can be absorbed by plant roots because the roots come in contact with them as they push their way through the soil.

Mass flow: The transport of solutes and ions by water that moves to the plant roots via convective flow as water is taken up from the soil by the plant.

Passive uptake: The uptake process whereby nutrient ions are absorbed without requiring exertion of energy, it happens due to either or both concentration and electrical gradients.

Photophosphorylation: The process whereby light induces an electron flow which provides the energy for the synthesis of ATP.

Plasmalemma or cell membrane: The external, limiting lipid bi-layer membrane of cells. It is a thin membrane around the living fluid content of the cell that controls passage of substances in and out of the cell.

Suberised roots: Roots of which their cell walls have been hardened by conversion to cork (suberin), making them less permeable to water and solutes.

Synergism: The stimulation of the uptake of an ion by the presence of another.

LITERATURE CITED

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