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Location & Regulation of Nitrogen In Trees

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From an energy standpoint, uptake and reduction of nitrogen with incorporation into an organic framework is one of the most expensive tasks a tree performs. It would hardly be worthwhile if usable nitrogen in the environment was not at a premium. Trees spends a great deal of energy and carbon chain stock in order to capture and control nitrogen. In this case, to move from soil nitrate to glutamine inside a tree cell requires at least 12 ATPs of energy per nitrogen. To reduce atmospheric dinitrogen gas into glutamine requires at least 16 ATPs of energy per nitrogen plus creation and maintenance of a microbial root nodule.

Under perfect conditions in a perfect world, a tree should spend about 1 glucose (6C) in respiration for every 2 nitrates processed. This cost does not include carbon skeletons used for nitrogen attachment, as well as the cost of uptake from soil. Generally, there is a 5:1 ratio of carbon spent for every nitrogen gained. In other words, a 2% nitrogen assimilation level in tree tissues required 10% of the tree's carbohydrate to build.

Reduction Location

Many herbaceous and rapidly growing annual plants ship captured nitrate within their xylem stream to leaves for processing. Leaves have readily available energy for nitrate reduction and incorporation of ammonium into amino acid frameworks. In trees, temperate species tend to process nitrate in roots, and tropical species tend to process nitrate in roots, stems, and leaves. Nitrate can be stored and transported. Ammonium can become easily toxic and is not usually stored or transported. Increasing ammonium concentrations inside cells dissipates pH gradients responsible for ATP (energy) production.

There is great variability in nitrogen processing locations partially because increasing nitrate concentrations are moved farther along the transpiration stream. The more nitrate available to, and taken-up by, a tree, the quicker root reduction ability is exceeded and the more nitrate is shipped upward to be reduced where energy sources are available. Xylem parenchyma serve as axillary nitrogen reduction centers. With excessive nitrogen sources in xylem transport, nitrates could reach leaves where direct light reduction products can be used.

In Roots

For most landscape trees in temperate areas, assume nitrate is reduced almost exclusively in root tissues. Nitrogen reduced and processed in roots is then added to the transpiration stream and sent up to the leaves. The cost for nitrogen reduction is paid by current phloem carbon contents (food shipped from leaves), and stored root carbon (food taken from local storage).

Glutamate, glutamine, asparagine, and aspartate are amino acid storage and transport forms for nitrogen in trees. Figure 1. Of these, asparagine and glutamine are the most effective and efficient for transport. Both have a high nitrogen / carbon ratio (asparagine = 2N:4C; glutamine = 2N:5C). Figure 2.

Root Plight

Dependence upon tree roots to reduce nitrates, except in times of excess, is of concern from an oxygen supply standpoint. Nitrate reduction is an energy-expensive and complex process. Good oxygenation around tree roots is required for effective processing. Under flooded, compacted, or water saturated soil conditions, oxygen can be quickly depleted in the rooting zone. Oxygen diffuses across water-filled soil 10,000 times slower than across a soil with 25% air-filled macro-pores. In addition, microbes can easily use any available oxygen quickly under oxygen limiting conditions, leaving tree roots under anaerobic conditions.

Respiration (stored carbon and oxygen use) rates double for every 18^{o}F increase in temperature. Warm summer nights under wet conditions, low oxygen, and nitrate presence can cause massive quantities of stored carbon in roots to be used. Figure 3. Intermediate products like ethanol and lactate build-up under these conditions. Under low oxygen levels in the rooting zone and moderate nitrate levels, 20 times more stored carbon must be used for processing nitrate and for root respiration than under normal oxygen conditions.

Control System

The control system within a tree for regulating nitrogen uptake is based upon cycling of amino acids formed in ammonium assimilation, and cycling of organic acids generated in photosynthesis and respiration. Amino acids and organic acids are the primary signal / products cycling between shoot and root in xylem and phloem. Figure 4.

If too much nitrogen is present in the system, amino-acids from the glutamate cycle begin piling-up. Figure 5. Alternatively with tree stress, growth slows and protein synthesis declines, leaving additional amino-acids available. Increasing amino-acid levels deliver a message to roots that tree nitrogen needs are satisfied. Given this amino-acid signal (generated locally and as transported in the phloem), nitrate uptake is slowed. Overabundance of nitrogen and tree stress that slows growth, generate the same signal in slowing nitrate uptake.

More Control

Increasing organic acid concentrations initiate nitrate up-take due to the release of carbonate anions ($HCO3^{-}$). Figure 6. An increasing level of organic acids signify a decrease in amino-acid production and/or a strong carbon production source. Carbonate anions are essential for the primary carrier of nitrate uptake to function. The key feature of nitrate up-take control systems is the integration of whole tree nitrogen and carbon status in determining a tree's response. Several amino-acids have been cited in this control process. Of the organic acids playing a role, malate is a good example.

Malate is an organic acid which can be stored in cell vacuoles, can generate carbonate anions for co-transport of nitrate, or can be used to balance electrostatic charges (malate carries two negative charges). Malate (not glucose or sucrose) from local sources moving into root cells from the phloem transport pathway, stimulates nitrate up-take.

Circulation

With increased nitrate uptake, nitrate reduction is stimulated and amino-acids are produced. The amino-acids are feed stock for protein synthesis. When growth slows and protein synthesis declines, unused amino-acids circulate and slow nitrate uptake. The nitrogen demand in a tree is the difference between the nitrogen reduction rate and the protein synthesis rate.

Control Scenarios

Inside trees is a feed-back control system using amino acids (transportable nitrogen) and organic acids. If one product recirculates and accumulates inside a tree, back to its inception point, it will slow further production. To appreciate nitrate uptake control, the following bullets provide five basic results: (Figure 7)

A) If amino-acids are used for protein synthesis in leaves (amino acid concentrations fall), then nitrate uptake increases.

B) If amino-acids concentrations increase in tree roots, then nitrate uptake decreases.

C) If organic acids increase in tree roots, then nitrate uptake is stimulated.

D) If organic acids are reduced in tree roots (less HCO3-), then nitrate uptake is reduced.

E) As trees become more stressed, growth rate is reduced, less organic acids are generated, less amino acids are used in protein synthesis, and more amino-acids recycle in a tree, causing nitrate uptake reduction.

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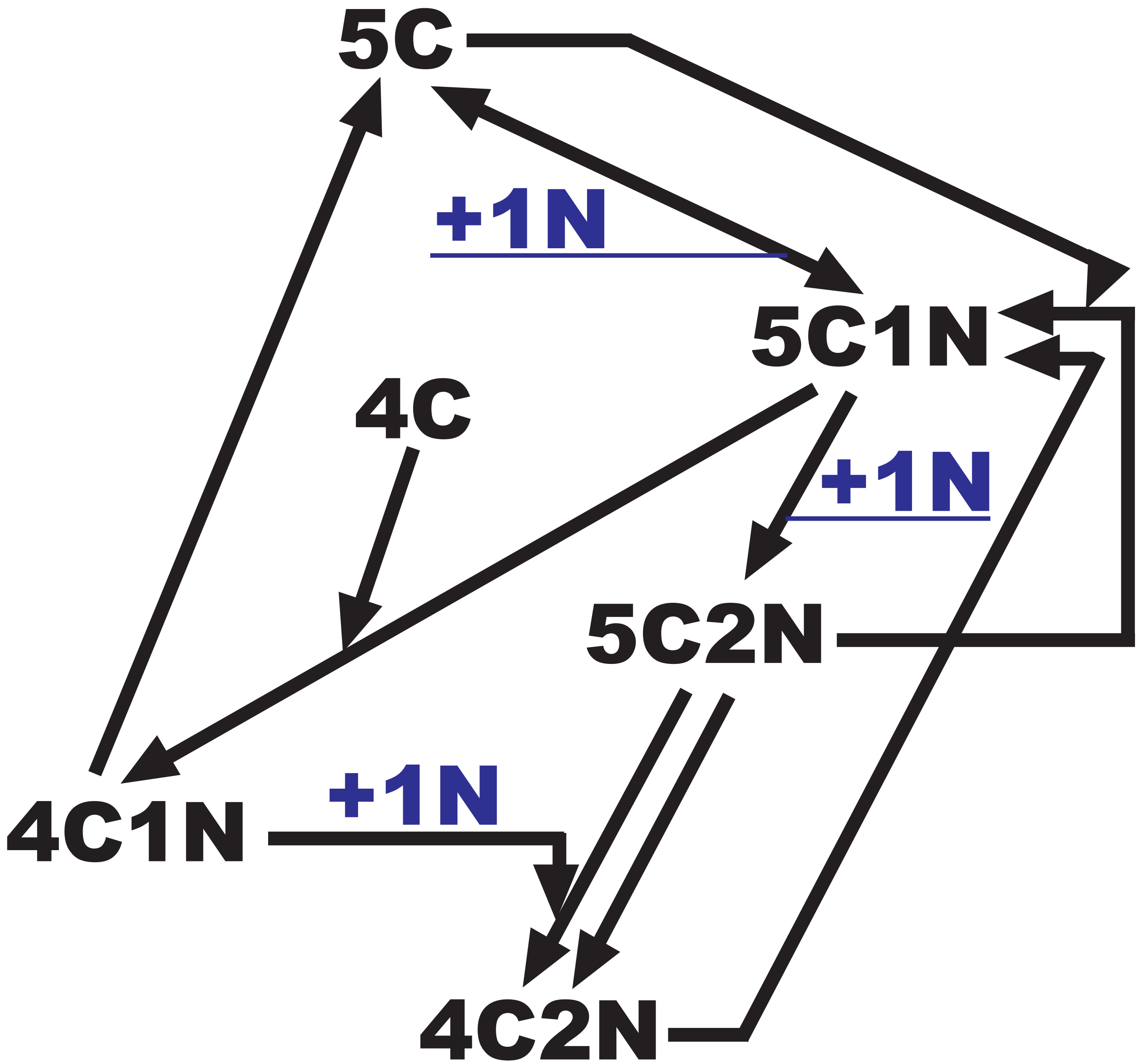

1N	=	ammonium
4C	=	oxalacetate
5C	=	oxogluterate
4C1N	=	aspartate
4C2N	=	asparagine
5C1N	=	glutamate
5C2N	=	glutamine

Figure 1: Ammonium ion (+1N) assimilation web in trees with transport and storage amino acids, and carbon chain feedstocks shown.

4C1N
aspartate

4C2N
asparagine

5C1N
glutamate

5C2N
glutamine

Figure 2: Primary transport and storage forms of nitrogen with number of carbons and nitrogens given.

temperature	relative amount of carbohydrate used in respiration (+N, $+O_2$)	relative amount of carbohydrate used in respiration (+N, $-O_2$)
40°F (4°C)	1X	20X
58°F (14°C)	2X	40X
76°F (24°C)	4X	80X
94°F (34°C)	8X	160X

Figure 3: Temperature effects on carbohydrate use in tree roots under ideal conditions, and carbohydrate use in tree roots under oxygen poor (near anaerobic) conditions when moderate nitrate levels are present in soil.
("2X" means two times the respiration rate at 40°F (4°C) under aerated conditions.)

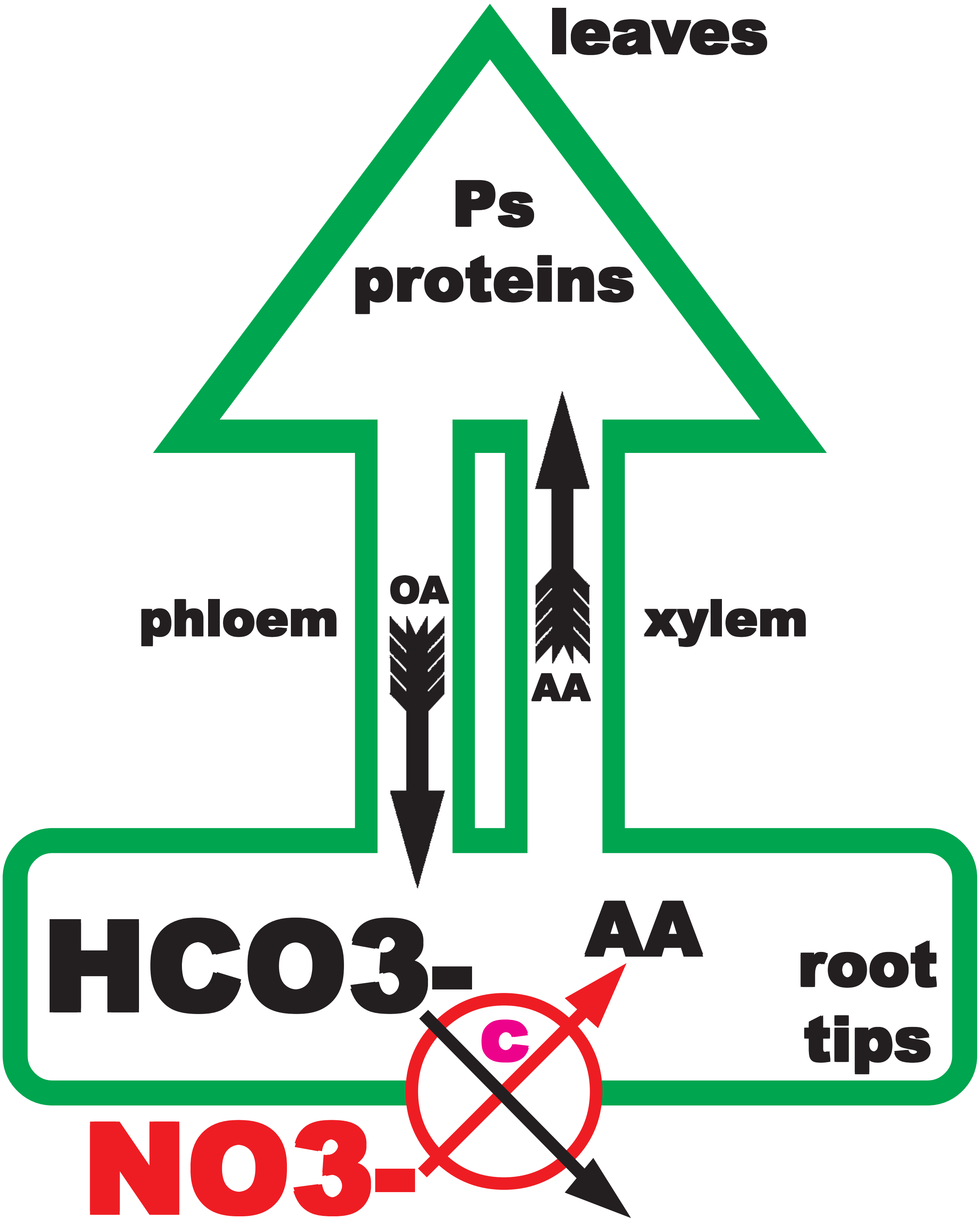

Figure 4: Nitrate uptake and control model inside a tree generating amino acids (AA) and using carbonate ions from organic acids (OA).

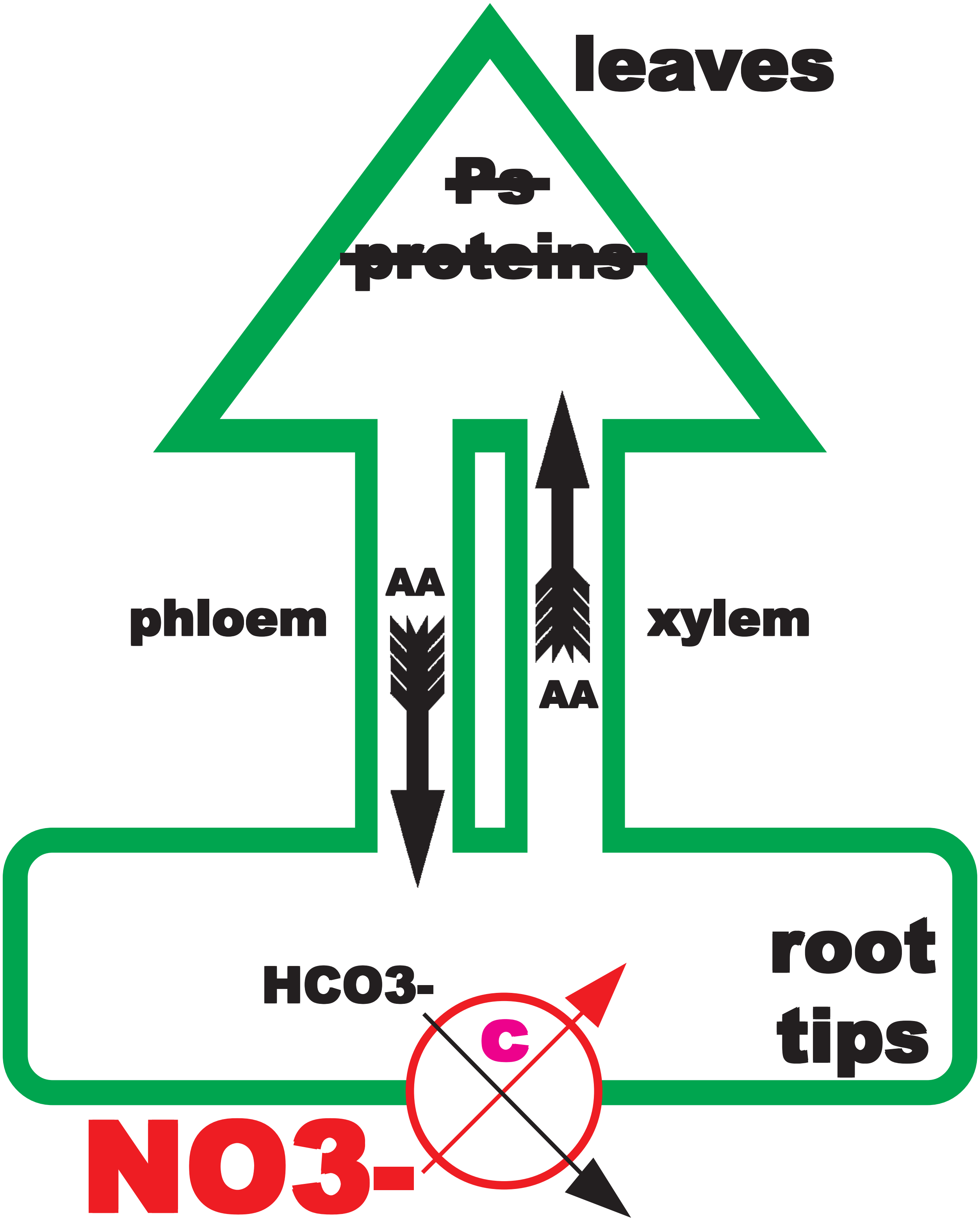

Figure 5: Nitrate uptake & control model inside a tree under photosynthetic & protein synthesis constraints, with stress causing recycling of unused amino acids (AA), slowing nitrate uptake.

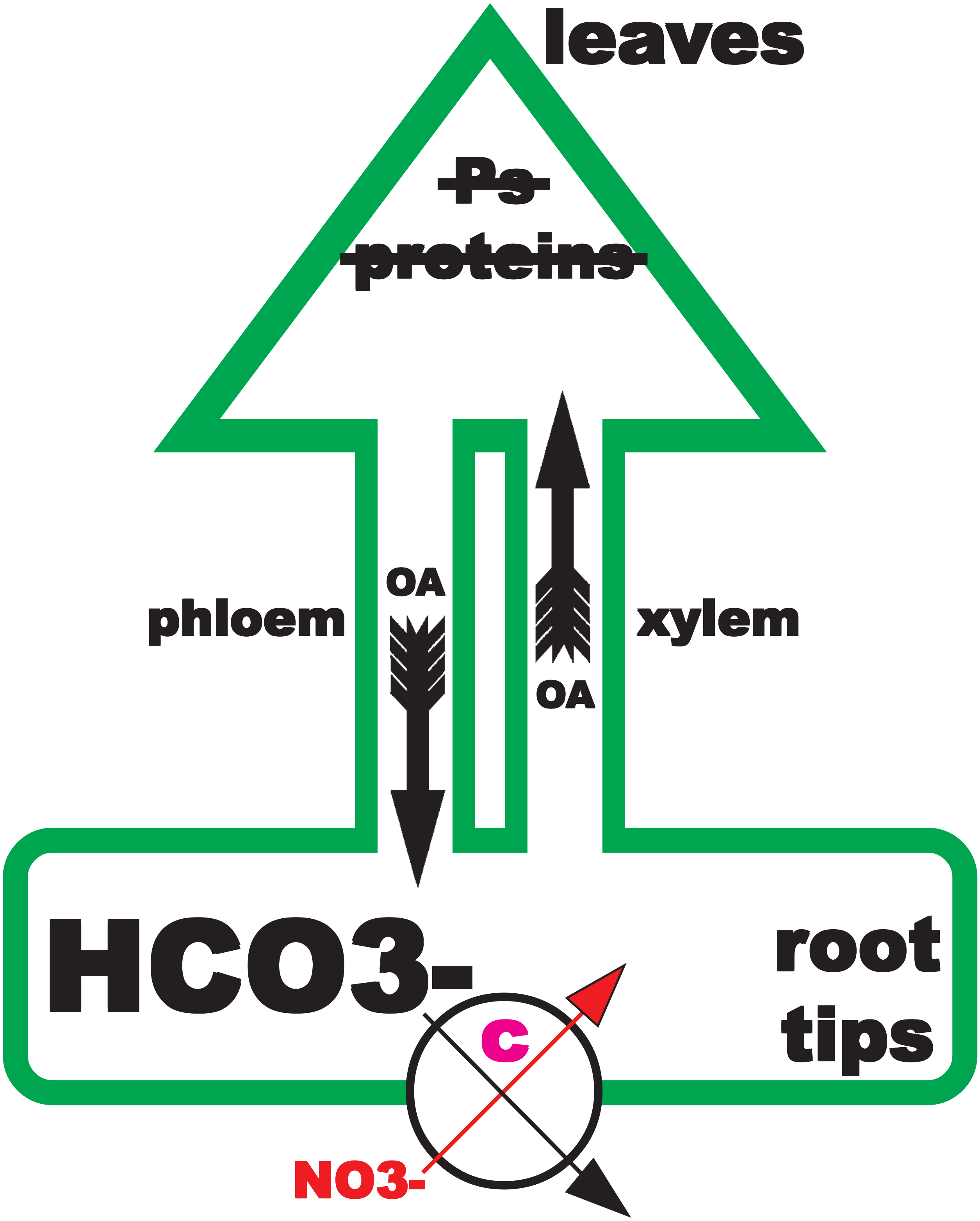

Figure 6: Nitrate uptake & control model inside a tree under nitrate availability constraints / stress causing recycling of organic acids (OA) which slows photosynthesis & protien synthesis.

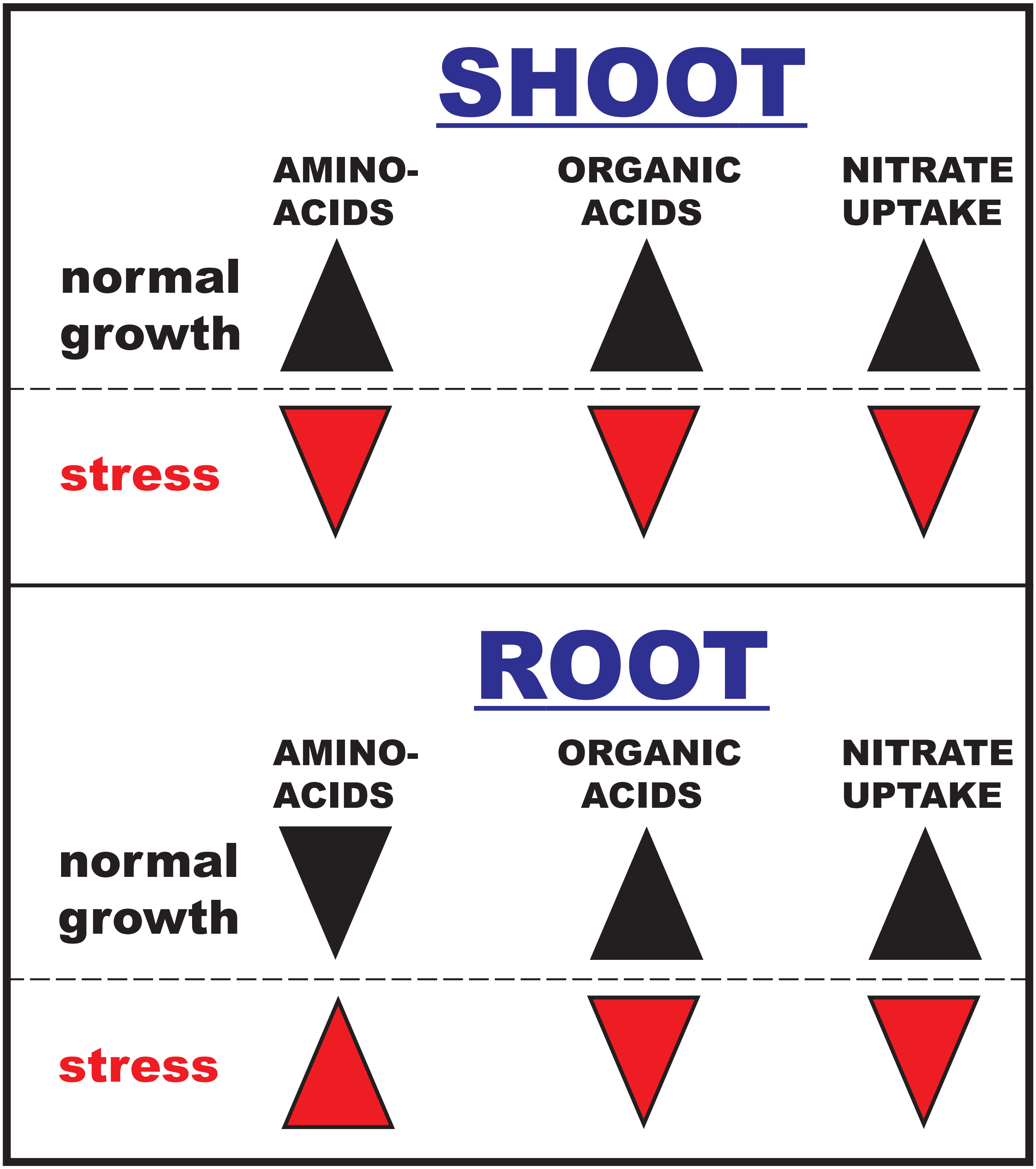

Figure 7: Example of normal and stress conditions changing amino-acid & organic acid concentrations, and their role in changing nitrate uptake within a tree.