UNIVERSITY OF GEORGIA
Warnell School of Forestry
& Natural Resources

Publication WSFNR-20-90C

October 2020

Nitrogen & Trees:

a learning manual

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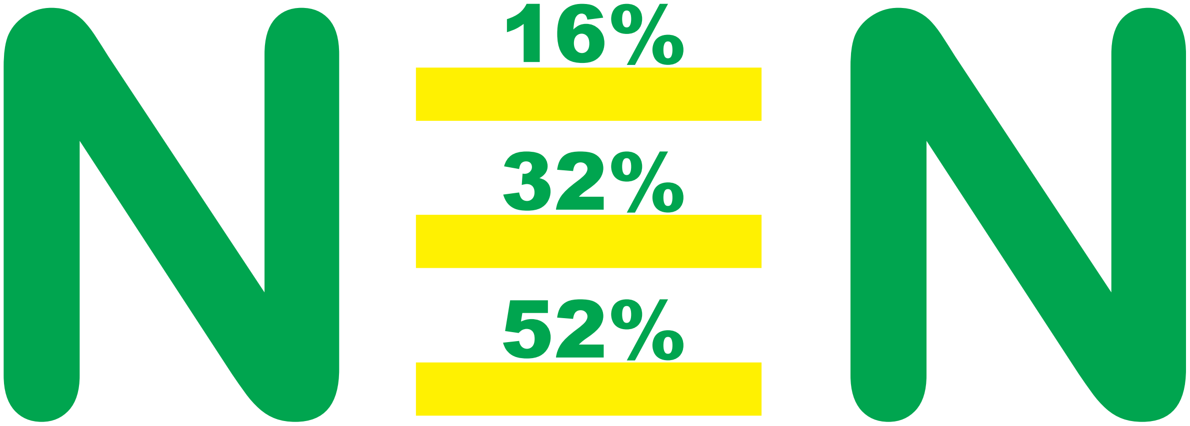


This publication is an educational product designed for helping tree health care professionals appreciate and understand the essential element nitrogen in tree / site systems. This product is a synthesis and integration of research and educational concepts regarding how sites process, and trees take-up and use, nitrogen. This educational product is for awareness building and professional development. This product does not present tree nitrogen fertilization applications or product formulations. This is not a tree health care fertilization standard.

At the time it was finished, this publication contained educational models concerning tree nitrogen thought by the author to provide the best means for considering fundamental tree health care issues surrounding nitrogen on sites, in soils, and in trees. The University of Georgia, the Warnell School of Forestry & Natural Resources, and the author are not responsible for any errors, omissions, misinterpretations, or misapplications stemming from this educational product. The author assumed professional users would have some basic tree and soil educational background. This product was not designed, nor is suited, for homeowner use. Always seek the advice and assistance of professional tree health care providers.

Citation:

Coder, Kim D. 2020. **Nitrogen & Trees: A learning manual.** University of Georgia, Warnell School of Forestry & Natural Resources Outreach Publication WSFNR20-90C. Pp.76.

Nitrogen & Trees: A learning manual

Described in its most basic form, a tree is a collection of carbon chains with a few other elements attached. There are many elements required for successful tree life. Some elements are needed in much higher proportions than others. What elements a tree requires for life may not be readily available within the environment in which it stands. Within terrestrial environments, usable nitrogen is usually in short supply — if not the most growth-limiting of all essential elements. Nitrogen is one of the key connectors between, and modifiers of, carbon chains.

Nitrogen affects molecular interactions, compound shapes and functions, and chemical symmetry of life-maintaining materials. In ecosystems, usable nitrogen is the most precious of elements — carefully used, relentlessly recycled, and biologically hoarded. If carbon represents the structure of life, nitrogen is the ignition key. Energy bound within organic carbons can only be held and retrieved by utilizing nitrogen.

History of Nitrogen

Trees are roughly 80% water, 19% carbohydrate, and 1% everything else. Figure 1. A major portion of the "everything else" component is nitrogen. Nitrogen has had a long history as a suspect in tree growth. A brief scientific history of nitrogen in trees would include:

1656 — nitrogen is found to be a chief nutrient of trees.
1699 — nitrogen is taken up from soil.
1747 — nitrite is detected in green tree parts.
1804 — nitrogen is found to be essential to trees.
1820 — nitrogen found to be the element usually in most limited supply.

Nitrogen is an essential component of tree life. Figure 2. Nitrogen is considered a myri-element averaging around 17,000 ppm in living tree tissues, and with only carbon, oxygen, and hydrogen found in greater quantities. Nitrogen has been shown to be essential to tree life in three ways: A) it is required for completing the life cycle of a tree; B) it is an essential part of life sustaining molecules in a tree; and, C) it is a component of essential processes in a tree. Nitrogen is found everywhere in a tree growing, living or dying. Nitrogen is commonly supplemented by humans in established landscapes.

Fertilize?

One of the first concerns in discussing nitrogen in tree systems is the practice of supplemental nitrogen enrichment — fertilizer! In natural systems, usable nitrogen is available at low levels through decomposition of organic matter, biological fixation, and/or atmospheric deposition. Nitrogen is carefully conserved and recycled by all organisms on and around a tree.

Recycling materials from decaying organic matter is probably the most important aspect to usable nitrogen supplies, as well as other essential elements. Organic materials contain many nitrogen atoms bound-up with carbon. Long-term soil genesis processes, leakage from living things, and organic matter decomposition represent significant nitrogen resources on a site. Figure 3. A healthy tree can effectively and efficiency capture and control a portion of this nitrogen. Most tree sites have nitrogen available for adequate health and growth, not optimum nor opulent levels.

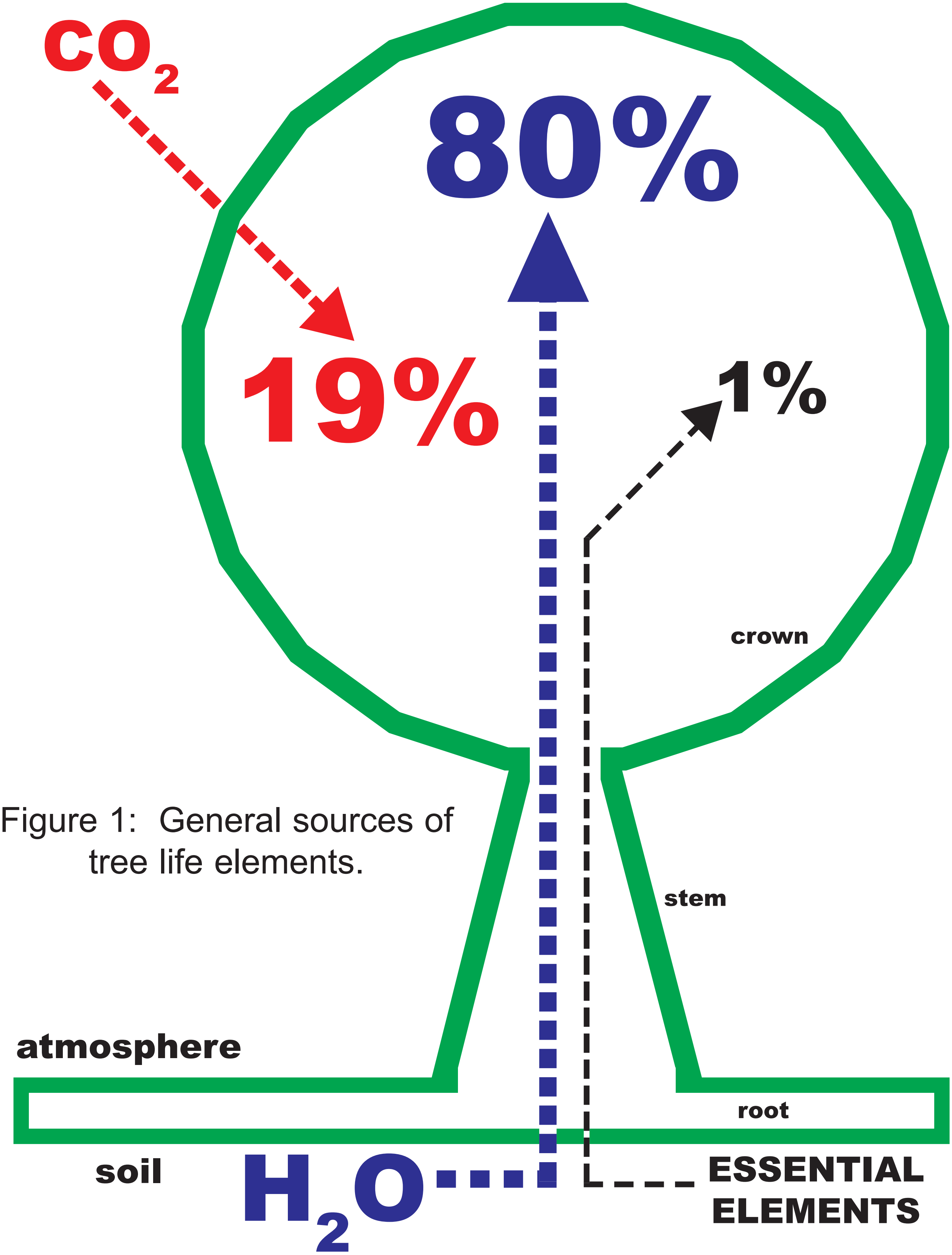


Figure 1: General sources of tree life elements.

element	symbol	average in tree (parts-per-million)	relative proportion in trees
group 1: (mega-)			
carbon	C	450,000 ppm	1,000,000
oxygen	O	450,000 ppm	1,000,000
hydrogen	H	60,000 ppm	133,000
group 2: (myri-)			
nitrogen	**N**	**17,000 ppm**	**38,000**
potassium	K	12,500 ppm	28,000
calcium	Ca	10,000 ppm	22,000
group 3: (kilo-)			
magnesium	Mg	2,500 ppm	5,500
phosphorus	P	2,250 ppm	5,000
sulfur	S	1,500 ppm	3,300
group 4: (hecto-)			
chlorine	Cl	250 ppm	550
group 5: (deka-)			
iron	Fe	75 ppm	170
manganese	Mn	45 ppm	100
zinc	Zn	38 ppm	85
boron	B	30 ppm	65
copper	Cu	20 ppm	45
group 6: (deci-)			
silicon	Si	0.7 ppm	1.5
molybdenum	Mo	0.5 ppm	1.1
nickel	Ni	0.4 ppm	0.9
cobalt	Co	0.2 ppm	0.4

Figure 2: List of tree essential elements divided into concentration groups (average concentration within trees), and relative proportion in trees with carbon and oxygen levels set at one million.

Human Objectives

In established landscapes, there are management objectives other than “adequate” tree growth. Because of human perceptions and expectations for tree performance, and the ability of trees to respond in specific ways to site resource enrichment, humans manipulate trees and sites to generate goods and services. The messiness and seeming chaos of the littered-strewn, ecologically rich natural soil surface layer is eliminated and replaced by hardscapes, heavy turf, neatly raked piles of organic carcasses and tree embryos, and damaged or limited soil volumes. Natural recycling of elements are short-circuited or stopped. Lack of nitrogen recycling and stringent tree performance objectives require supplemental nitrogen enrichment.

Being cost-effective and biologically correct in supplying nitrogen is important. Biological correctness involves understanding tree / nitrogen interactions. For trees, nitrogen represents a good news / bad news problem. The good news is the atmosphere surrounding trees is at least 78% nitrogen gas (dinitrogen or N2). Every acre of land has a blanket of more than 36,000 tons of nitrogen overhead. The bad news is almost all this nitrogen is tightly bound together and acts as an inert gas with low chemical energy. Atmospheric dinitrogen gas is held in a two atom, triple-bonded molecule. Figure 4. Few living systems have the biological machinery necessary to break apart nitrogen gas. For trees, nitrogen is everywhere, but not a molecule to use.

Making N Usable

Living tree systems must utilize fixed or reduced nitrogen (energized N) for incorporation into amino acids, nucleic acids, and proteins. Reduced nitrogen has been energized and made chemically reactive by addition of electrons. Reduced nitrogen is electron-dense and viable as a biological building component or a reaction coupler inside a tree. Reduction, fixation, or change in oxidation states, are essential for nitrogen use by a tree.

For example, nitrate (NO3-) is a common nitrogen containing anion in soil and is often enriched on sites. The nitrogen portion of nitrate must go through four major changes in form, each with an associated energy addition (increasing electron density), before that nitrogen can be used within a tree. In this case, oxidation state values must be forced from a +5 in NO3- (low energy, fairly benign nitrate anion) to -3 in NH4+ (a small, high energy, potentially toxic ammonium cation), an eight electron input difference.

Natural Fix

Nitrogen used by living systems does have its ultimate source in the huge ocean of atmospheric nitrogen. But, nitrogen must be “fixed” or “reduced” into biologically usable forms in one of several ways. Most nitrogen is made usable to trees through a biological fixation process (termed “nitrogen fixation”) which must occur under near anaerobic conditions. Biological fixation of nitrogen is engineered by many soil organisms, summarized into three primary groups:

-- free-living nitrogen fixing bacteria and algae (both aerobes and anaerobes);
-- symbiotic nitrogen fixing organisms (Rhizobia, Actinomycetes, cyanobacteria); and,
-- nodule forming nitrogen fixing bacteria (Rhizobia spp.). Note Rhizobia is the generic term for all species of nitrogen fixing bacteria in legume nodules.

Specific tree associated biological fixation examples include alder (Alnus spp.) nitrogen fixing actinomycetes, and some tree legumes and their Rhizobium bacteria. Both these tree systems sequester

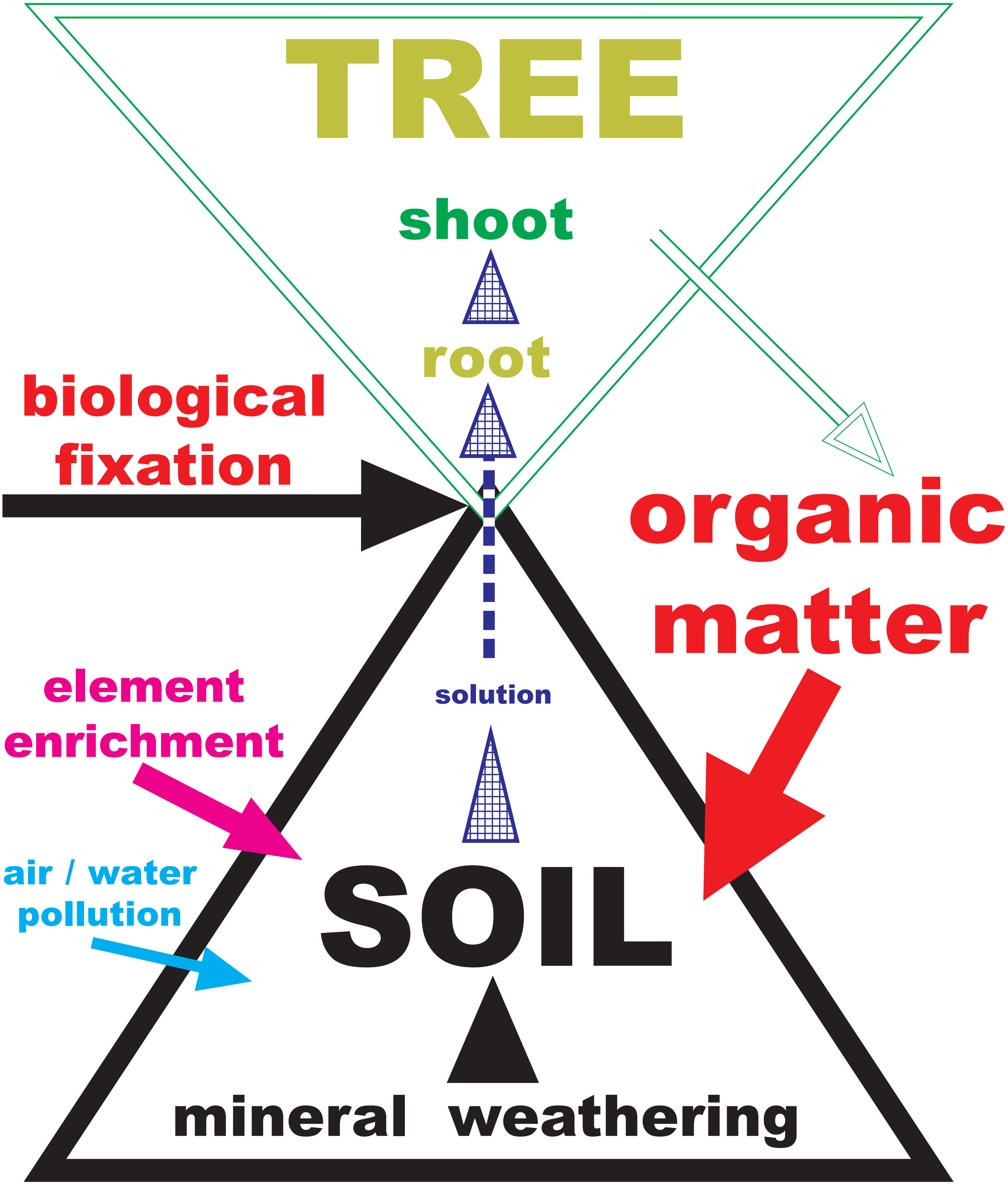


Figure 3: The primary sources of reduced (energized) nitrogen in a soil / tree association.

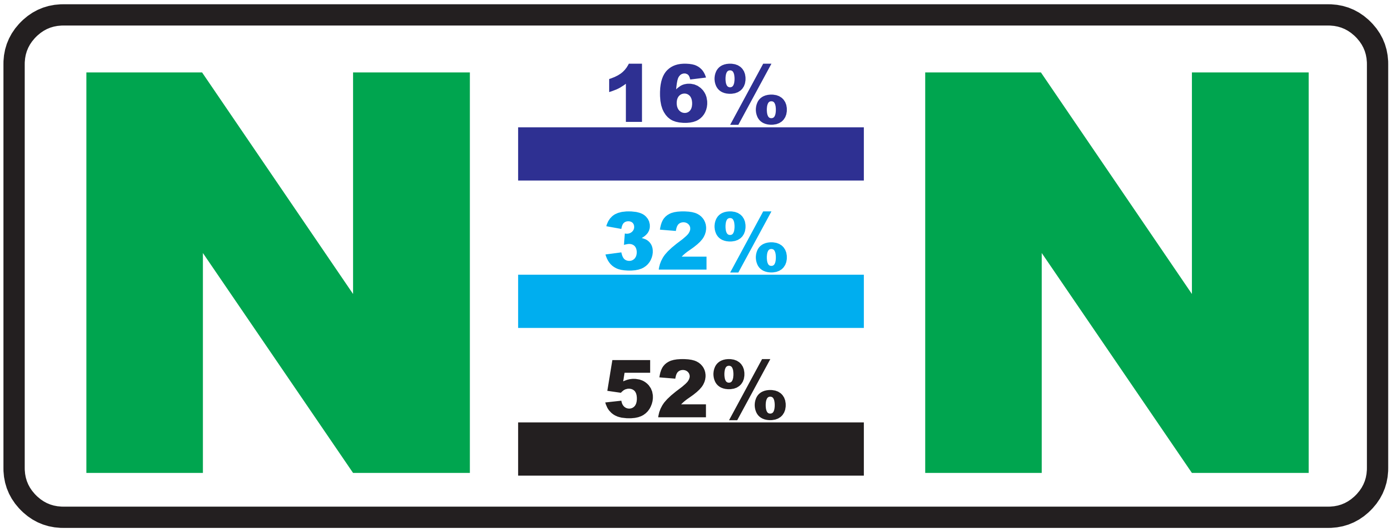


Figure 4: Atmospheric dinitrogen gas (i.e. low energy, almost inert, tightly bound) listed with the relative energy required to break each bond.

nitrogen fixation activities in localized root areas where oxygen can be kept at bay. Biological fixation of nitrogen is energy expensive and can amount up to 20% of tree energy production through photosynthesis.

Total Fixed

The final biological fixation product from atmospheric nitrogen gas is usually ammonium ions (NH_4^+) processed by an enzyme called nitrogenase. Nitrogenase is a slow processing (~5 N_2 per second) enzyme which uses a large amount of energy (16 ATPs) to generate two ammonium ions and dihydrogen gas (H_2). Twelve carbons are required for every dinitrogen (N_2) fixed. Additional means of natural nitrogen fixation includes lightning generated materials and high altitude photo-chemical transformations. The total natural nitrogen fixation is composed of 90% biological fixation, 9% lightning fixed, and 1% photo-chemical fixation.

Human Made

Artificial fixation by humans also generates significant sources of reduced nitrogen used by living things. The equivalent of roughly 15% of the total amount of natural nitrogen fixation is generated by industrial fixation. Additionally, in our modern world, atmospheric and water pollution problems provide some fixed nitrogen sources. Any advantage of this pollution-source nitrogen is usually off-set by dose, timing, pH, and toxicity problems. Figure 5.

Industrial fixation uses energy-expensive high temperatures (400°F) and high pressures (200 atms) to crack atmospheric nitrogen (N_2) into ammonia (NH_3). Ammonia in water yields ammonium ions ($NH_3 + H_2O = NH_4^+$). A total of 38 cubic feet of nitrogen gas is needed to fix one pound of nitrogen. It is biologically interesting how living systems fix nitrogen in oxygen-filled, ambient temperature, and atmospheric pressure with only biological catalysts. One way of thinking about nitrogen energy relations is to consider transforming ammonium nitrate (NH_4-NO_3) quickly back into dinitrogen gas (N_2). This nitrogen compound is the basis for a number of explosives.

Organic N

Usable nitrogen is a rare commodity for trees. Mineral soil and soil parent materials contain little nitrogen. While animals consume plants and other animals for their reduced nitrogen, trees must collect usable nitrogen from the environment. Much of soil nitrogen is held within living bodies of bacteria, fungi, animals, and plants, all of which try to defend their nitrogen stash. A large amount of nitrogen, in various usable stages or forms, is found in decaying organic materials in soil.

The organic matter pool of nitrogen in soil is valuable to all living things in the area. This biological (ecological) pool of nitrogen represents a bank account of "life" capital that can be used in growing trees. If this pool becomes depleted, for any of a number of reasons, short-term (acute) or long-term (chronic) shortages will develop and impact tree growth and health.

N Competition

Almost all organisms must take already energized (fixed/reduced) nitrogen from the environment. Unfortunately, the environment is a highly competitive place. All life forms need the rare usable forms of nitrogen, all for the same reasons. Different organisms have different strategies for collecting usable nitrogen. Nitrogen is not made nor destroyed, just recycled from organism to organism. Each time nitrogen passes through a living organism, another organism tries to grab it before the nitrogen is completely oxidized and returned to the atmosphere as an inert gas (N_2).

Natural Fixation	
Biological Fixed	**90%**
Lightning Fixed	**9%**
Photo-Chemical Fixed	**1%**
sub-total	**100%**
Artificial Fixation	
Industrial Fixed	**15%**
Pollution Delivered	**0.5%**
grand total	**115.5%**

Figure 5: Sources of new reduced nitrogen in tree ecosystems.

Nitrogen nutrition in trees involve a tree and site in an elaborate exchange of materials. Almost 60% of all nitrogen gathered by a tree is recycled internally. Once in a reduced form, nitrogen is used and maintained in its reduced form. Only upon organ death, such as with absorbing root turn-over or in shed tissues, will some valuable nitrogen escape. Quick catastrophic accidents, such as an untimely freeze killing leaves preventing a tree from withdrawing nitrogen supplies from damaged parts to be shed, can be a serious drain on whole tree resource levels.

Passages

Usable / reduced / energized nitrogen is available for capture by a tree when an organism dies and decays, excretes nitrogen containing wastes, or sheds materials and parts. The organic matter breakdown and nitrogen release process can be a long and drawn-out set of steps in which nitrogen passes from one living system to another.

For example, nitrogen in a decaying tree root can be captured by a detritus feeding insect — then passed to a bacteria — then moved to another bacteria upon the first bacteria's death, and on to a fungi — to a soil arthropod — back to an insect — to a mammal — and finally back to a living tree root again. Healthy ecological systems have a closely conserved nitrogen recycling network.

Terms of Loss

Nitrogen is kept close to living things because of its value in manufacturing the stuff of life, and its expense in preparation. As living cells die, there is a time period when nitrogen is available to whomever can capture it effectively. Nitrogen can be <u>immobilized</u> in organic matter and living organisms for a while, and not directly available to other organisms. But as life declines away, nitrogen can become available for short periods.

As organic materials are consumed and decay, nitrogen finally may pass through, by <u>mineralization</u>, into inorganic forms like ammonium ($NH4+$) or nitrate ($NO3-$). The pool of inorganic nitrogen compounds in a soil is usually quite small and is the target of many organisms seeking nitrogen. It is enrichment of the inorganic or organic soil pools of usable nitrogen to which people make additions with nitrogen containing fertilizers.

Changing Forms

Organic forms of nitrogen on any site are usually locked into complex and tightly held compounds. Most of these organic forms of nitrogen are unavailable for tree use. Tree-available and uptakable forms of inorganic nitrogen are primarily ammonium ($NH4+$) and nitrate ($NO3-$). Note it is possible for organic nitrogen forms like urea and free amino acids to be taken up by trees to a limited degree. Between unusable organic nitrogen forms and tree-preferred inorganic nitrogen forms, lie many soil organisms (almost exclusively bacteria). These bacteria use whatever nitrogen source is accessible to live and, in the process, transform nitrogen into another form. Figure 6.

Nitrogen transformation steps include a long line of aerobically respiring organisms incorporating nitrogen into their organic bodies. The decay, breakdown, and transformation process (mineralization) yielding usable inorganic nitrogen can be summarized into three steps: Figure 7.

1) <u>aminization</u> where proteins are decomposed to simple amine ($NH2$) containing materials and carbon dioxide ($CO2$);

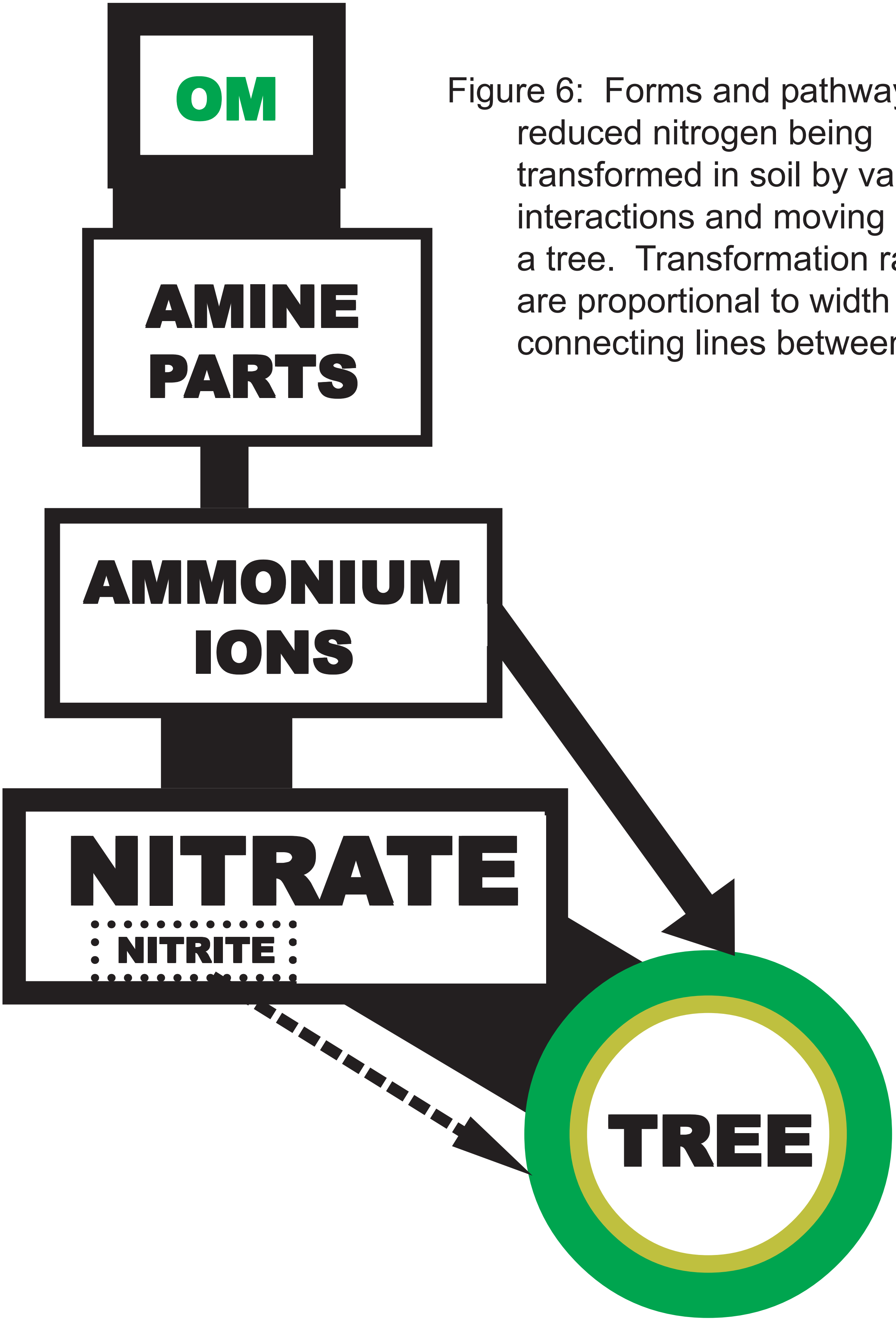


Figure 6: Forms and pathways of reduced nitrogen being transformed in soil by various interactions and moving into a tree. Transformation rates are proportional to width of connecting lines between boxes.

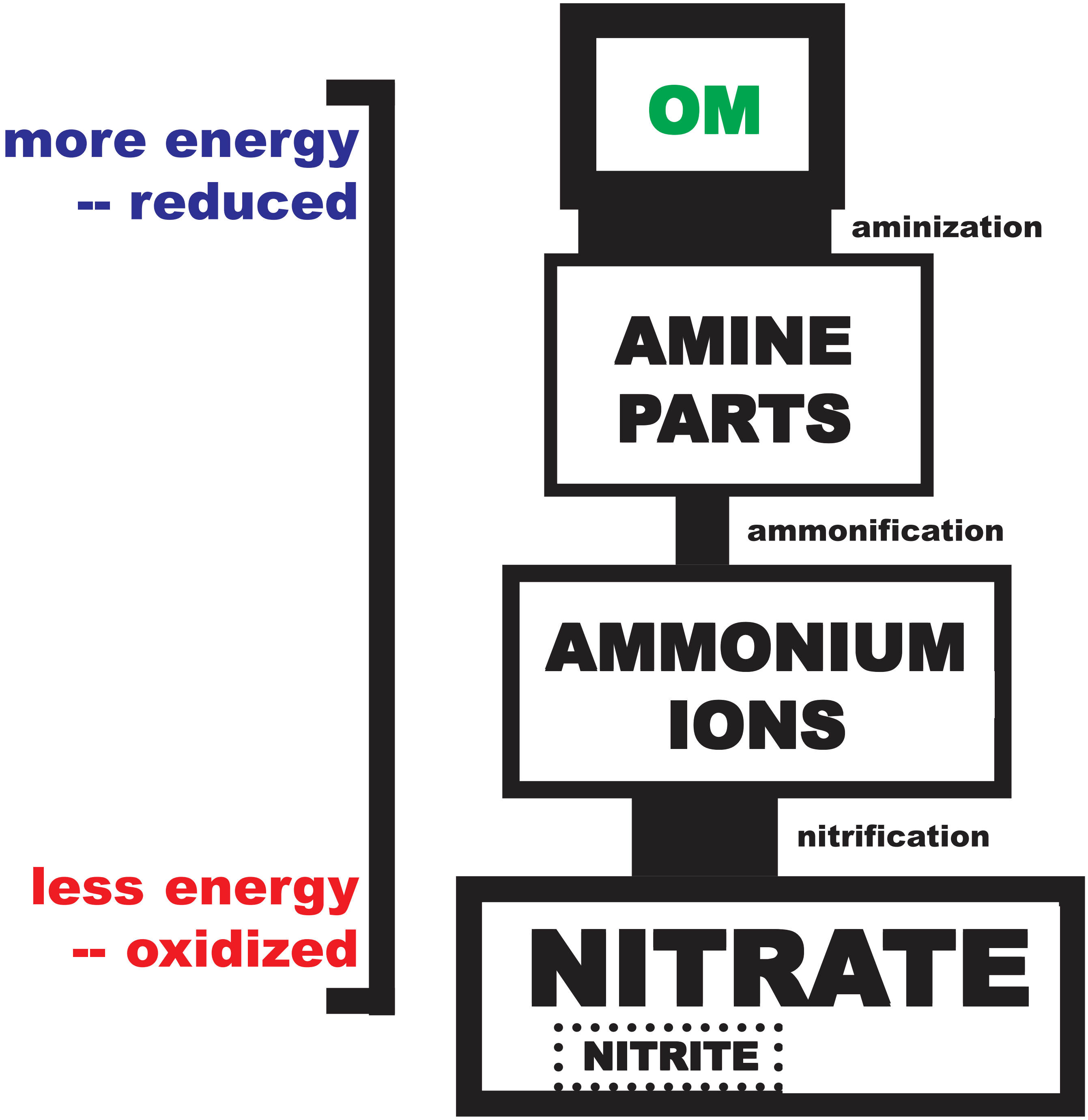


Figure 7: Forms and pathways of reduced nitrogen being tranformed by predominantly bacteria in soil from more energy dense materials in decaying organic matter (OM) to a less energy dense material (oxidized) nitrate.

2) ammonification where amine containing materials (NH2) and water (H2O) are transformed into ammonium cations (NH4+) and an OH- unit; and,
3) nitrification where ammonium cations (NH4+) and oxygen (4O) are transformed into nitrate anions (NO3-), water (H2O), and 2(H+) units.

Final Forms

Each transformation step is performed by a different set of soil bacteria which generate energy for themselves from this process. Note nitrification process (step 3 above) requires plenty of oxygen (O2) and generates two proton units of acidity. Because of the involvement of specific bacteria in mineralization of nitrogen — soil pH, oxygen content, and temperature all play an important role in determining the amount of inorganic nitrogen made available.

The native nitrogen source used by trees tends to be associated with soil pH. Neutral and high soil pH values favor microorganisms generating nitrate. Acidic pH soil values tend to inhibit nitrate generation by microorganisms and favor ammonium as a reduced nitrogen source in trees. Nitrate is considered the preferred bulk nitrogen source for trees, especially in more artificial landscapes. Usually any nitrogen source available is quickly moved toward the nitrate form in healthy soils. Ammonium is quickly pushed to nitrate in aerobic soils, but in wet and poorly drained soils, ammonium is a good tree nitrogen source because nitrification is slow. Urea in most soils is pushed to ammonium within 3-5 days. Figure 8.

Problems?

There are some soil treatments that can prevent nitrogen transformations by interfering with the activity of specific groups of bacteria. These chemicals have been utilized primarily in agriculture to slow or prevent transformations until crops can utilize available nitrogen. Acid soils (<5.5 pH), poorly drained or flooded soils, and cool temperatures all slow or stop the mineralization processes. Low soil oxygen contents, as in wet, organic, or compacted soils, can lead to a nitrogen conversion termed "denitrification" where nitrates ($NO3^-$) are directly converted into inert nitrogen gas (N2). Figure 9. Small amounts (~0.15%) of nitrite in soil can be released as nitrous oxide (N2O).

Soil is filled with tree roots, plus roots from all other plants in an area. In addition, roots are surrounded with millions of soil-living organisms most of which need oxygen. Poor drainage, water saturation, or a flood event when soil is warm (growing season temperatures) can cause all available oxygen to be used-up within a few hours. Microbes act as oxygen sponges, using any available oxygen before tree roots. As oxygen is consumed, microbe respiration progresses to using other materials like nitrogen, manganese, iron, sulphur and carbon. Nitrogen is the first major element used for respiration by soil microbes when oxygen is depleted. Nitrogen respiration in warm saturated soils can cause available nitrogen from enrichment to be turned into inert gas within a few days.

Figure 10 represents the external path of reduced nitrogen within a tree / soil system.

Ionic Changes

Once mineralized, and in an usable inorganic form, available nitrogen is prey to other problems in soils. The ammonium cation (NH4+) and nitrate anion (NO3-), by definition, have different electrostatic charges generated in water solutions (represented by the "+" or "-" symbols). Clays and organic material surfaces in soils generate negative charges, collectively called cation exchange sites. Organic material surfaces also generate a limited number of positively charged sites responsible for anion ex-

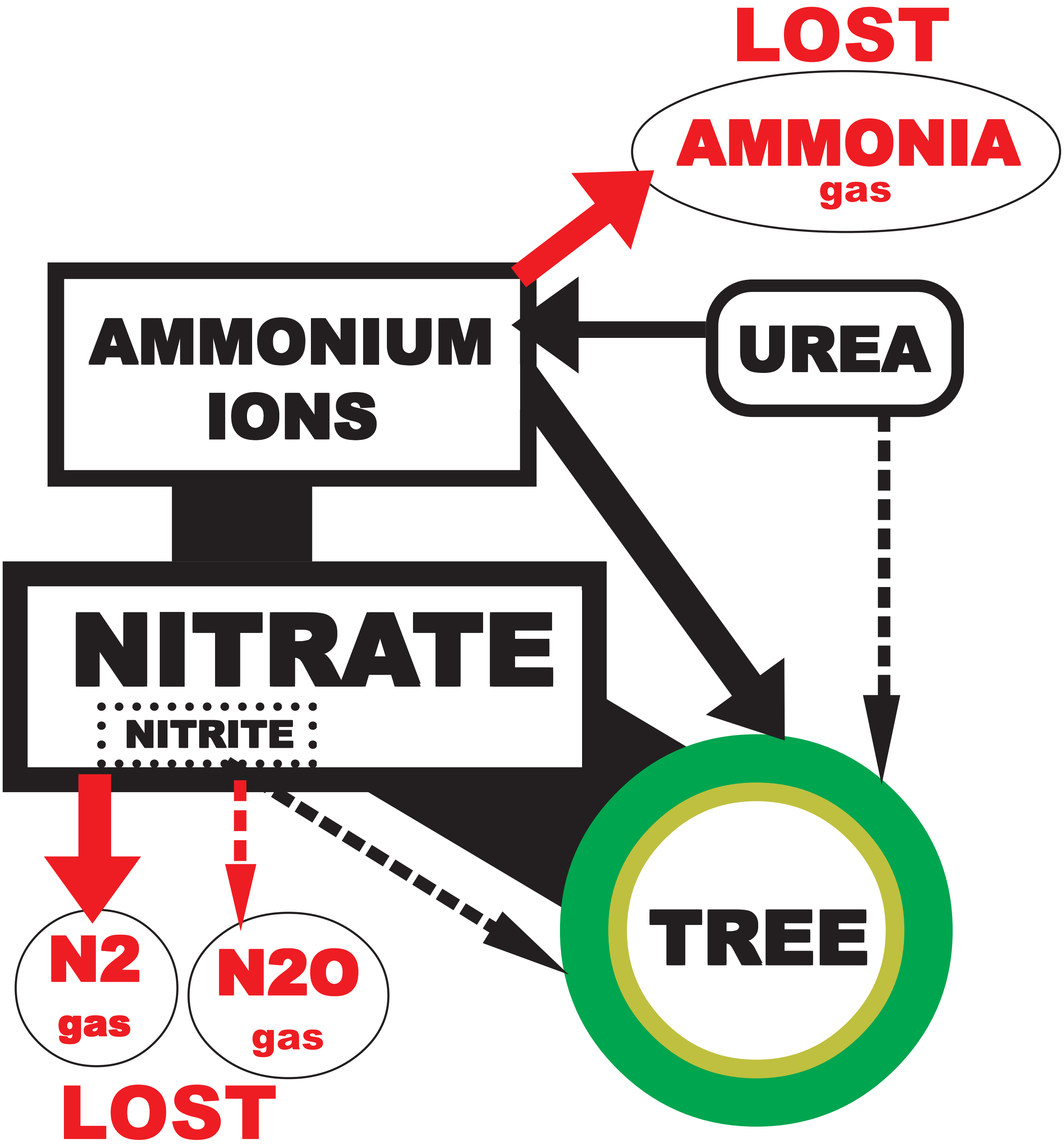


Figure 8: Possible pathways of reduced nitrogen in soil transformed from urea fertilizer and moved into a tree or lost to the atmosphere.

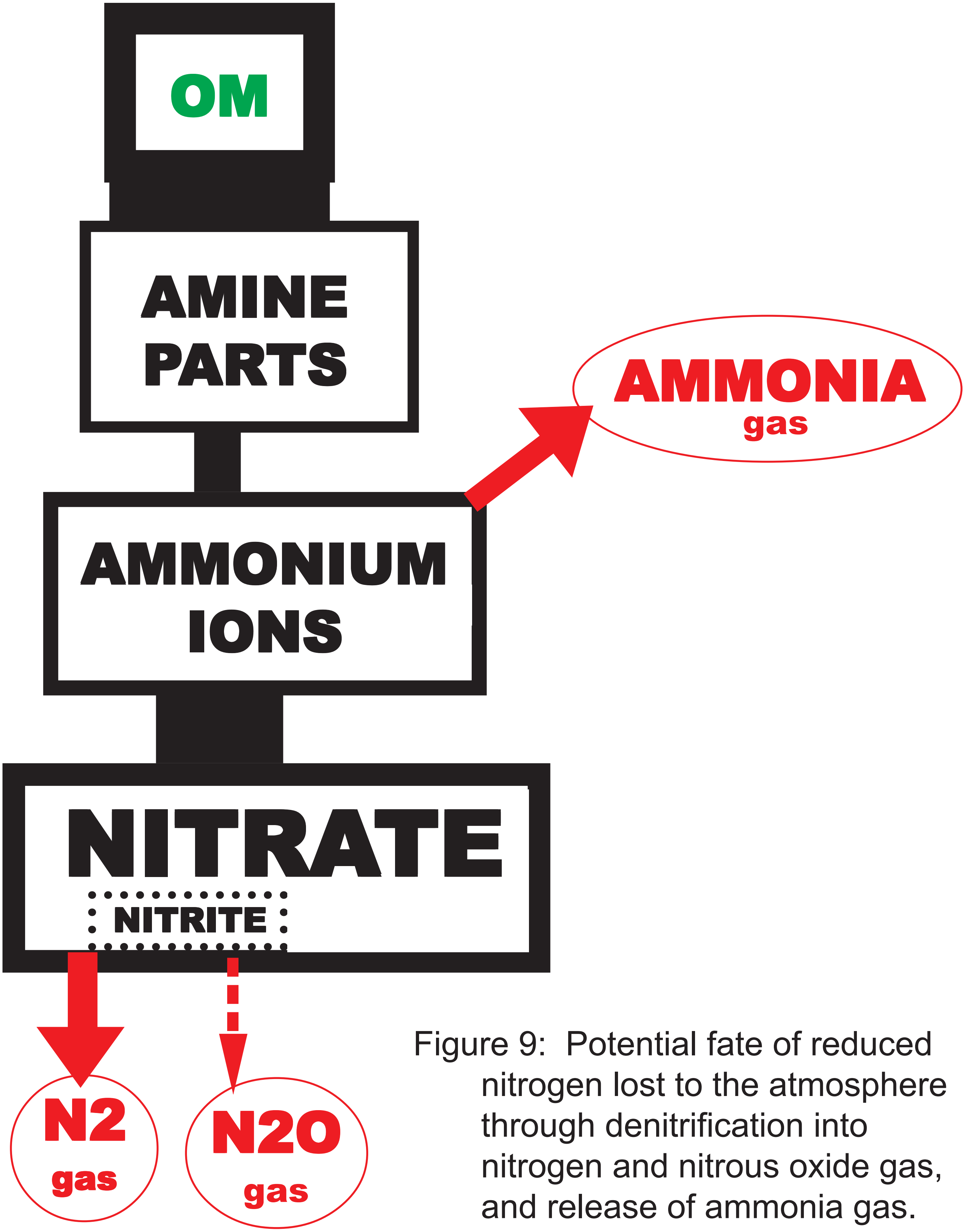
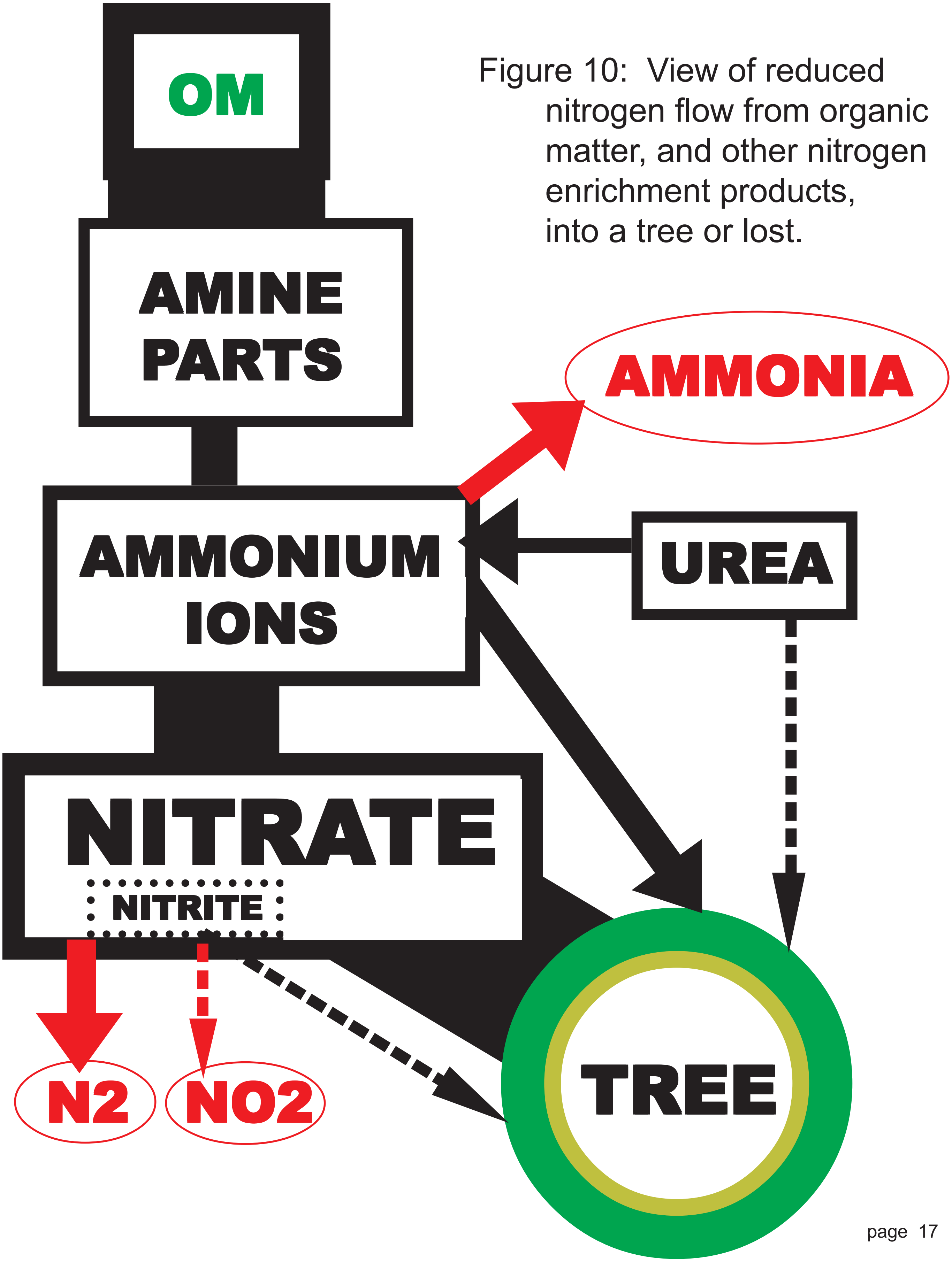


Figure 9: Potential fate of reduced nitrogen lost to the atmosphere through denitrification into nitrogen and nitrous oxide gas, and release of ammonia gas.

Figure 10: View of reduced nitrogen flow from organic matter, and other nitrogen enrichment products, into a tree or lost.



change sites. In most soils, cation exchange capacity (negative charge bank) is large and greatly affects availability and leachability of charged elements. Anion exchange capacity (positive charge bank) is usually small in its effect.

The negatively charged nitrate (NO3-) is electrostatically repelled by soil and organic matter surfaces making tree-available nitrate prone to leaching out of soils by water. The positively charged ammonium (NH4+) is electrostatically attracted by soil and organic matter surfaces allowing ammonium to remain loosely bound in soil and resistant to leaching. As temperatures increase, more ammonium is converted to nitrate, allowing warm season rains to wash available nitrogen (in nitrate form) away.

Soil Interactions

As water passes through a soil, more leaching of valuable nitrate ions occur. As trees take-up more essential elements, less valuable ions may be left loosely bound near soil charges surrounding tree roots. Cations of essentials elements can be bumped away from negative exchange sites and replaced by acidic elements (such as aluminum (Al), hydrogen protons (H^+), and manganese (Mn)) which tends to lower soil pH. Leached soils tend to become more acidic and less valuable in supplying essential elements for tree growth over time.

Figure 11 demonstrates how the changing availability of nitrate (NO3-) or ammonium (NH4+) causes significant changes among other tree essential elements. For example, as nitrate availability and concentrations rise, calcium (Ca), cobalt (Co), potassium (K), magnesium (Mg), molybdenum (Mo), and sulfur (S) availability increase, while chlorine (Cl), iron (Fe), manganese (Mn), silicon (Si), and zinc (Zn) availability declines. Element interactions with changing nitrogen availability and enrichment (and nitrogen form) are difficult to predict accurately. Ecological tuning of enrichment applications must be cautious to minimize undesirable or unexpected outcomes.

Changing pH

Soil pH is affected by the type of inorganic nitrogen present in a soil. High levels of organic materials or ammonium concentrations tend to accelerate a drop in soil pH. Ammonium sources surface-applied to high pH soils, recently limed soils, or soils with free calcium carbonate are transformed into ammonia gas which escapes into the atmosphere.

The nitrification process generates two protons (2H+ units -- acidity as measured by pH) for every nitrate transformed from ammonium. High nitrate concentrations initiate an increase in soil pH from OH- and HCO3- excretion by the tree through ion transport systems. Internally, tree pH is maintained by organic acid production with potassium transport used to keep the tree slightly electrostatically negative. Addition of any fixed nitrogen source can disrupt and change soil / tree interactions.

Depletion Zones

As inorganic nitrogen ions are taken-up by a tree, soil areas close to tree roots quickly become depleted of nitrate and ammonium. Limited amounts of nitrate can move with water around roots, while ammonium ions remain closely bound near exchange sites, shifting toward roots. The nitrogen depletion zone increases the difficulty with which trees take-up nitrogen and requires continuous root growth to maintain supplies (also true of phosphorus (P).)

Supply and demand for reduced nitrogen in a tree are based upon instantaneous needs, with only a small amount in storage. Continuous dosing is the process which emulates roots through their elongation growth. A tree attempts to keep nitrogen and phosphorus at steady-state concentration levels. This

tree essential element	nitrogen ion added to soil NITRATE	 AMMONIUM
B	--	--
Ca	S	A
Cl	A	S
Co	S	S
Cu	--	--
Fe	A	S
K	S	S
Mg	S	A
Mn	A	S
Mo	S	A
Ni	--	--
P	--	--
S	S	S
Si	A	A
Zn	A	A

Figure 11: Tree essential element availability interactions for nitrate and ammonium. (listed by chemical symbol).

"A" = antagonistic where addition of nitrogen decreases availability of another element.
"S" = synergistic where addition of nitrogen increases availablility of another element.
"--" = no apparent change in element availability.

requires more or less continuous growth to control and capture nitrogen and phosphorus resources, or "hiring" a symbiont to capture resources.

Steady-State Levels

A steady trickle of nitrogen, rather than large bursts of availability, are normal for a tree / soil system. Internal tree growth correlation systems are designed for controlling resource gathering processes. Swamping (overdosing) these sensor systems and sequestering processes for nitrogen within a tree can modify many tree responses to the environment. Some of these responses will have a negative impact on tree health and survival.

Over-all tree health, rather than individual measures of growth, should be the targeted goal of nitrogen enrichment. A tree can be made to have dark green foliage and to profusely grow shoots with nitrogen additions. From a whole tree perspective, utilizing (obsessing upon) a simple growth goal or threshold system, while disregarding tree system health and efficient function can be damaging.

High / Low

The amount of inorganic nitrogen present in soil has a direct effect on tree health and growth. At decreasing concentrations, beginning well before visual symptoms are present (because of internal recycling and reallocation of nitrogen), represents nitrogen deficiency. At high nitrogen concentrations, toxicity and physiological disfunction can be problems.

There is an intermediate zone of moderate nitrogen concentrations where tree health and growth is "adequate" for sustained growth. This adequate zone is the target for management activities. The adequate zone is narrower and the toxic zone is more easily reached with supplemental ammonium nitrogen sources, as compared to nitrate sources. Figure 12.

Soil Systems

Trees do impact (passive) and change (active) their own rhizospheres with organic additions. These added materials are comprised of everything in a tree (because everything can leak out), and everything outwardly shed from a tree. Micro-flora and fauna of the rhizosphere are fed, housed, and killed by tree materials and exudates. All the microorganisms of soil help cycle and recycle elements and life co-factors needed by a tree. Some microorganisms are invited to infect roots in order to present a larger tree rooting area at a smaller cost to the tree.

Mulch and composted organic matter have strong roles to play with nitrogen availability around tree roots. A thin, tree / wood derived, well aerated and mixed, composted organic layer over the rooting area, covered by a thin course textured organic mulch layer, can be helpful in recycling nitrogen. Use of tree litter and other organic components provide food-stocks for soil organisms which break-down and recycle essential materials.

Slowly decaying organic materials, like bark, should be used only in small proportions and only for the top mulch layer. Inorganic and dense materials should be avoided. Supplemental nitrogen enrichment can be broadcast over top of a mulch / compost area.

Ecological Management

Supplemental nitrogen enrichment, loss of organic matter, detrimental soil changes, and landscape maintenance chemicals can disrupt the tree / soil ecological community. Carefully tuning nutrition within a tree by nitrogen enrichment, and through nitrogen sources in composted organic matter, can

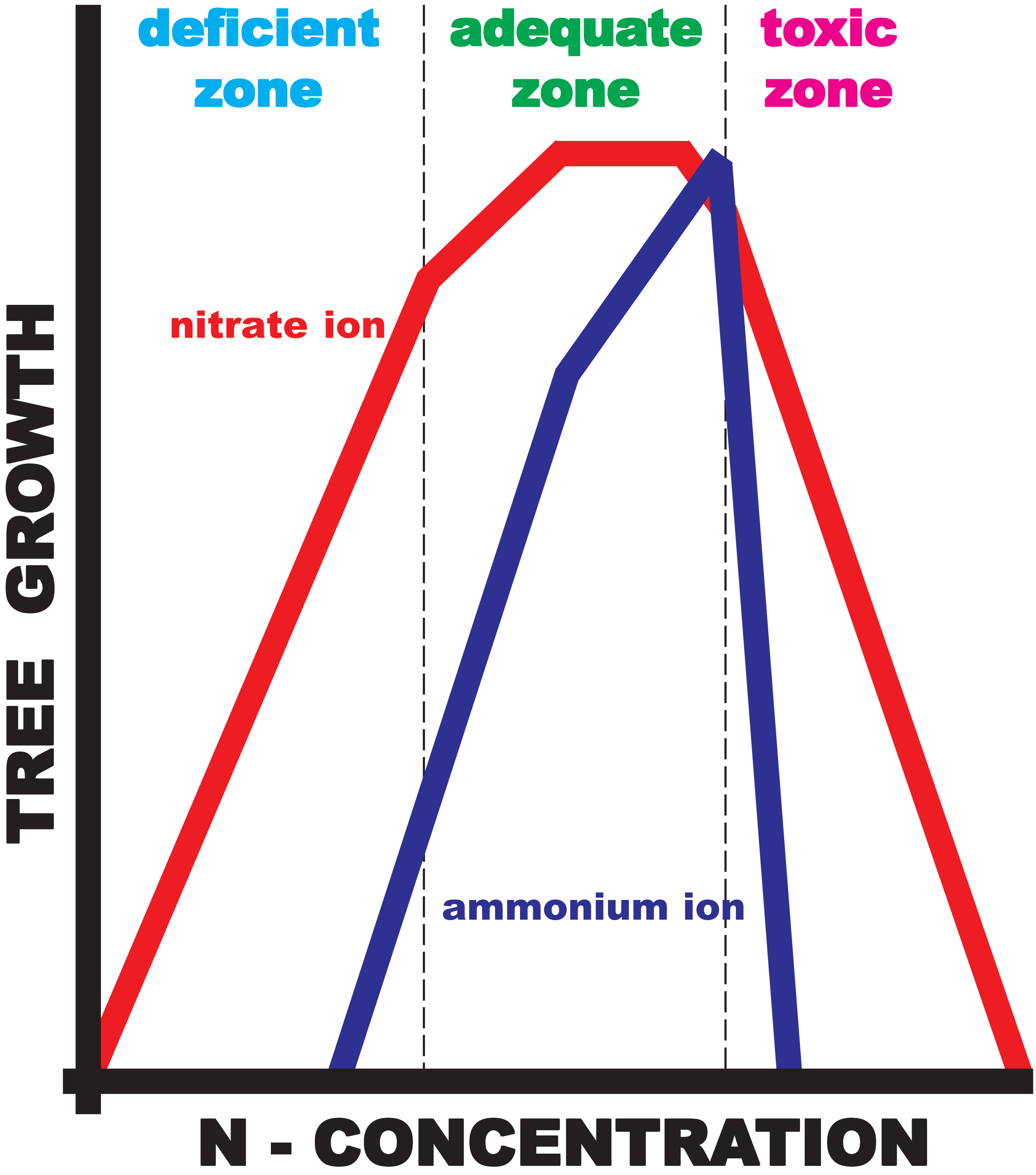


Figure 12: Nitrogen concentrations and availability for tree growth following an essential element growth curve form from deficiency to toxicity. Note ammonium cation curve (dotted line) shows a much narrower space between deficiency and toxicity than does nitrate.

provide many advantages of a healthy soil. Abusive soil management practices can leave trees open to deficiencies, toxicities, and pest attack.

Come On In !

Adequate availability of nitrogen in soils is but one problem facing trees. Moving nitrogen inside a tree presents a number of unique constraints and solutions. Transporting some materials across root cell membranes can be accomplished by simple diffusion where materials move from high concentrations to places of low concentrations. Transport can also be associated with moving electrostatically charged ions from places with like-charges to places of opposite-charges. Active transport systems are used by root cells for nitrogen uptake.

Active transport mechanisms require energy for maintenance and for moving individual items. These transport mechanisms function both at cell membranes and at internal tonoplasts (vacuole membrane). Carriers on membranes are used to move materials, while cells attempt to maintain a near neutral internal electric charge balance. Active transport is required for uptake of anions ($NO3^-$, Cl^-, $H2PO4^-$, $SO4^{2-}$); excretion of selected cations (Na^+, Ca^{++}, Mg^{++}); and, not required for potassium ions (K^+) which serve as universal charge balancing.

Nitrate Forms

Ecologically, most nitrogen compounds are quickly converted to nitrates under aerobic conditions. Ammonium is a small molecule, is easily available on exchange sites in soil, and is already in a reduced state. Unfortunately, ammonium can quickly initiate toxicity problems. Urea can be taken up as applied to a limited extent, but is quickly (3-5 days) converted to ammonium in soil.

Urea should not be applied directly to soil or plant surfaces, especially turf, or high pH soils. Various types of nitriform products bind nitrogen within various length carbon chains which must be broken apart biologically to allow nitrogen to be released and used.

Nitrate ($NO3^-$), and to a lesser degree ammonium (NH4+), uptake into a tree from soil is an energy dependent process. Nitrate is taken into a tree against concentration, hydrostatic pressure, and electrostatic charge gradients. This uptake process is not simple diffusion, but an active process requiring energy to transport nitrate across cell membranes, as well as energy to produce and maintain a carrier system.

Carried

The presence of nitrate in soil stimulates carrier activity (and its own uptake by a tree.) Nitrate uptake also stimulates production of nitrate reduction machinery inside root cells. Nitrate presence in the root area is a signal to a tree to expend energy for transport and processing of nitrate. Tree roots without adequate energy and carbon chain supplies will be stressed by nitrate presence in the soil. Actual nitrate uptake is usually much less (4-5X) than the full nitrate uptake capacity of tree roots.

Nitrate can not move into tree root cells passively with water, as do many of the other essential elements. Nitrate, because of its mass, size, and charge must be actively transported into tree root cells using one of three specialized carrier systems:

1) a low capacity carrier always available and present in the absence of nitrate;
2) a inducable carrier generated under low nitrate concentrations. (Note this carrier is not generated and maintained unless there is nitrate present in the rhizosphere.); and,
3) a carrier which functions at high nitrate concentrations.

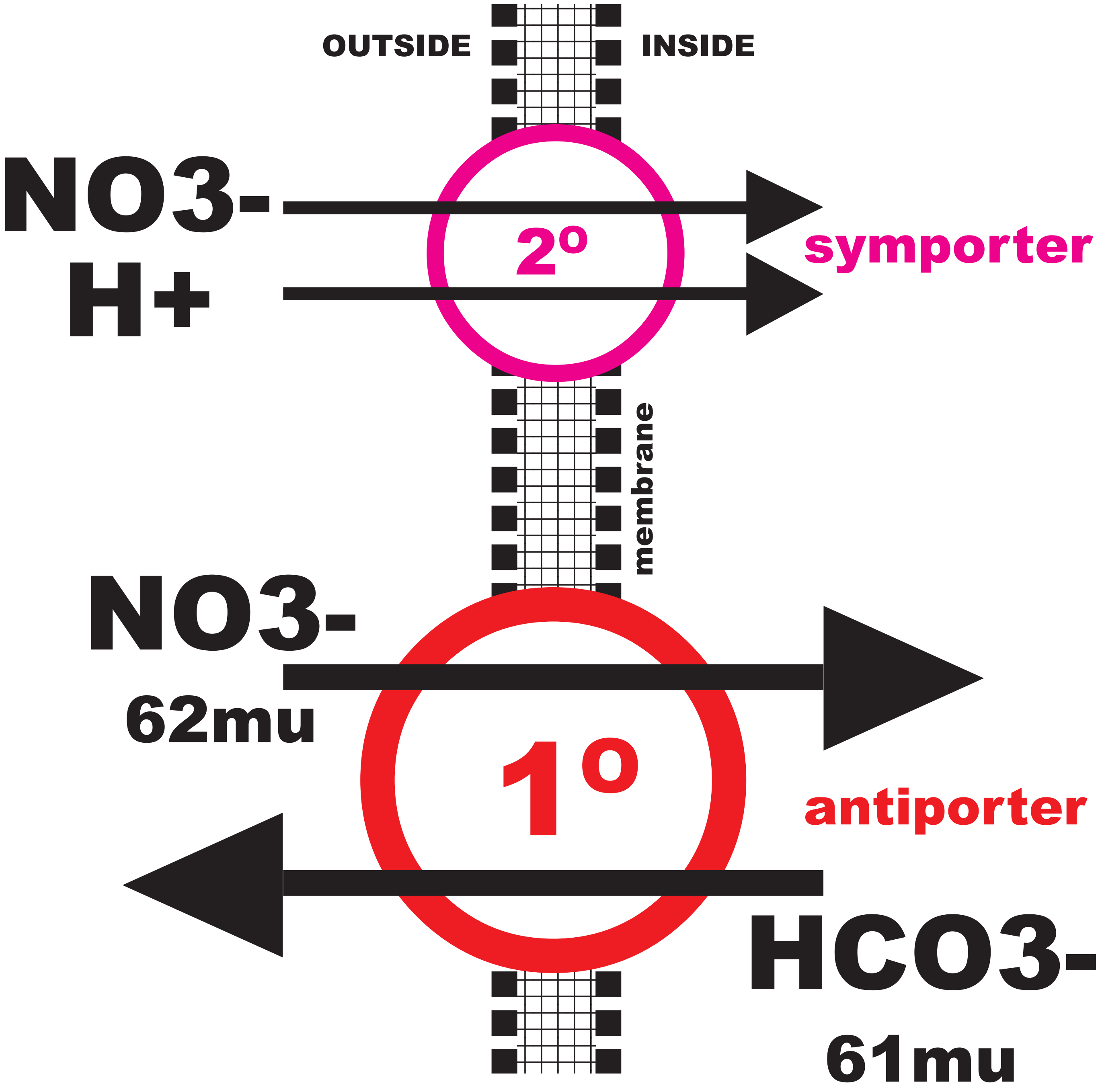


Figure 13: Secondary nitrate (NO3-) symport carrier transports nitrate and proton (H+) simultaneously into cell maintaining electrostatic charge balance. Primary nitrate (NO3- & 62 mass units) antiport carrier transports nitrate inward and carbonate (HCO3- and 61 mass units from organic acids) outward maintaining a mass and charge balance.

Easing Transport

Nitrate is transported using carriers which breach cell membranes. Figure 13 shows two primary types of carriers used by tree cells to move nitrate from one side of a membrane to the other (either apoplast / symplast interface or symplast / symplast interface). Symporters move two items in the same direction usually maintaining a balanced charge across the membrane. Antiporters move two items in opposite directions usually maintaining a mass and / or charge balance.

Nitrate can be moved into a tree by a symporter carrier, where a molecule of nitrate is transported into a cell simultaneously with a proton (H+) to maintain the balance of electrostatic charges. This leaves an OH- outside in the soil. Nitrate (NO3- mw = 62 mass units) is primarily transported by antiports move nitrates into a cell and an ion of like charge (and similar size) outward.

This cotransported ion of similar charge and size is a carbonate anion (HCO3- mw = 61 mass units) from organic acid origins. The presence of HCO3- inside root cells stimulates nitrate uptake and is essential for operation of the primary nitrate carrier.

Ammonium is positively charged and small enough to enter tree root cells with water. Because of nitrogen demands, ammonium ions can also be actively transported into tree root cells using two types of carriers, one transports ammonium under low concentrations and one function at high ammonium concentrations.

Nitrate Reduction

Once inside root cells, nitrate is reduced by nitrate reductase (NRe) enzyme, which is the first step in reducing nitrates into a usable form. Figure 14. This process is accelerated and maintained by light, CHO, cytokinin, high CO2 concentrations, and anaerobic conditions. This process is inhibited by darkness, glutamine build-up, oxygen, magnesium ions, and low CO2 concentrations.

NRe is a monstrous, enzymatic catalyst which requires molybdenum (Mo) and iron (Fe) to function. This enzyme is the only major use for Mo in a tree and its requirement can be circumvented (if required) by adding only ammonium-based nitrogen. NRe is energy-expensive to construct and maintain with a half-life of only a few hours. NRe activity is initiated within 40 minutes of nitrate presence in the soil and reaches a maximum after three hours. It is estimated up to 25% of tree energy from photosynthesis is used in nitrate assimilation. NRe only purpose is to make the initial reduction step on nitrate.

To accomplish the first step in nitrogen reduction, NRe facilitates transfer of two electrons (energy from carbon respiration) to nitrate (NO3-), which yields nitrite (NO2-). This process occurs in root cell cytosol. When excess nitrate is available, nitrate is moved beyond the initial cell of uptake and reduced in xylem parenchyma. In some tree species, a small portion of nitrate (usually the remains of excessive loads) are shipped to leaves for reduction. NRe is not a limiting factor for tree nitrogen utilization (availability of nitrate to roots is limit).

Nitrite Reduction

Nitrite (NO2-) is moved quickly to plastids (cell organelles) to minimize toxicity. The next three steps in nitrogen reduction is facilitated by nitrite reductase (NitRe), an enzymatic catalyst which requires iron (Fe) and sulfur (S). NitRe facilitates the reduction of nitrite by transferring six electrons (3 electron transfer molecules -- ETMs) which yields ammonium (NH4+).

Ammonium can easily reach toxic levels in a tree cell, and is not readily stored. Ammonium is not normally freely transported in xylem unless large amounts are present and can not be processed in roots. Ammonium is quickly moved into an organic framework (carbon skeleton) with the result called

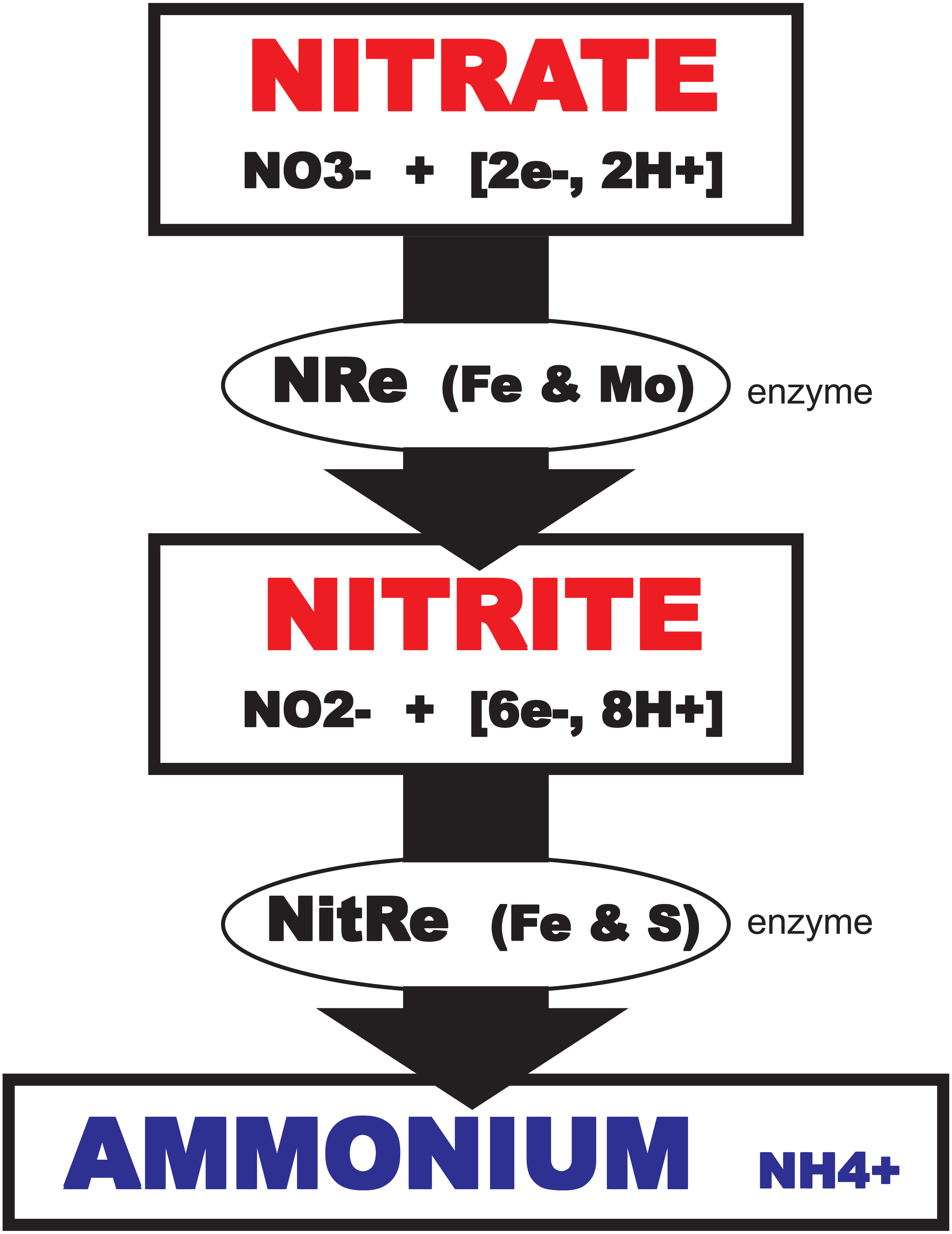


Figure 14: Pathway inside tree cells moving nitrate taken from soil to ammonium ions sequestered in cellular pool.

idealized formula	name
2C1N	glycine
3C1N	serine
3C1N	alanine
3C1N	cysteine (S)
4C1N	aspartate
4C1N	threonine
4C2N	asparagine (A)
5C1N	glutamate
5C1N	valine
5C1N	methionine (S)
5C1N	proline
5C2N	glutamine (A)
6C1N	leucine
6C1N	isoleucine
6C2N	lysine
6C3N	histidine
6C4N	arginine
9C1N	tyrosine
9C1N	phenylalanine
11C2N	tryptophan

Figure 15: Basic amino acids used in trees for enzyme and protein structures (considered structural amino acids).
"C" = carbon; "N" = nitrogen; (S) = sulphur containing; (A) = amide.

normal ammonium processing

$1N_{(NH4+)} + 5C1N = 5C2N$

(glutamate) (glutamine)

high ammonium processing

$1N_{(NH4+)} + 5C = 5C1N$

(oxoglutarate) (glutamate)

occasional ammonium processing

$1N_{(NH4+)} + 4C1N = 4C2N$

(aspartate) (asparagine)

Figure 16: Three primary ammonium ion insertion points onto carbon chains generating amino acids.

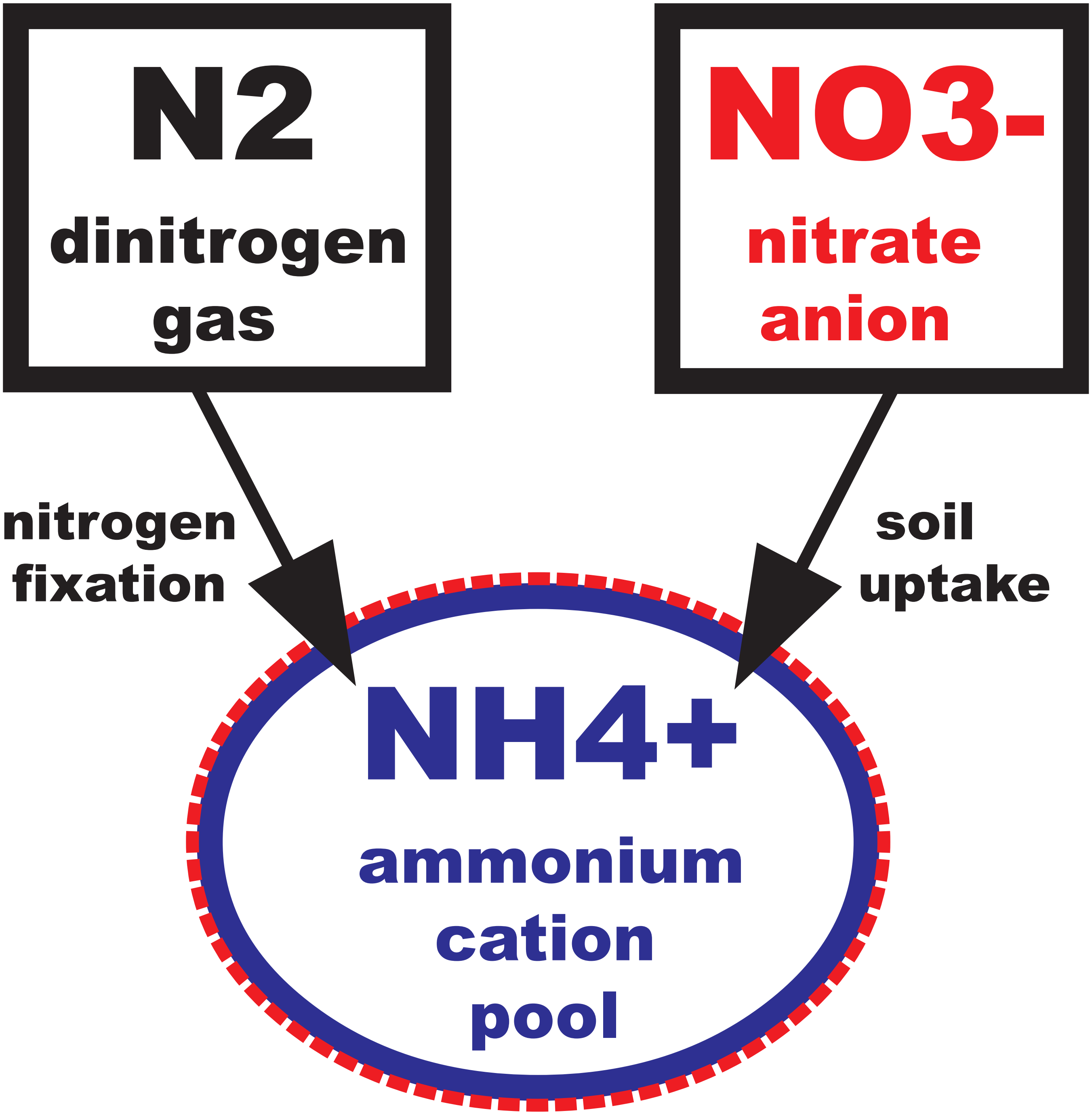


Figure 17: Primary external nitrogen sources supporting the ammonium cation pool inside tree root cells.

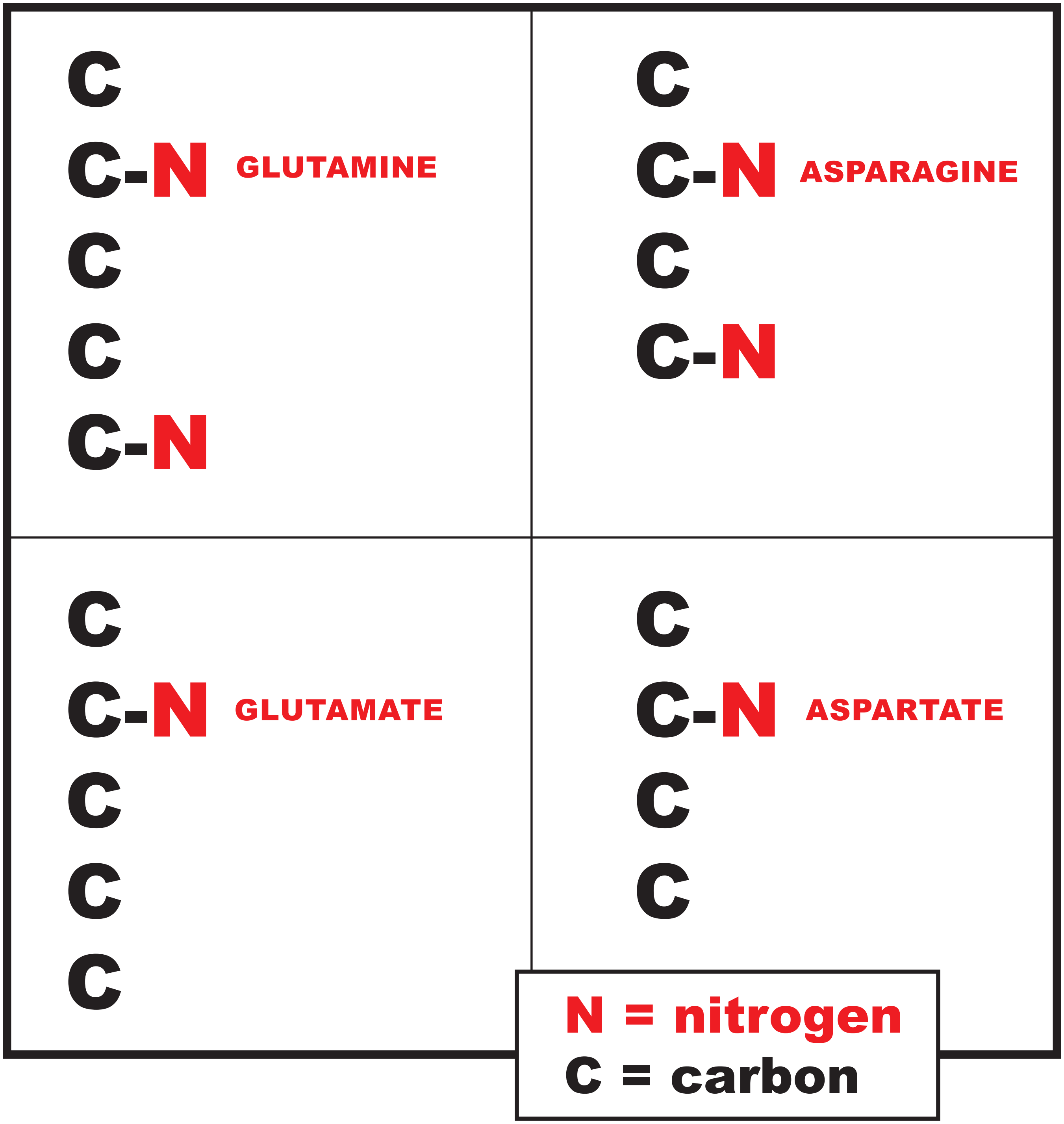


Figure 18: Example idealized structure of nitrogen transport and storage amino acids showing the location and number of nitrogen attachments.

(Structural amino acids can carry 1, 2, 3, or 4 nitrogens.)

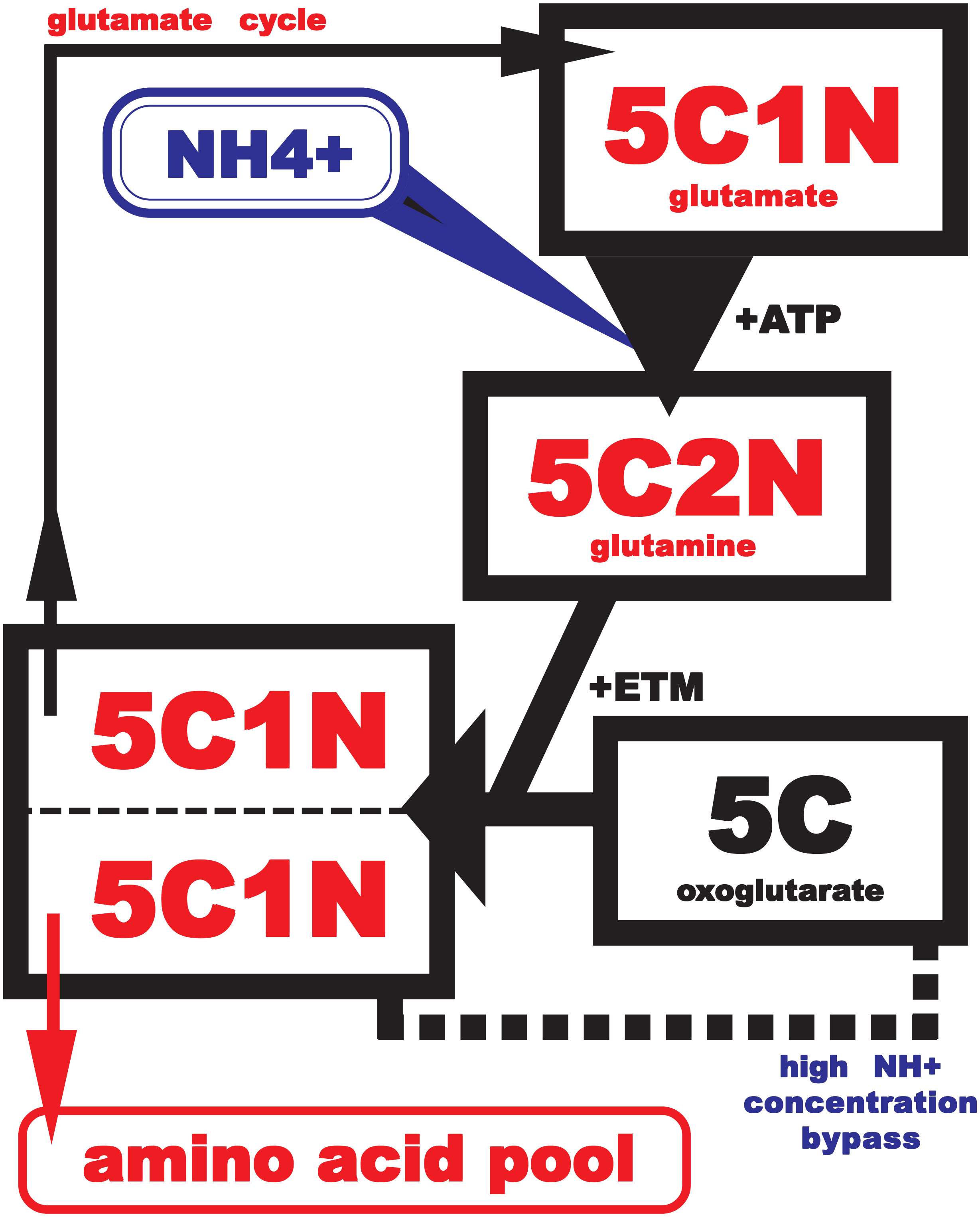


Figure 19: Pathway inside tree cells for accumulated ammonium ions (NH4+) being consolidated into a carbon framework generating two amino acids. (i.e. glutamate cycle)

an amino acid. Figure 15. Amino acids can be used as building blocks for other compounds, for storage, or for transport out of a cell and throughout a tree. Cellular assimilation of ammonium ions requires a strong and continuous carbon chain source transported from the photosynthetic process and from local storage materials. Figure 16.

Locking-Up Ammonia

Because of ammonium toxicity potential, there are two primary pathways (and one secondary pathway) for utilizing this reduced nitrogen compound. Figure 17. The first primary system for incorporation of ammonium into an amino acid is called the glutamate cycle (requiring magnesium (Mg) and zinc (Zn)). Ammonium is added to glutamate (a 5C1N amino acid) and energized (with 1 ATP) to produce glutamine (a 5C2N amide), which is a transport and storage form of nitrogen. Figure 18.

Glutamine (5C2N) and oxoglutarate (5C) are then combined to produce two glutamates (two 5C1N). Figure 19. One of the two glutamates generated is used to start the ammonium assimilation process again, while the other is shipped away for tasks like protein synthesis. The net result is one ammonium successfully incorporated into an amino acid which can be stored or used to transport nitrogen throughout a tree.

Glutamate (5C1N) is the feedstock leading to the other 19 amino acids (actually 18 amino acids and an amide) a tree's life is built around. There are over 200 amino acids in trees, although only 20 are structural forms used for enzymes and proteins. Glutamate is the starting material for amino acids, proteins, nucleic acids, nucleotides, coenzymes, and porphyrin rings (chlorophyll and phytochrome). Both glutamate (5C1N) and glutamine (5C2N) can be safely stored for later use or transported to the rest of a tree.

Alternative Assimilation

The second primary system for incorporation of ammonium into an amino acid is a direct carbon chain addition when ammonium ion concentrations are at high levels approaching toxicity (ammonium overdose). Ammonium is added to oxoglutarate (a five carbon organic acid from photosynthesis -- 5C) to generate a glutamate (5C1N). This pathway quickly moves toxic ammonium into storable and transportable glutamate (5C1N) but is energy-expensive and only functions at relatively high levels of ammonium. Figure 20. Figure 21 shows a further step in shifting amino nitrogen to another storage and transport form called asparagine (4C2N).

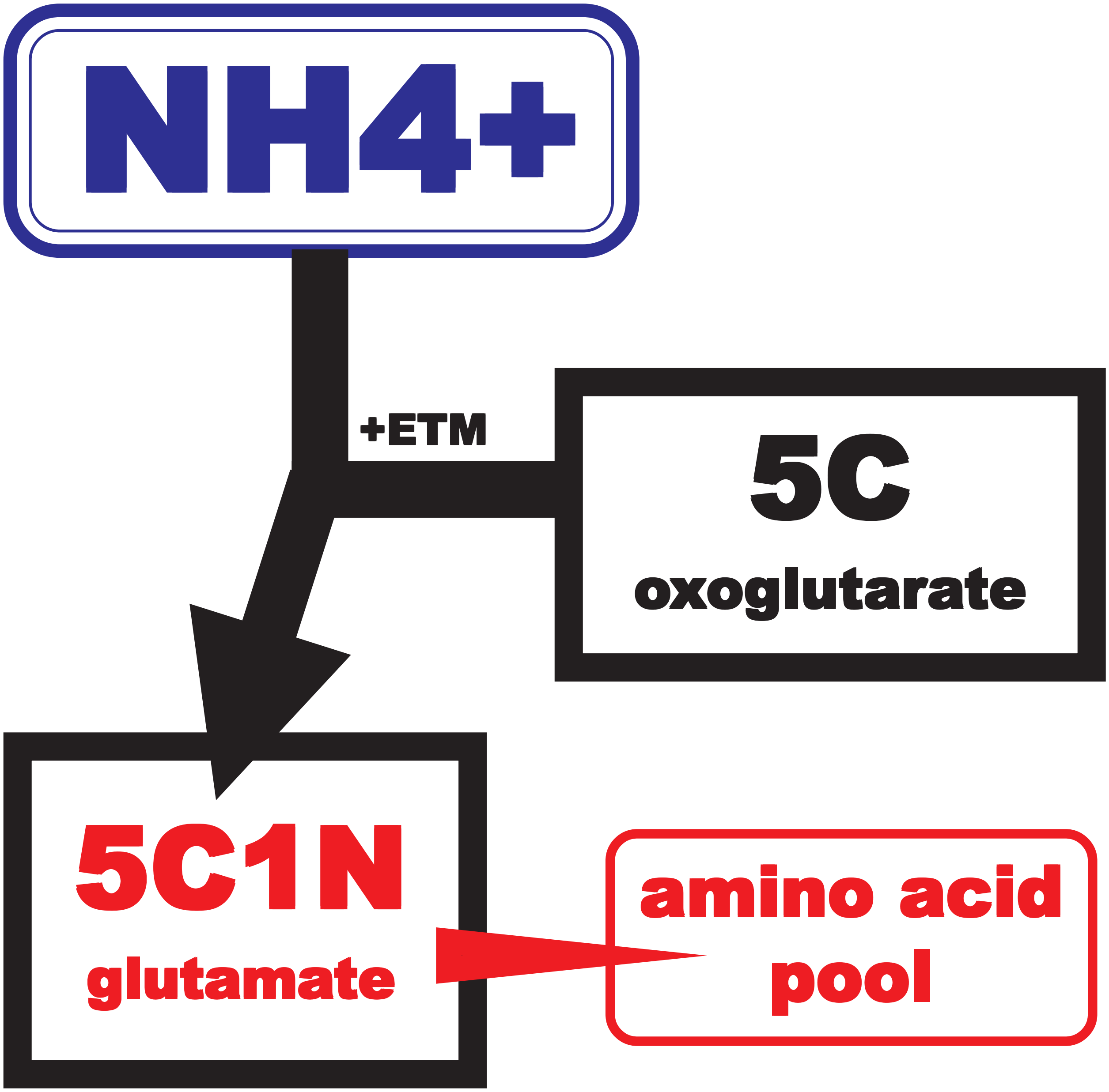
Third Assimilation

A third ammonium incorporation pathway (of secondary importance) is the aspartate / asparagine process. This pathways is usually used for transferring amino-nitrogens, not assimilating ammonium ions. Ammonium is added to amino acid aspartate (4C1N) and generates asparagine (4C2N), a amide transport and storage form of nitrogen. Asparagine is used for nighttime nitrogen storage. In daylight, and with strong protein synthesis in a tree, aspartate is continually moved to asparagine. Figure 22.

Accounting

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

High NH4+ Concentration Bypass



NH4+

+ETM

5C
oxoglutarate

5C1N
glutamate

amino acid pool

Figure 20: Pathway inside tree cells for high concentrations or excess ammonium ions (NH4+) accumulation being consolidated into a carbon framework generating one amino acid. (i.e. high NH4+ concentration bypass)

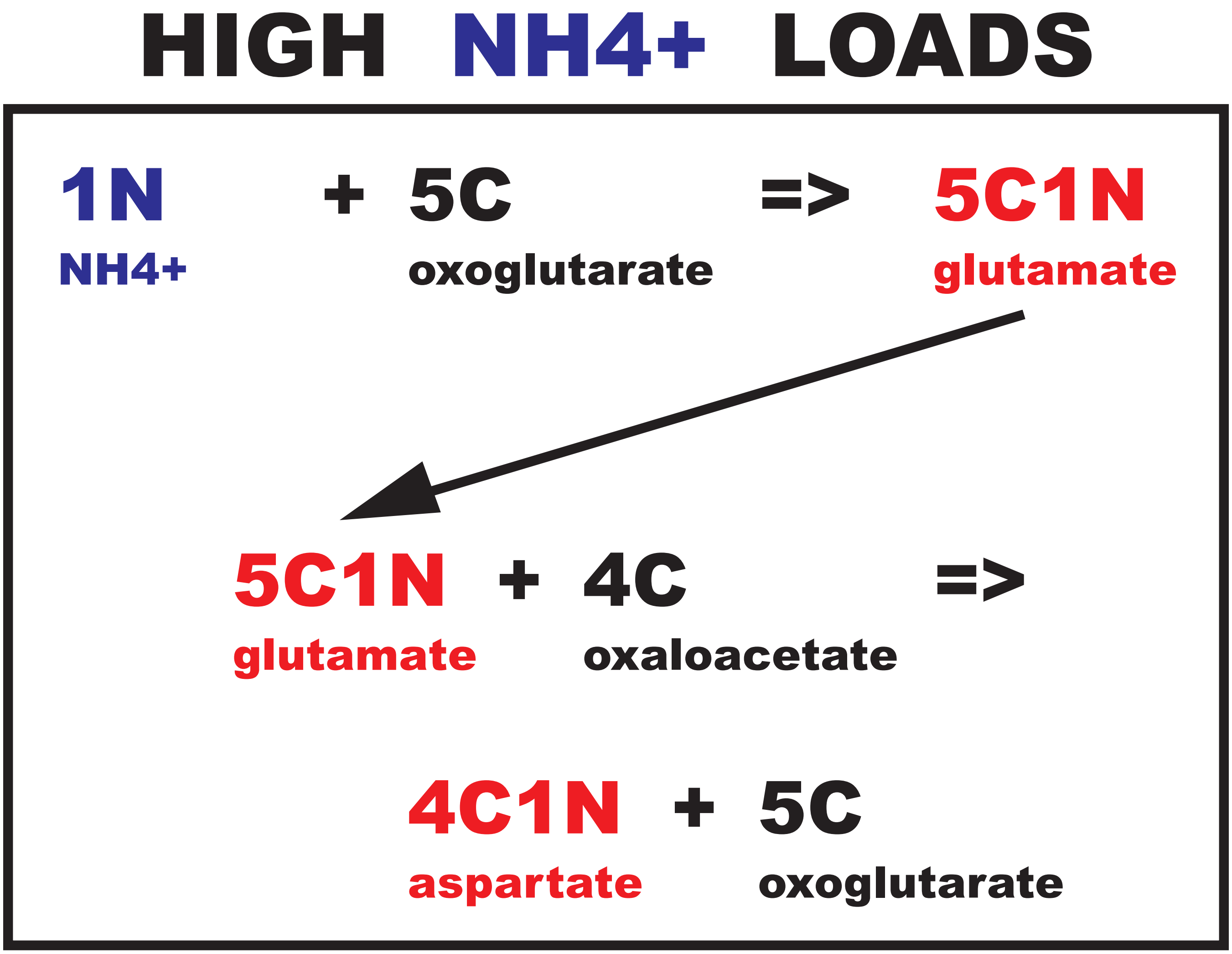


Figure 21: Ammonium assimilation under high concentration loads directly to glutamate using a carbon chain (5C), and shifting of nitrogen to aspartate using a glutamate source combined with a carbon chain (4C).

LOW TREE ENERGY

1N + **4C1N** => **4C2N**
NH4+ **aspartate** **asparagine**

OR

4C1N + **5C2N** =>
aspartate **glutamine**

4C2N + **5C1N**
asparagine **glutamate**

Figure 22: Ammonium assimilation to generate asparagine, a major transport form of nitrogen, and recombination of nitrogen to generate asparagine and glutamate. Asparagine is generated under low light, low carbohydrate levels, and low energy levels.

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 the microbe 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. Actually, there is at least 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 the pH gradients responsible for ATP (energy) production.

There is great variability in processing location 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

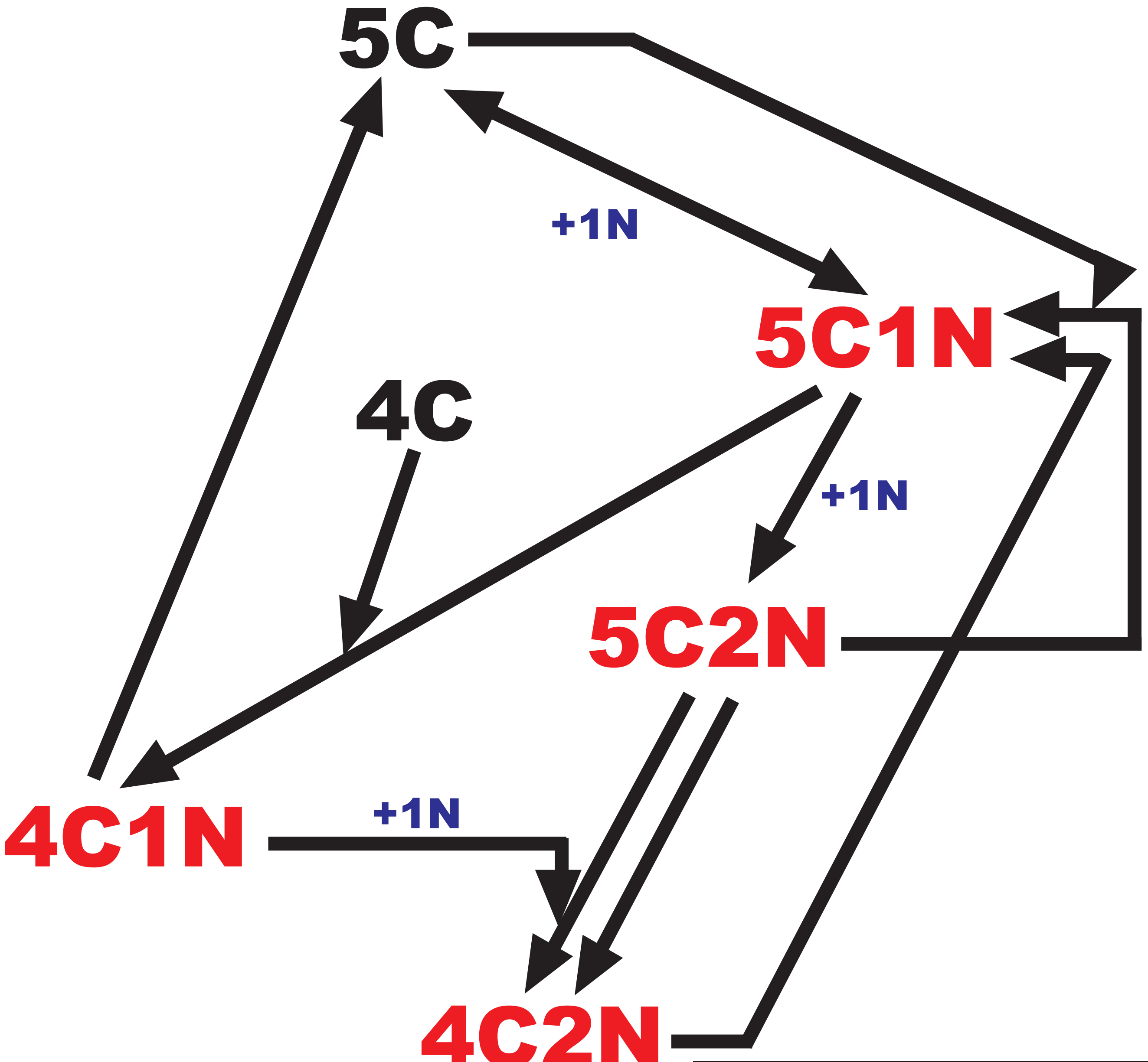
For most landscape trees in temperate areas, assume nitrate is reduced almost exclusively in root tissues. Nitrogen reduced in roots is then added to the transpiration stream and sent up to leaves. The cost for nitrogen reduction is paid by current phloem carbon contents (food shipped from leaves), and 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 23. Of these, asparagine and glutamine are the most effective and efficient. Both have a high nitrogen / carbon ratio (asparagine = 2N:4C; glutamine = 2N:5C). Figure 24.

Root Plight

The 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) doubles 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 25. Intermediate products like ethanol and lactate build-



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

Figure 23: Ammonium ion (+1N) assimilation web in trees with transport and storage amino acids and carbon chain feedstock pools shown.

4C1N
aspartate

4C2N
asparagine

5C1N
glutamate

5C2N
glutamine

Figure 24: Primary transport and storage forms of nitrogen with the 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 25: 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.)

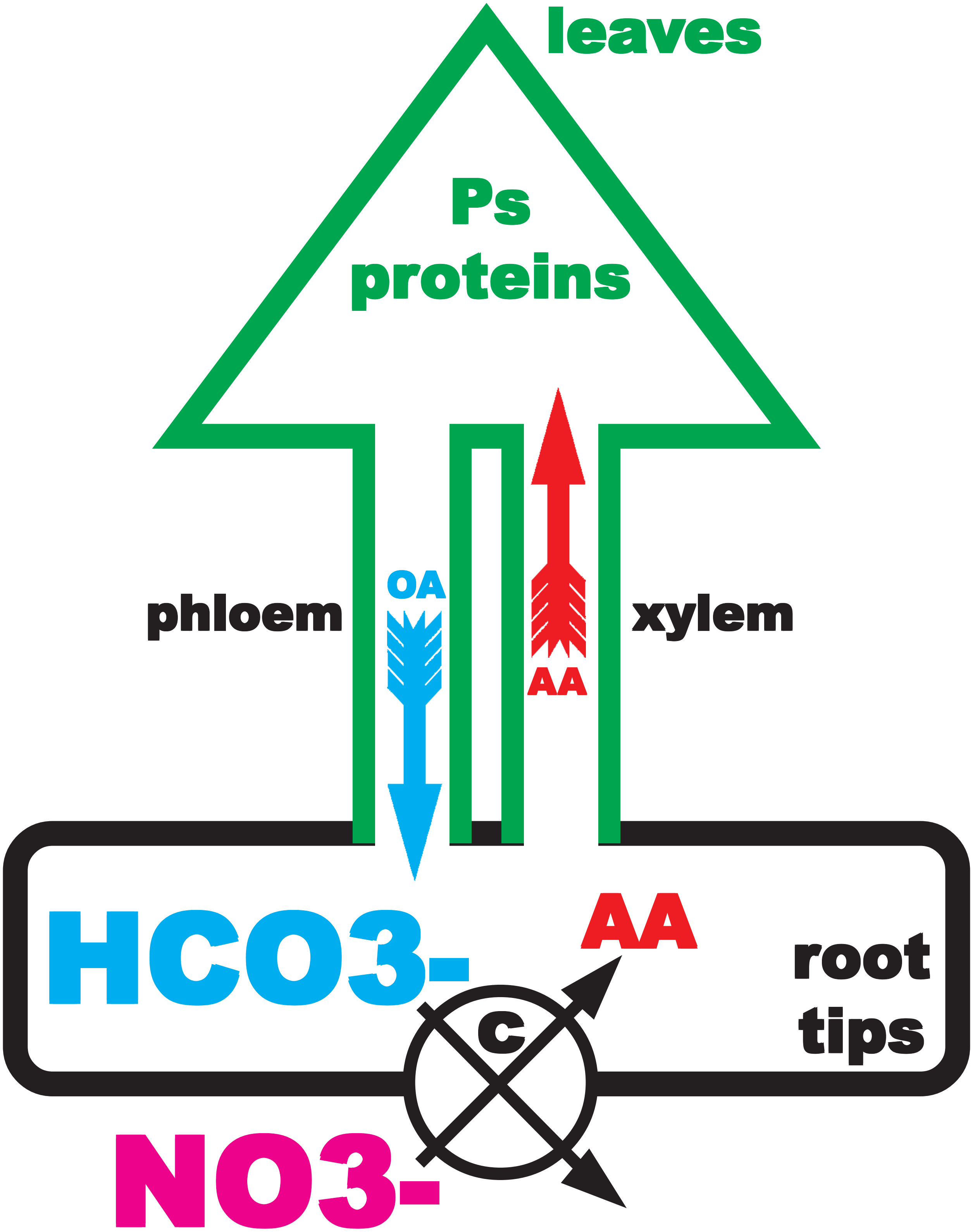


Figure 26: Nitrate uptake and control model inside a tree generating amino acids (AA) and using carbonate ions from organic acids (OA).

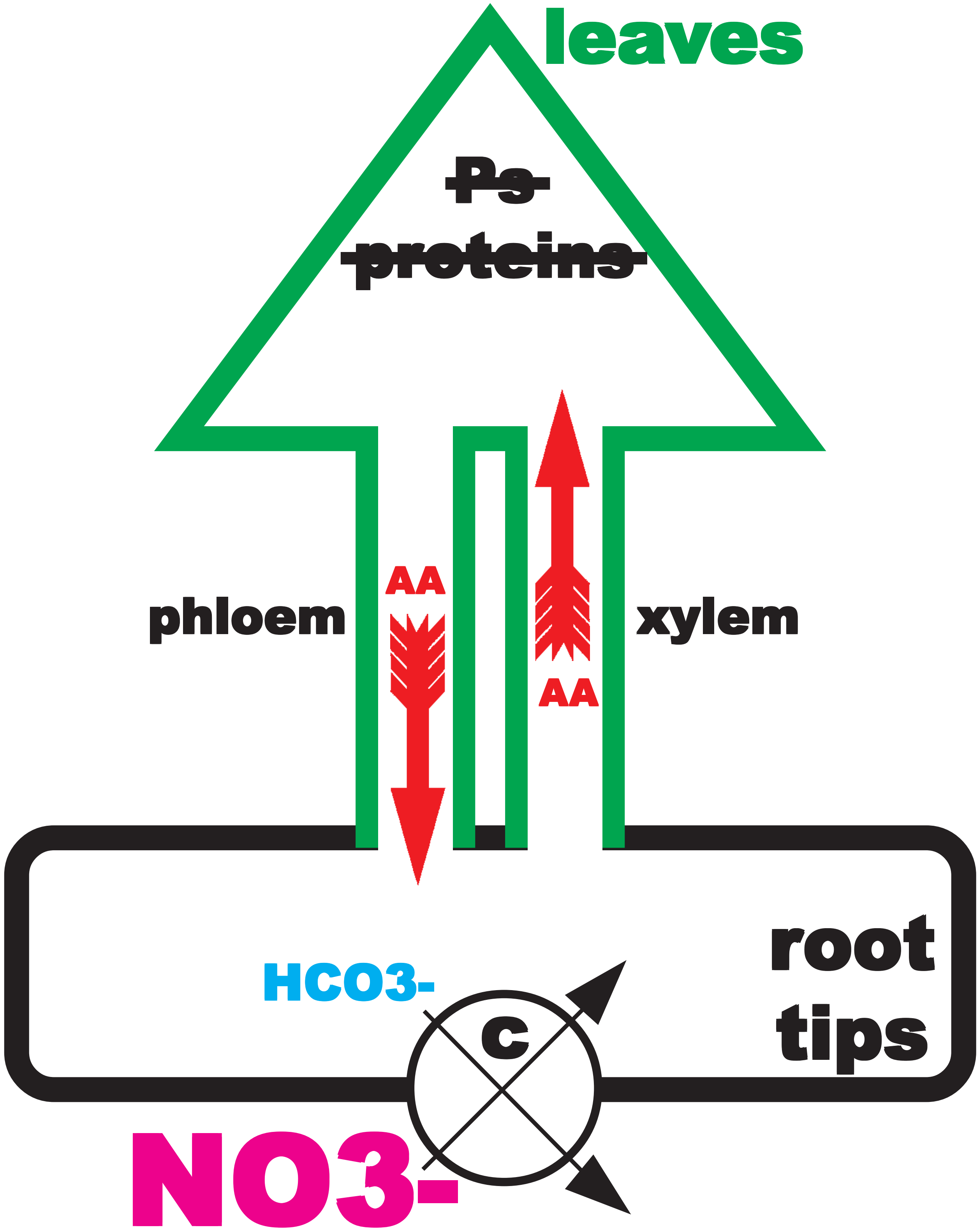


Figure 27: Nitrate uptake and control model inside a tree under photosynthetic and protein synthesis constraints or stress causing recycling of unused amino acids (AA) slowing nitrate uptake.

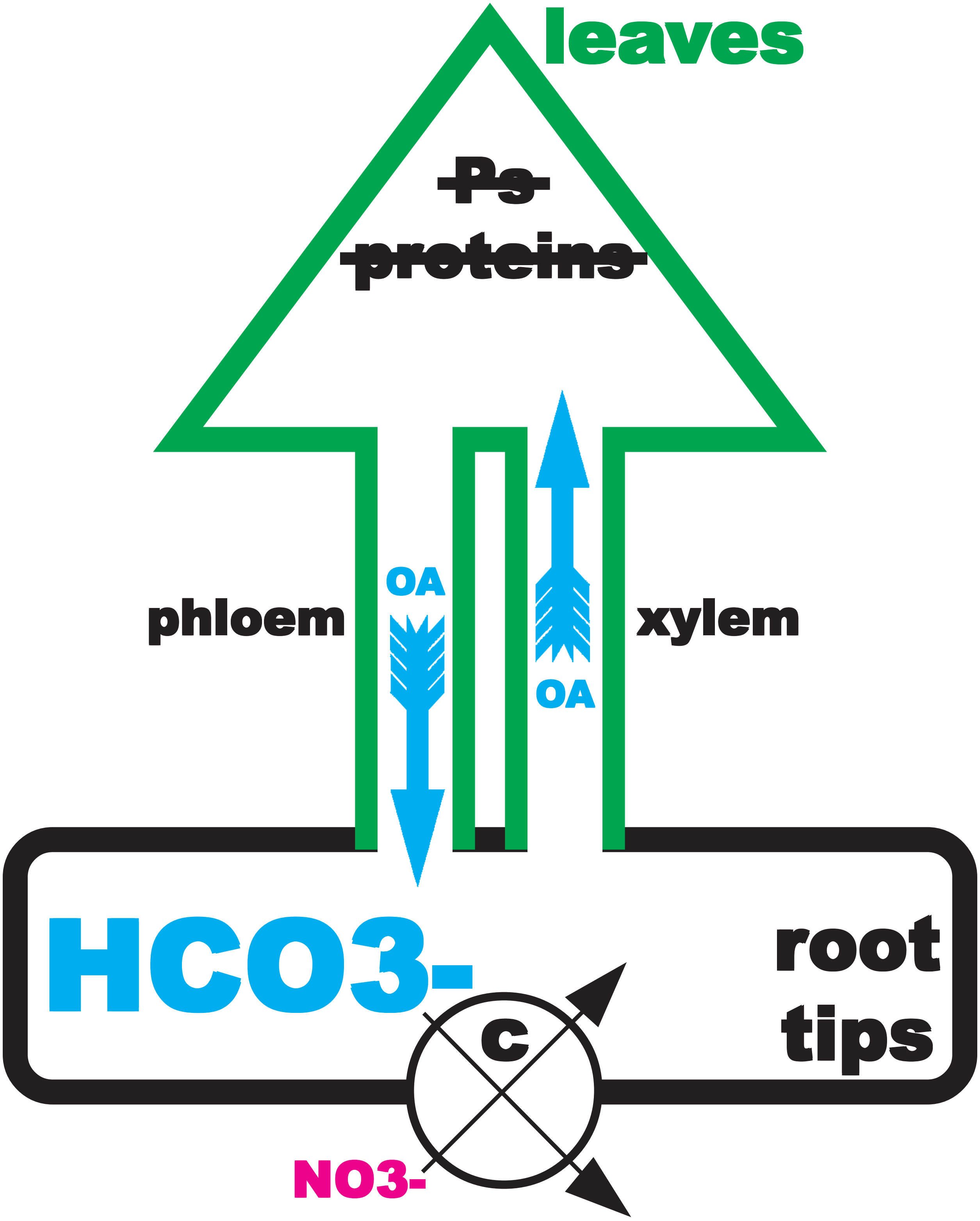


Figure 28: Nitrate uptake and control model inside a tree under nitrate availability constraints / stress causing recycling of organic acids (OA) which slow photosynthesis and protien synthesis.

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 concentrations.

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 26.

If too much nitrogen is present in the system, amino-acids from the glutamate cycle begin piling-up. Figure 27. 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 transported in phloem), nitrate uptake is slowed. Overabundance of nitrogen and tree stress which 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 28. 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 that 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 at its inception point, it will slow further production. To appreciate nitrate uptake control, the following bullets provide five basic results:

A) If amino-acids are used for protein synthesis (amino acid concentrations fall), then nitrate uptake increases.
B) If amino-acids concentrations increase in roots, then nitrate uptake decreases.
C) If organic acids increase, then nitrate uptake is stimulated.

tree part	relative tree nitrogen concentrations
leaf	68%
branch	9%
stem	9%
sapwood	6%
heartwood	3%
periderm	14%

Figure 29: Average relative nitrogen distribution in above ground parts for four species of hardwoods (dogwood, red maple, red oak, yellow-poplar).

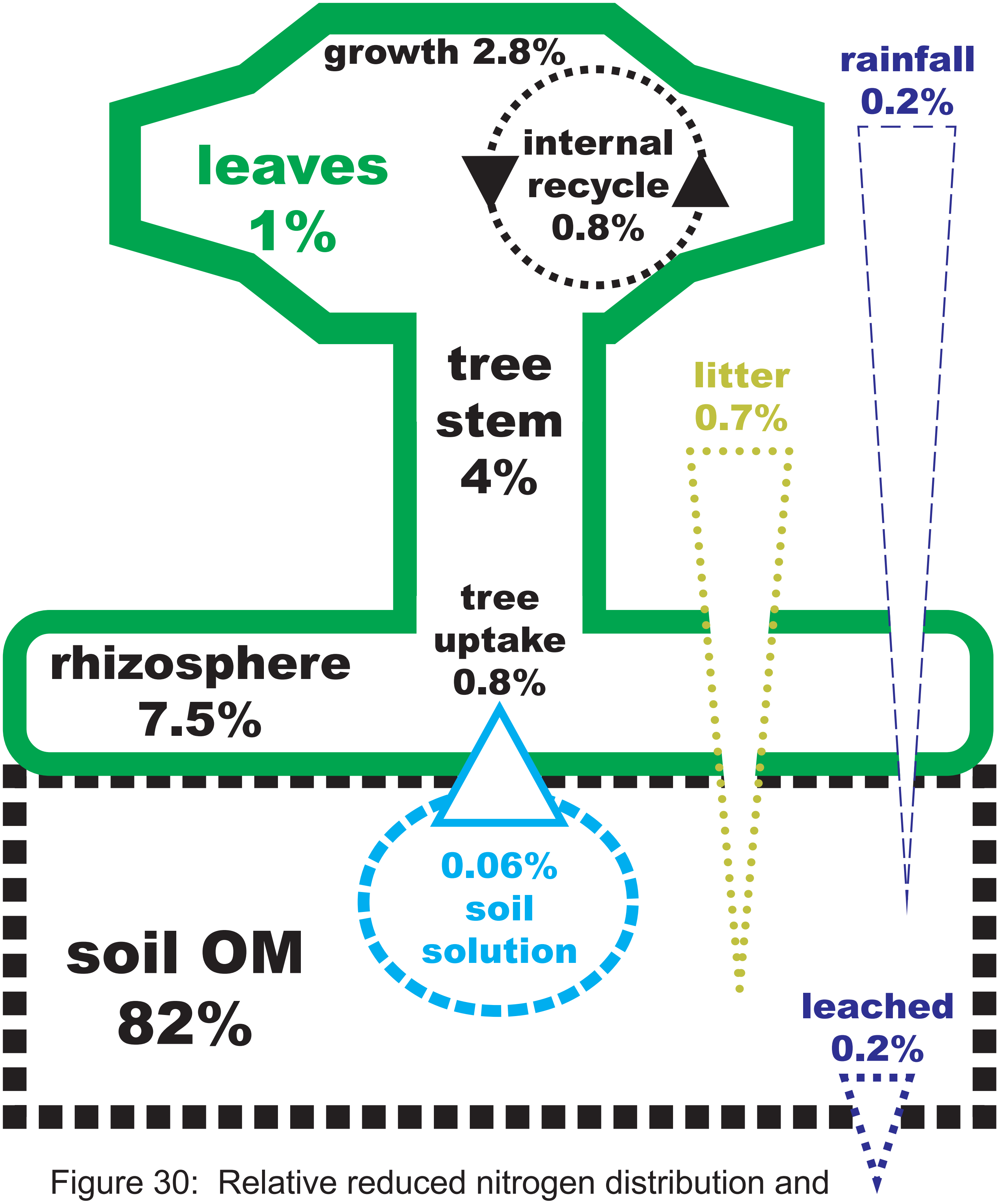


Figure 30: Relative reduced nitrogen distribution and annual changes within a tree / soil system with soil organic matter (OM) set at 82% of site's reduced nitrogen pool.

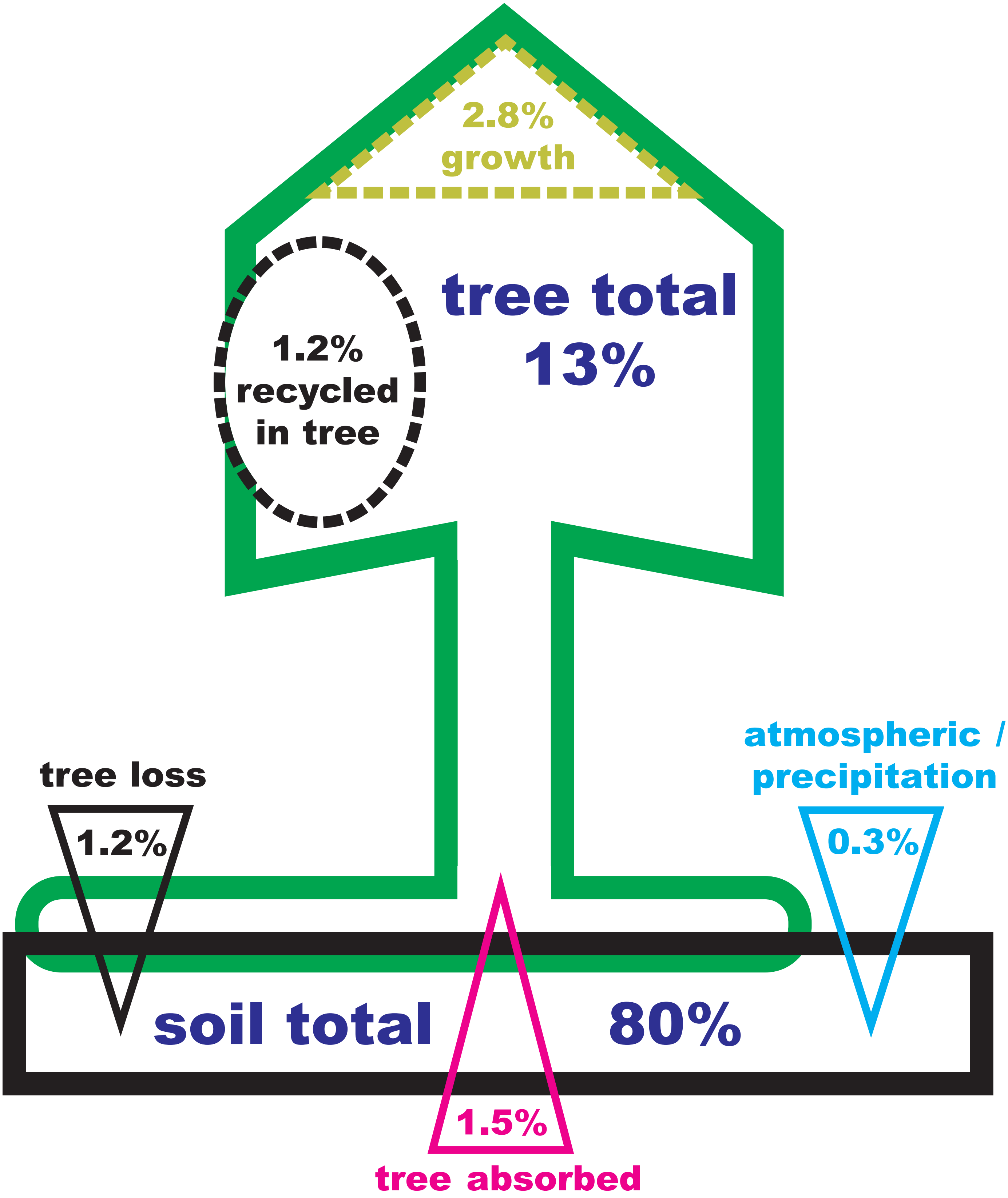


Figure 31: Relative reduced nitrogen distribution and annual changes within a tree / soil system.

D) If organic acids are reduced (less HCO3-), then nitrate uptake is reduced.
E) As trees become more stressed, growth rate is reduced, less amino acids are used in protein synthesis, and more amino-acids recycle in a tree, causing nitrate uptake reduction.

Where's Nitrogen

Nitrogen stress and deficiency in trees can initiate early senescence and abscission of leaves. This process remobilizes nitrogen compounds within tissues to be shed and pulls nitrogen back into twig, branch, and stem areas behind shed leaves. Approximately 60% of nitrogen in a tree is remobilized and reallocated on an annual basis. The internal living environment of a tree carefully stores and uses nitrogen materials. Nitrogen, for the most part, remains portable and transportable to where needs are greatest and conservation most sure. Nitrogen is a valuable prize, once captured it is carefully protected from loss.

For example, Figure 29 provides the average relative amounts of nitrogen in above ground parts of four temperate hardwoods. Note leaves contain most of a tree's reduced nitrogen. The reduced nitrogen in periderm is concentrated in the secondary cortex area. Figure 30 is a composite of nitrogen distribution and annual changes in trees. Inputs to a site's reduced nitrogen are rainfall, litter, and organic matter. Outputs of a site's reduced nitrogen are leaching, denitrification, and erosional processes.

Figure 31 provides a different view of reduced nitrogen distribution annually around a tree.

In The Pool

The tree maintains three compartments or pools for carbon and nitrogen:

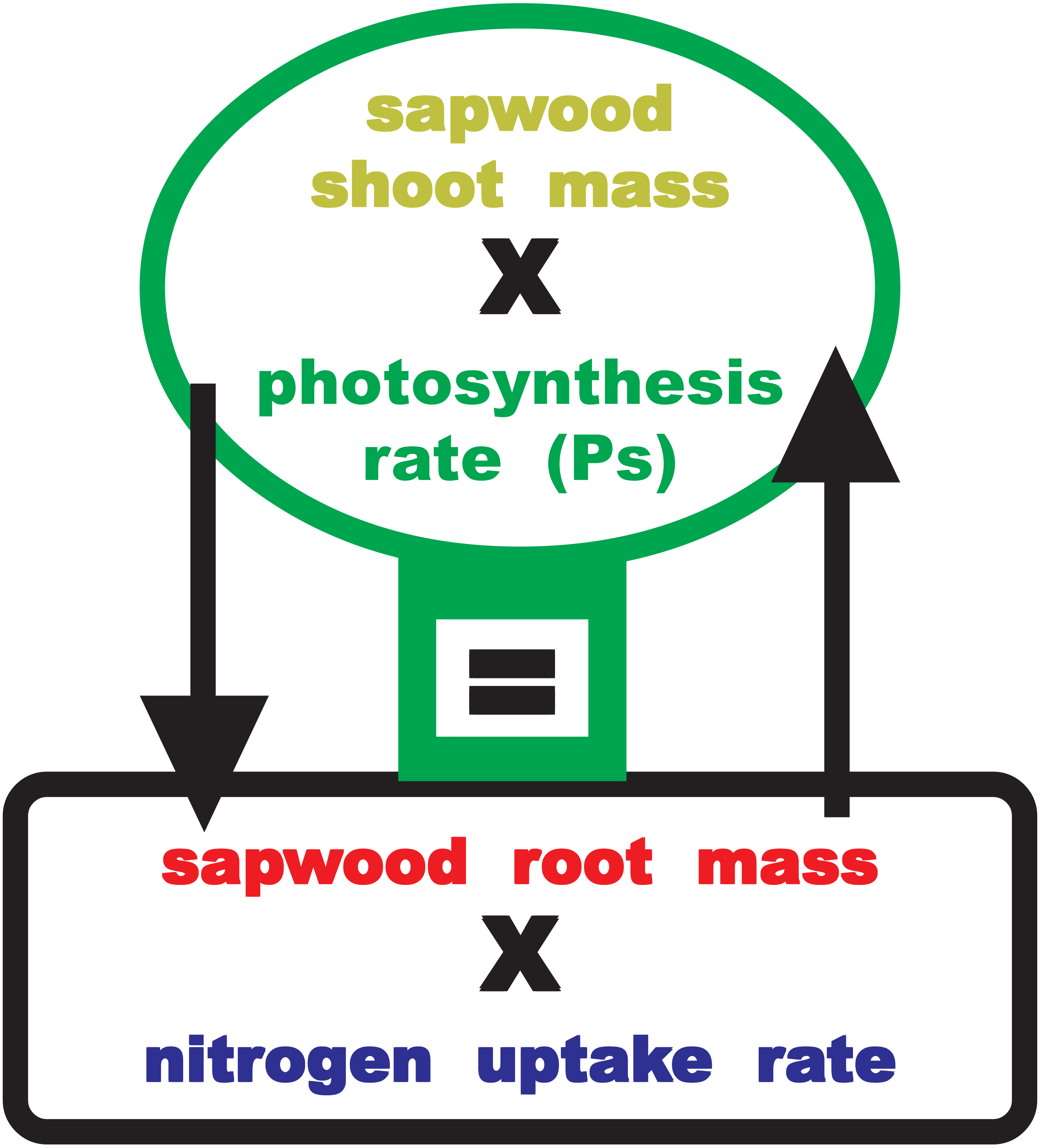
1) fine roots	(0.5% of total tree weight, 35% of tree nitrogen);
2) leaves and buds	(0.5% of total tree weight, 50% of tree nitrogen);
3) storage reserves	(99% of total tree weight, 15% of tree nitrogen).

Average tree nitrogen contents (dry weight basis) under an intensively managed landscape regime are: 2.25% leaves; 1.25% stem; and, 1.75% roots. An appropriate nitrogen percent measured in woody angiosperm tissue to use as a target is ~1.75%. Gymnosperm tissue target is ~1.3% nitrogen in tissue.

A strong combined carbon and nitrogen balance in a tree among these three pools will maintain good vigor; improve tree reactivity to changes; decrease effectiveness of pests; and, decrease the chances of environmental damage to a tree. Changing the balance among these three carbon and nitrogen compartments can radically change tree growth dynamics. For example, nitrogen enrichment can decrease both internal and external nitrogen fixation, reduce symbiotic associations, and advance pests.

Think Trees

The unique features of trees and their interactions with nitrogen, allow a tree health care provider to better care for tree and site resources. Specific tree features manipulated by health management include: shoot/root ratios; skin/core aspects; and, growth rate concerns. Each of these features affect, and are effected by, nitrogen availability in a tree and on a site. A number of physiological and pest effects in trees can be consolidated to provide an understanding of whole tree nitrogen.



functional balance in tree

Figure 32: Thornley model for the functional balance between living components of shoot and root systems in a tree which are dependent upon interacting nitrogen uptake rates and photosynthetic rates.

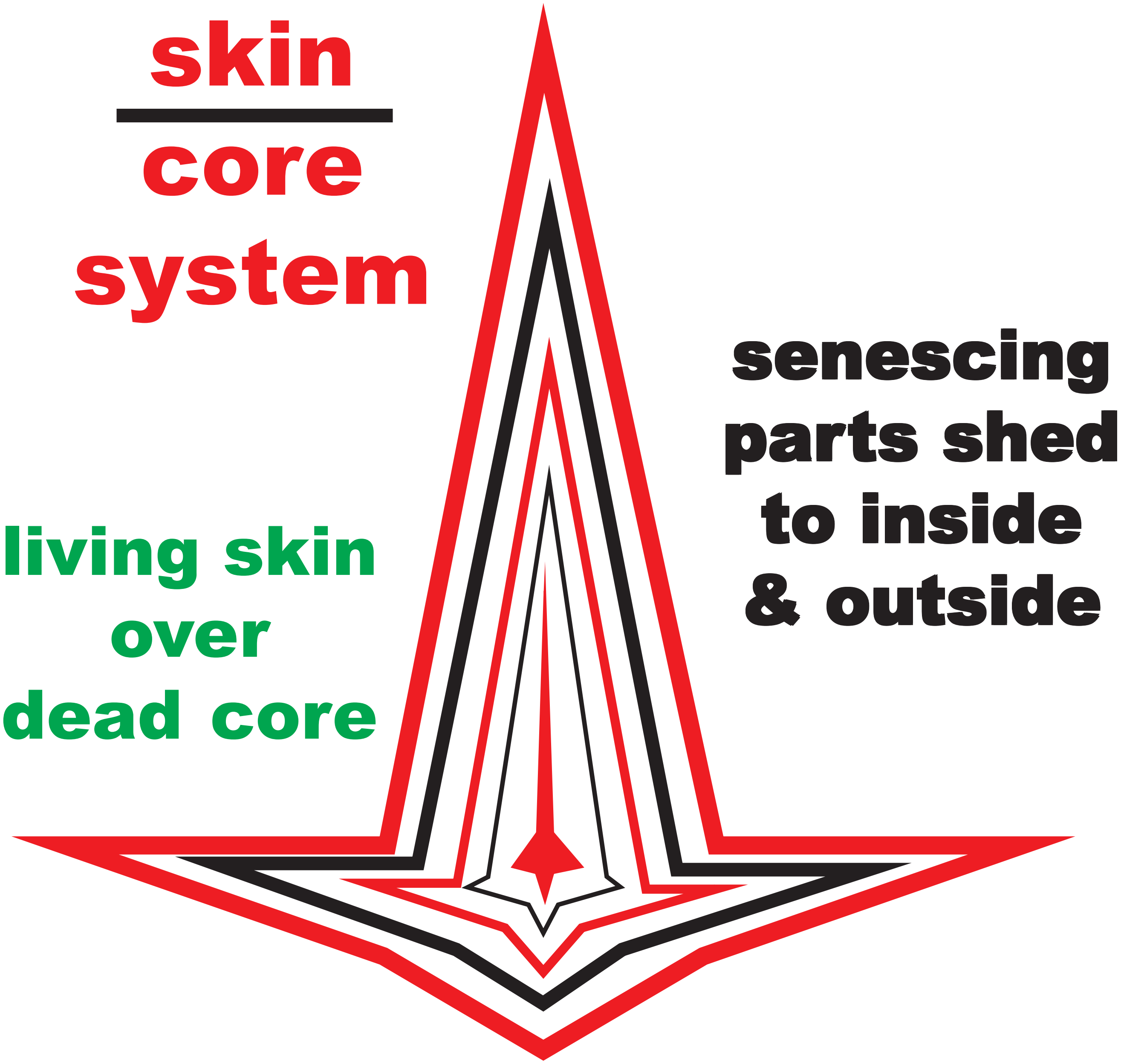


Figure 33: Tree annual growth is a thin sheath of living tissue over a framework of previous growth increments. The more exterior sapwood area is functionally proportional to productivity and inversely proportional to stress.

Shoot / Root Balance

Nitrogen up-take and use in a tree have been examined using shoot/root models. The most tested and effective is called the Thornley model. To recognize resource allocation patterns in trees between shoot and root (approaching a functional balance), only four components are required: sapwood shoot mass, sapwood root mass, photosynthesis rate, and nitrogen uptake rate. Figure 32.

Trees attempt to balance shoot mass and photosynthesis rates against root mass and nitrogen uptake. A tree will adjust living mass of roots or shoots to correct any deficiency in photosynthesis rates or nitrogen uptake rates. Carbohydrate shortages and/or nitrogen increases will initiate more shoots — nitrogen shortages and/or carbohydrate increases will initiate more roots.

Balancing Disaster

Both benchmark processes (and associated tissue masses) in the Thornley model must always be functionally balanced across a tree. For example, as nitrogen absorption declines, what nitrogen remains is concentrated more in roots and used preferentially. This leads to less shoot growth and more root growth. Even before growth is noticeably reduced, a tree is reallocating nitrogen to vital processes. One vital need is absorbing roots where more rapid turn-over is occurring as nitrogen concentrations fall.

With nitrogen enrichment, root growth declines and shoot growth increases. In addition, the added nitrogen causes a decline in starch storage and an increase in transport sugars. Increased sugar contents and additional nitrogen availability generate improved access and attack conditions for a number of pests.

Skin / Core Games

Nitrogen needs of a tree are affected by many circumstances. One of the most significant, but often overlooked conditions changing nitrogen requirements is the fundamental perennial growth form of a tree. When trees are young, their whole mass is filled with living cells with significant nitrogen demands. As trees age, they begin to shed inefficient parts and tissues, concentrating nitrogen into those tissues that provide positive benefits to the whole organism. The shedding process includes branch self-pruning, leaf and twig abscission, and heartwood formation.

Parts of a tree, including inner core areas, are shed to minimize total respiring mass of a tree. This concept of a living active skin over a dead core has been successfully tested in trees. Figure 33. Trees have a much smaller living mass than outward size would suggest. Constant nitrogen loads (or increasing loads) after a tree has reached its full site respiration load and begins to shed can be wasteful of any nitrogen resource added and disrupt effective tree functions. The skin / core model well represents tree reactivity to internal and external changes in resources.

Nitrogen Demands

The skin / core model of tree growth can be used to approximate the living mass of a tree and its nitrogen demands. The skin / core ratio can be estimated by calculating the mass of nitrogen in a tree (an estimate of the skin portion) divided by an estimate of the total mass of a tree (the core estimate). This process has shown young trees have skin/core ratios of 1.0, while older trees with branch shedding and heartwood development approach a skin/core ratio value of 0.66, or less. The results of the skin / core model shows nitrogen demand is not represented by a tree's entire mass but by some exterior, living, nitrogen using portion of that mass. Nitrogen additions should be tuned to actual living mass needs.

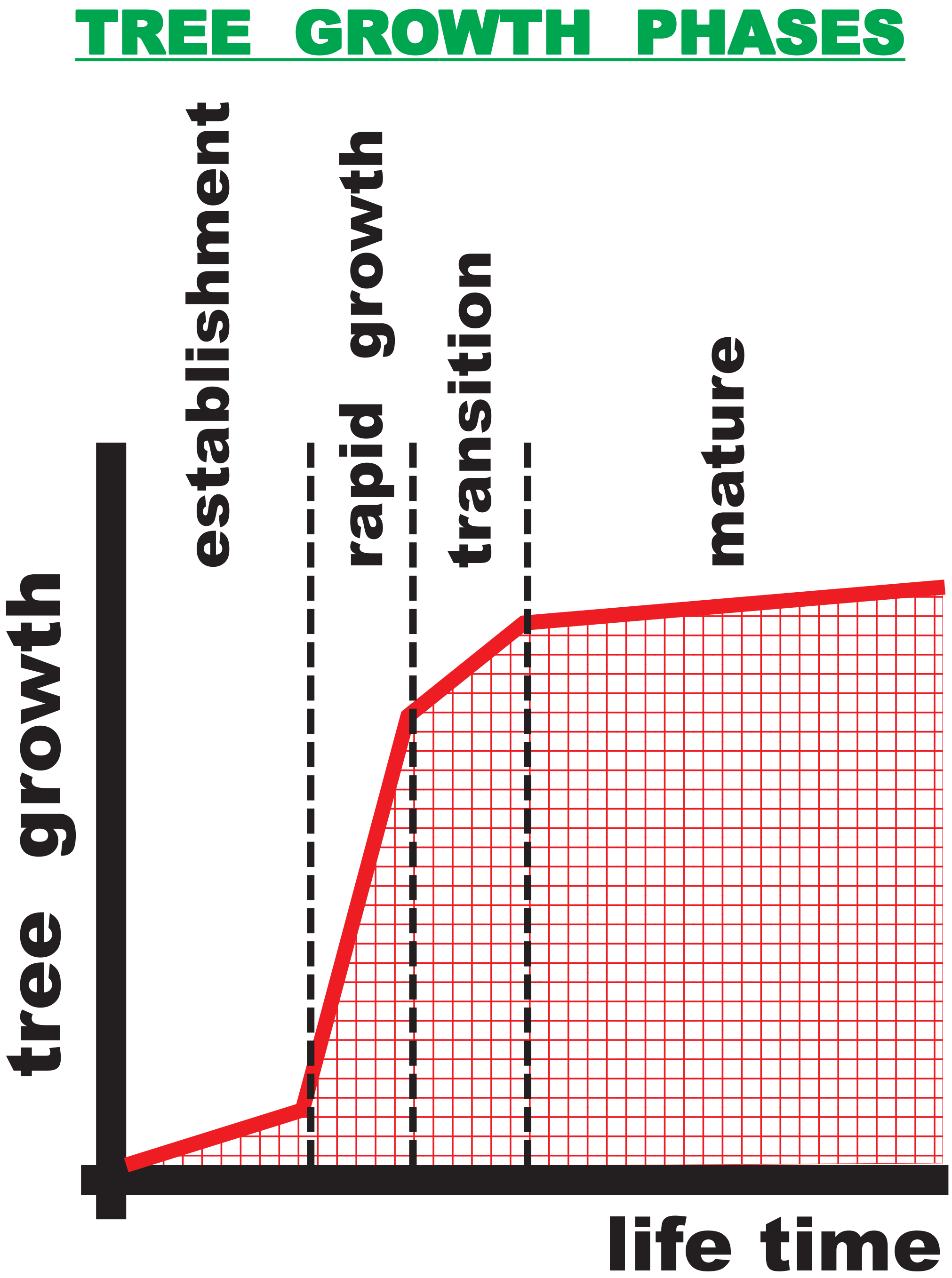


Figure 34: Tree growth phases over its life.

DBH	R1	R1.5	R2	R2.5	R3	R4	R5	R7.5	R10	R12.5	R15	R17.5	R20
6 in	16 in^2	11	8.6	7.0	5.9	4.5	3.6	2.5	1.9	1.5	1.2	1.1	0.9
7	19	13	10	8.3	7.0	5.3	4.3	2.9	2.2	1.7	1.4	1.2	1.1
8	22	15	12	9.6	8.0	6.1	4.9	3.3	2.5	2.0	1.6	1.4	1.2
9	25	17	13	11	9.1	6.9	5.5	3.7	2.8	2.2	1.9	1.6	1.4
10	28	20	15	12	10	7.7	6.2	4.1	3.1	2.5	2.1	1.8	1.6
11	31	22	17	13	11	8.4	6.8	4.5	3.4	2.7	2.3	2.0	1.7
12	35	24	18	15	12	9.2	7.4	5.0	3.7	3.0	2.5	2.1	1.7
13	38	26	20	16	13	10	8.0	5.4	4.1	3.2	2.7	2.3	2.0
14	41	28	21	17	14	11	8.7	5.8	4.4	3.5	2.9	2.5	2.2
15	44	30	23	18	15	12	9.3	6.2	4.7	3.7	3.1	2.7	2.3
16	47	32	24	20	16	12	9.9	6.6	5.0	4.0	3.3	2.9	2.5
17	50	34	26	21	17	13	11	7.0	5.3	4.3	3.5	3.0	2.7
18	53	36	28	22	19	13	11	7.5	5.6	4.5	3.7	3.2	2.8
19	57	38	29	23	20	15	12	7.9	5.9	4.8	3.9	3.4	3.0
20	60	41	31	25	21	16	12	8.3	6.3	5.0	4.1	3.6	3.1
21	63	43	32	26	22	16	13	8.7	6.6	5.3	4.3	3.8	3.3
22	66	45	34	27	23	17	14	9.1	6.9	5.5	4.5	3.9	3.4
23	69	47	35	28	24	18	14	9.6	7.2	5.8	4.8	4.1	3.6
24	72	49	37	30	25	19	15	10	7.5	6.0	5.0	4.3	3.8
25	75	51	39	31	26	19.	16	10	7.8	6.3	5.2	4.5	3.9
26	79	53	40	32	27	20	16	11	8.1	6.5	5.4	4.7	4.1
27	82	55	42	33	28	21	17	11	8.5	6.8	5.6	4.8	4.2
28	85	57	43	35	29	22	18	12	8.8	7.0	5.8	5.0	4.4
29	88	59	45	36	30	23	18	12	9.1	7.3	6.0	5.2	4.5
30	91	61	46	37	31	23	19	13	9.4	7.5	6.2	5.4	4.7
31	94	64	48	39	32	24	19	13	9.7	7.8	6.4	5.6	4.9
32	97	66	50	40	33	25	20	13	10	8.0	6.6	5.7	5.0
33	101	68	51	41	34	26	21	14	10	8.3	6.8	5.9	5.2
34	104	70	53	42	35	27	21	14	11	8.5	7.0	6.1	5.3
35	107	72	54	44	36	27	22	15	11	8.8	7.2	6.3	5.5
36	110	74	56	45	37	28	23	15	11	9.0	7.5	6.4	5.6
37	113	76	57	46	38	29	23	15	12	9.3	7.7	6.6	5.8
38	116	78	59	47	39	30	24	16	12	9.5	7.9	6.8	6.0
39	119	80	61	49	41	30	24	16	12	9.8	8.1	7.0	6.1
40	123	82	62	50	42	31	25	17	13	10	8.3	7.2	6.3
45	138	93	70	56	47	35	28	19	14	11	9.3	8.1	7.1
50	154	103	78	62	52	39	31	21	16	13	10	9.0	7.8
55	170	114	86	69	57	43	34	23	17	14	11	9.9	8.6
60	185	124	94	75	62	47	38	25	19	15	12	11	9.4
65	201	135	101	81	68	51	41	27	20	16	14	12	10

Figure 35: Area increase in cross-sectional inches per single growth increment by tree diameter (DBH). Diameter growth rate ranges from 1.0 growth increment per inch (R1) to 20 growth increments per inch (R20).

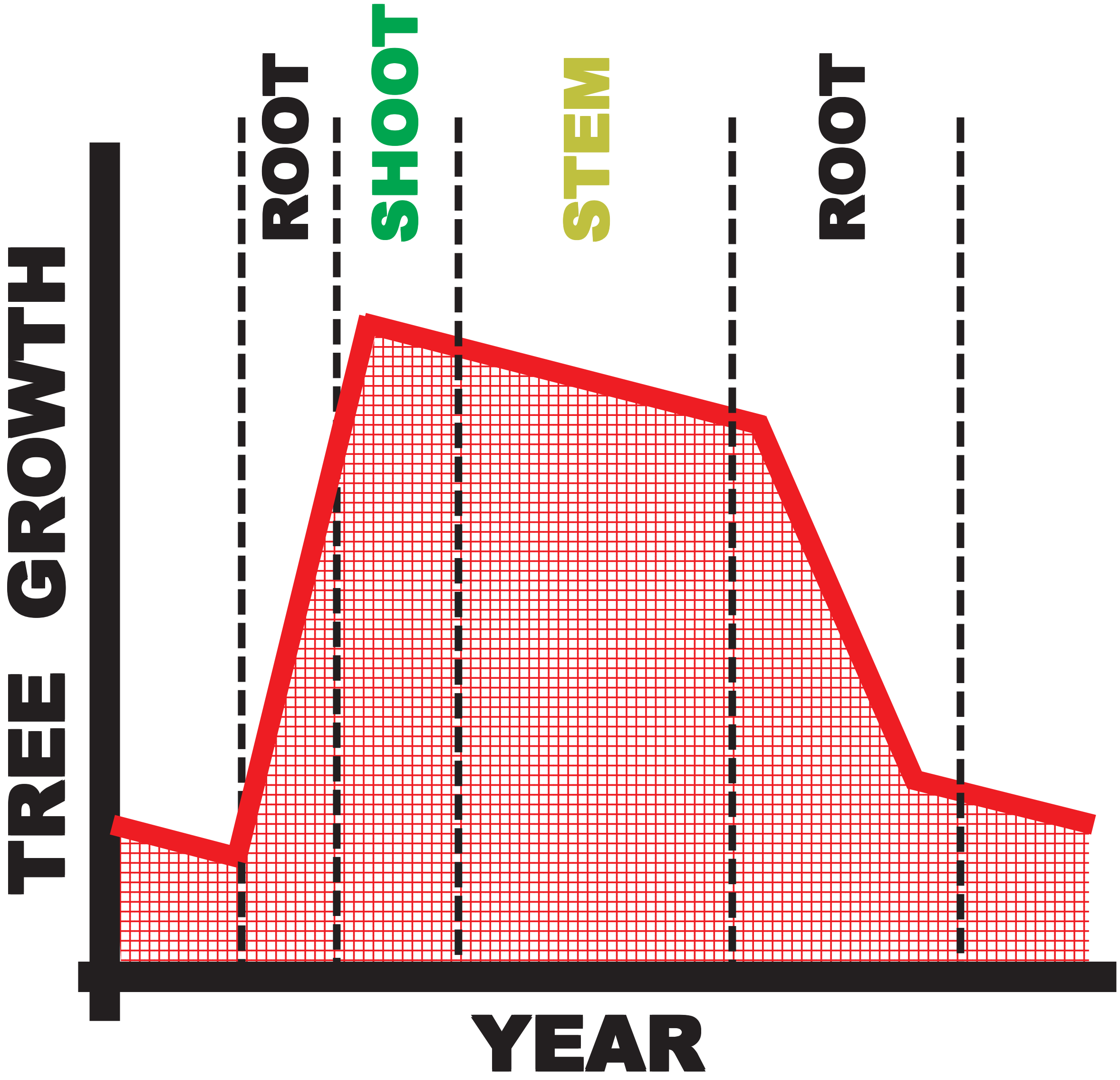


Figure 36: Generalized tree energy requiring and energy producing activities summarized over a growing season divided among root, stem, and shoot components.

Whole Tree Reactions
<u>INCREASED</u> Nitrogen:

— Increased shoot size.
— More foliage growth stimulated.
— Photosynthesis & stomates sensitive to water stress.
— Lengthened growing season.
— Increased amino-nitrogen content.

— Decreased starch in whole tree.
— Increased pest effectiveness.
— Decreased defensive materials produced.
— Carbon allocation to fine roots delayed.
— Decreased carbon allocation to roots.

— Root carbon storage reduced.
— Root sugar concentrations increase.
— Decreased root reactivity to damage and stress.
— Reduced cold tolerance in root system.
— Increases stored starch use -- not always photosynthesis increase.

Figure 37: Whole tree reactions to moderate / large concentrations of nitrogen availability and uptake.

Growth Rate Changes

Another critical feature of nitrogen requirements in a tree involves annual growth rates and timing of growth periods. Because of its rarity in nature, nitrogen will be taken-up in the best and most expedient way possible. Sometimes nitrogen uptake occurs at the costs of other processes, regardless of growth and time of the growing season. Nitrogen is most important for actively growing tissues, but it is also needed for maintenance activities. The growth rate of a tree is both a cause and effect of nitrogen uptake and use.

Trees continue to grow, but eventually reach biological and physical limits to total living mass on any particular site. Figure 34. At this point, growth rates (percentage rate of growth) begin to decline. Annual increment radial thickness declines for trees even if the same total amount of wood is being produced. The same amount of wood grown over a larger surface spreads out growth and decreases annual increment (growth ring) width. Figure 35. As site resources are gathered and controlled, less resources may be available, greatly decreasing growth rates and nitrogen needs. As absolute growth rates decline, nitrogen requirements decline.

Have An Episode

Nitrogen requirements in a tree also are affected by episodic growth of different tree parts. Although generic in their nature, seasonal growth models can help clarify nitrogen requirements in different areas of a tree over the year. Those tissues actively growing with significant carbon supplies, can most readily assimilate any nitrogen additions. Figure 36. This period is just after full leaf expansion.

Minimizing waste of nitrogen resources, preventing competitors and pests from utilizing available nitrogen, and ensuring a tree can effectively handle added nitrogen are all critical management features. Use nitrogen enrichment when total biological costs / benefits are lowest for a tree. In addition, be sure nitrogen enrichment activities do not damage surrounding natural resources or reach untargeted organisms or areas.

Whole Tree Reactivity

Whole tree reactions to significantly increased nitrogen levels through enrichment include increased growth, size, and amino acid content. There is a trade-off between increased pest effectiveness and a decreased production of defensive materials. Generally shoots are emphasized over roots and food storage. Figure 37. Whole tree reactions to nitrogen shortage are not simply opposite of high nitrogen loads. Tree reactions include a decrease in most growth except for absorbing roots. Food storage is given priority. Figure 38. Lower nitrogen contents generate a number of stress-resisting reactions within trees, which allows a more conservative approach to resource allocation and use.

Prescribing N

Supplemental nitrogen enrichment should be treated as a fined-tuned, carefully considered, constantly modified, whole tree prescription process. The whole tree wins or loses with changing reactions of one major organ or resource. Nitrogen prescription involves prudent and reasonable treatments carried out in a timely manner without site and tree damage.

The nitrogen dose provided by supplemental additions, and its timing, are part of a comprehensive management prescription which should vary primarily by ecological season of the year, a tree's ability to successfully and effectively utilize nitrogen additions, and by the life stage of a tree. These

Whole Tree Reactions
Nitrogen SHORTAGE:

— Decreased overall growth of tree.
— Increased total storage reserves.
— More sulfur containing proteins made.
— More fine root production.

— Increased root weights.
— More carbon allocated to fine roots.
— Shortened time span of fine root growth.
— Earlier seasonal carbon storage in roots.

Figure 38: Whole tree reactions to low concentrations / slight deficiency of nitrogen availability and uptake.

considerations deal with successful capture and use of nitrogen by a tree as it grows, and with minimizing environmental impacts to untargeted systems (i.e. nitrogen to weeds, streams, and soils).

No Dumping

Dosing trees correctly with supplemental nitrogen involves discarding dumping concepts. Trees try and maintain a steady-state, internal nutritional balance governed by nitrogen demand and carbon availability. Under this internal system, one large application of nitrogen dumped on a tree makes little biological sense. Ecologically and chemically, chances are greater for more of any massive dose to go to nontarget species or processes, such as weeds, pests, erosion, and denitrification. The total nitrogen provided at one time is not as critical as the nitrogen recycling rate through the tree / site system.

A monetary analogy would be a steady, controlled cash flow (of nitrogen) rather than a one-time, disruptive lottery jackpot. For example, animals are not given a once-a-season (or once every two or three seasons) feeding. Under these conditions, food can not be effectively used, and may be wasted or used by other organisms. Trees should not have a valuable resource dumped onto a site when and where a tree can not effectively use it, nor control its distribution.

Ecological Investment

The further away from ecological equilibrium a site is kept, the more management and resource investments must be supplied. Over time it is easy to forget how the tree / soil system is propped-up by resources from outside a site. Large doses of resources supplied over a number of years can generate both a chronic ecological addiction to added resources, and a human perception of resources needed far removed from actual natural site processes.

When management and resource inputs are removed or drastically changed by new owners, different objectives, or due to climbing expenses, a tree / site can undergo a number of highly variable / chaotic changes as it falls back into equilibrium with the environment. Tree health may be sacrificed in this process. In addition, the perceived values of nitrogen enrichment in large doses can decline over time as the site uses and discards more nitrogen (i.e. “big dump” syndrome.)

Dosing Schedules

Throughout a growing season, a tree’s nitrogen requirements, and its ability to effectively utilize nitrogen, declines until the first sign of senescence presents in Fall (first visible leaf color changes with leaves still green!) or 80% of the growing season has past. At the first sign of senescence, nitrogen additions should be cut back to dormant season maintenance levels.

Even though many supplemental nitrogen enrichments are listed on a per year basis, applications for the greatest benefit to cost ratio for a tree occur during the growing season. The growing season for nitrogen enrichment is counted from just after full leaf expansion until the first sign of senescence (or 80% of growing season is past). Figure 39. Maintenance levels of supplemental nitrogen vary by geographic location and activity of roots, but should be minimized to prevent use of food reserves, to reduce run-off, and to prevent soil systems from destroying usable nitrogen availability (conversion of nitrogen dollars into nitrogen gas!)

Mature Dose

In a mature tree there are nitrogen needs, but at reduced levels from earlier life stages. Figure 40. Growth rate is less, compartmentalization more complex, and many site resources are already under

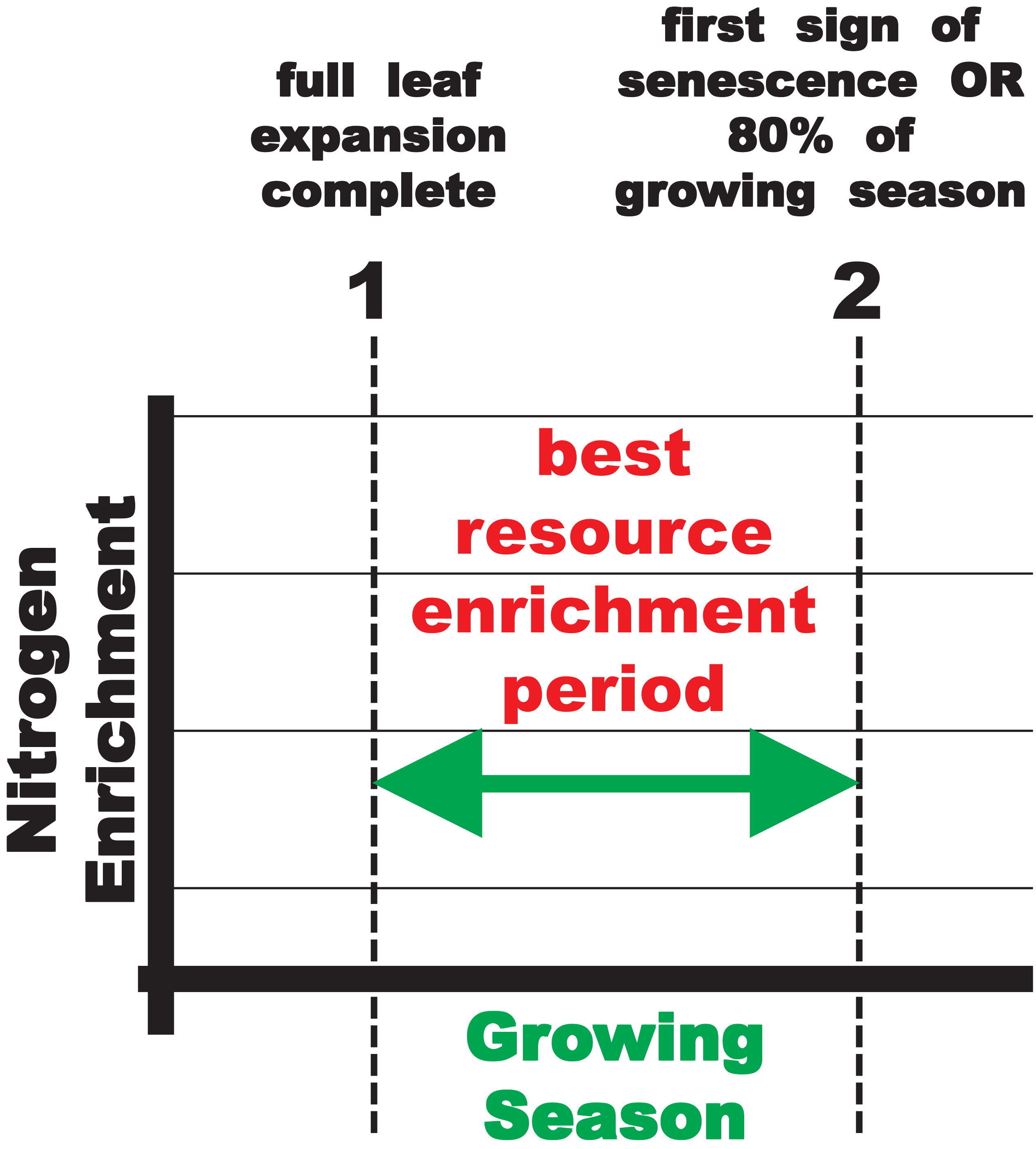
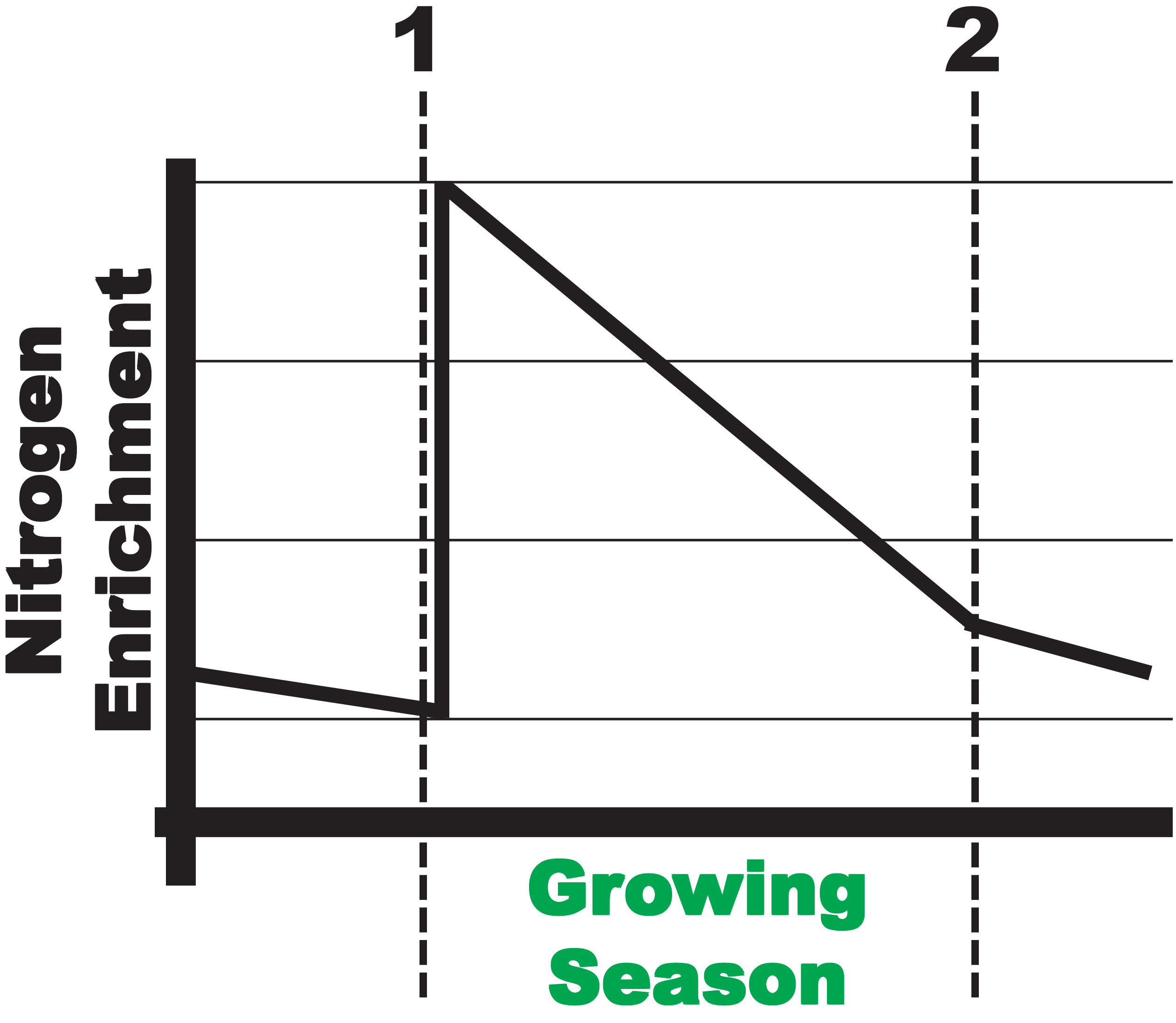


Figure 39: Initiation and suspension targets for nitrogen enrichment in trees for the most effective and efficient element uptake and utilization.

MATURE

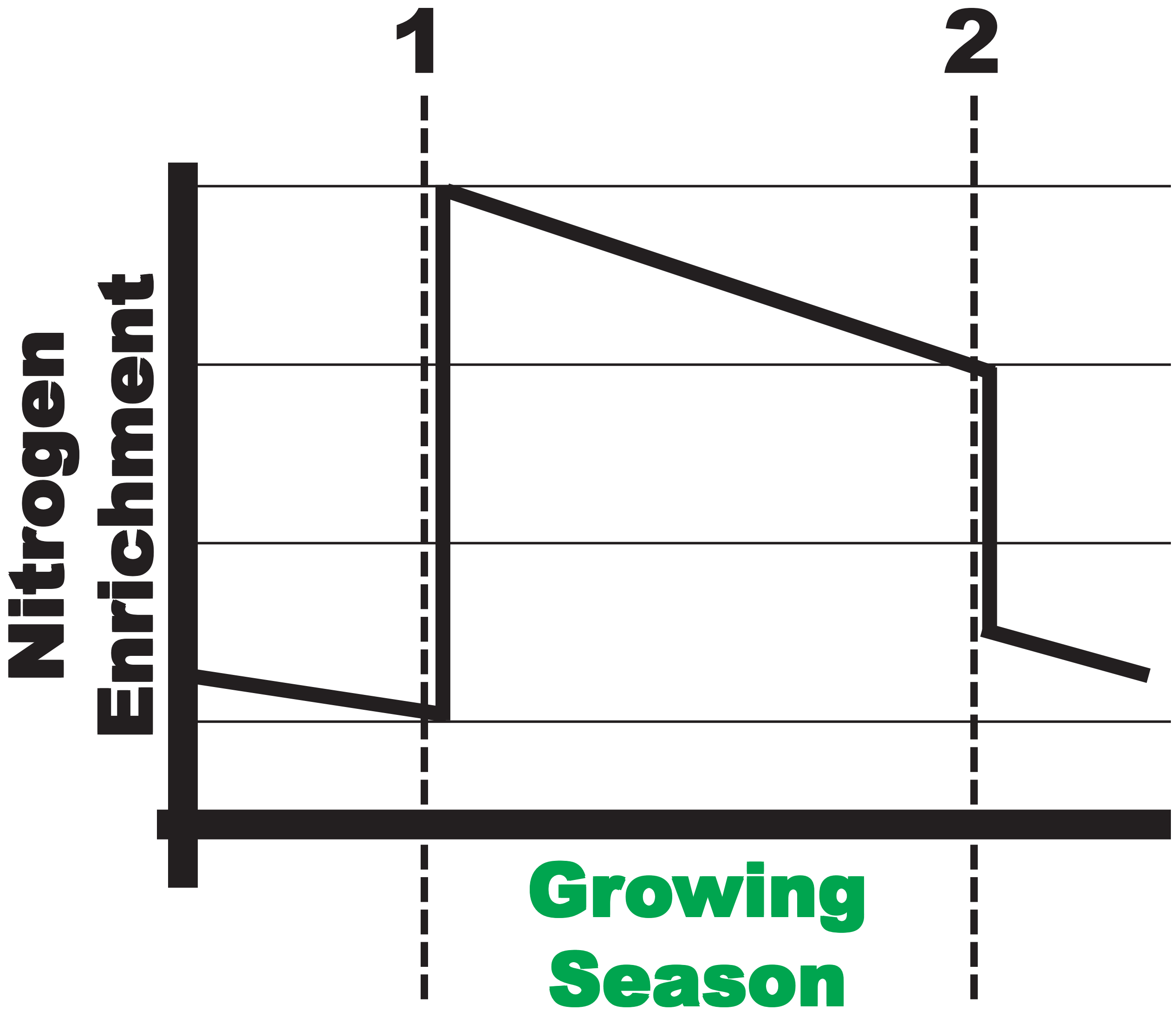


1 = full leaf expansion complete
2 = first sign of senescence /
80% of growing season past

Figure 40: Most effective and efficient period for nitrogen enrichment in mature trees.

RAPID GROWTH

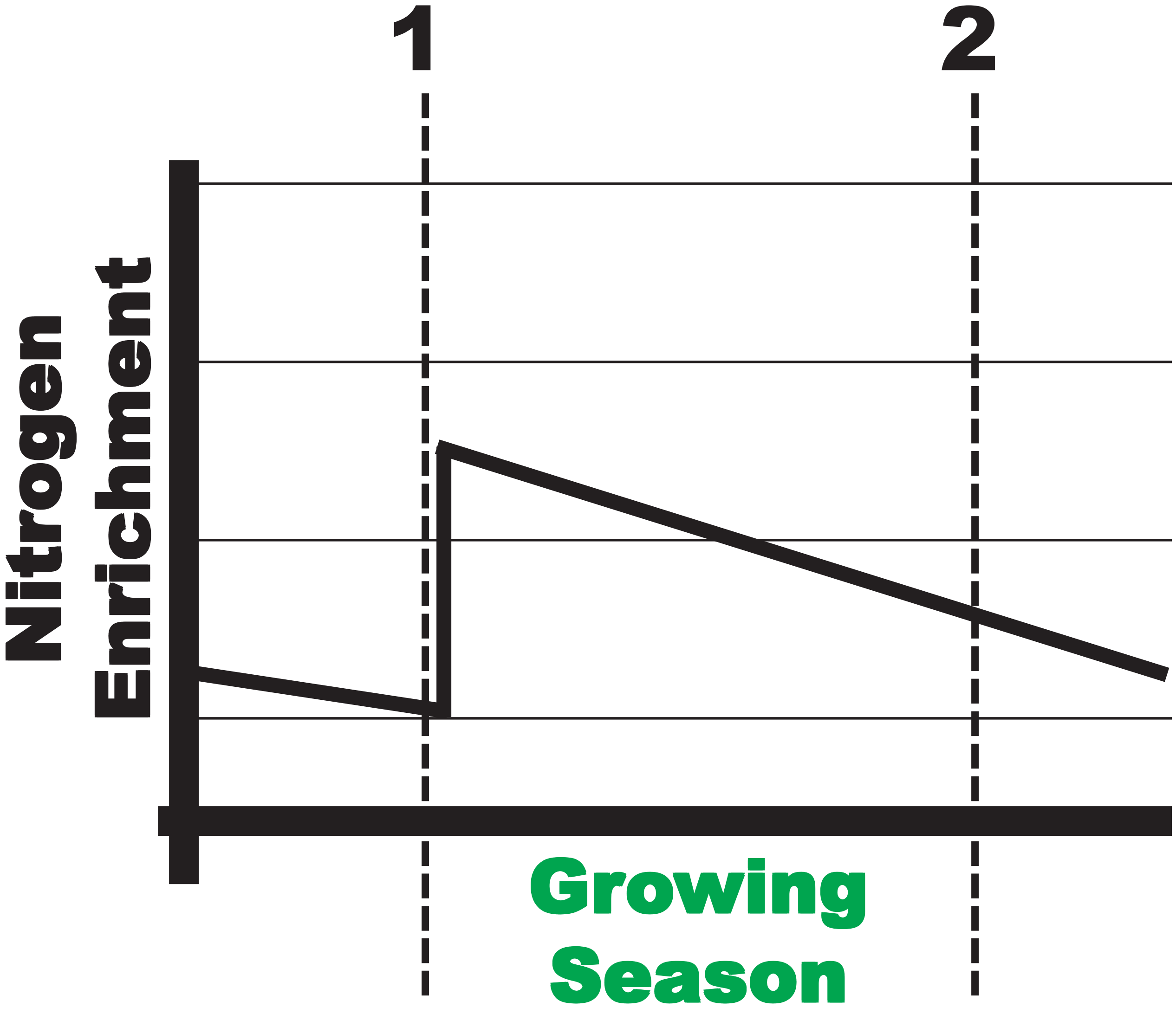
(At least one to two full growing seasons since planting.)



1 = full leaf expansion complete
2 = first sign of senescence / 80% of growing season past

Figure 41: Most effective and efficient period for nitrogen enrichment in trees out of their establishment phase and in their rapid growth phase.

ESTABLISHMENT



1 = full leaf expansion complete
2 = first sign of senescence / 80% of growing season past

Figure 42: Most effective and efficient period for nitrogen enrichment in trees during their establishment phase.

control in a mature tree. The model of nitrogen dosing for a mature tree presents opportunities for low maintenance applications during the dormant season with a jump to full loading just after full leaf expansion. This is the point when a tree is at its full productive potential and carbon supplies are rebounding after Spring start-up.

The Young

Young trees, once completely established (after at least one full growing season in diffuse-porous trees and two full growing seasons in gymnosperms and ring-porous trees), can move into a rapid growth stage of life. Figure 41. Timing targets for growing season nitrogen additions are the same as for mature trees. After full leaf expansion, a young tree will be able to handle nitrogen additions effectively and these additions can be maintained through the growing season. At first sign of senescence, nitrogen additions should be dropped to dormant season levels.

Establishment

Another life stage of a tree requiring careful consideration when adding nitrogen is during establishment. Figure 42. It is critical newly planted trees be allowed to sense and respond to site resource levels, and to internal resource changes, before superimposing a carbon- and energy-expensive treatment like supplemental nitrogen enrichment. Low rates of nitrogen addition should be used which hover near dormant season maintenance levels. Just after full leaf expansion, a slightly increased rate of nitrogen enrichment can be used that gently fades into dormant season levels as Fall approaches.

Life Stages

When prescribing nitrogen enrichment using tree life stages, remember total nitrogen amounts can be added in one dose or many progressively smaller doses. Dosing throughout the year in small additions, rather than in one "dump" is an appropriate ecological response. Nitrogen additions at low levels will pass through a tree / soil ecological system with some losses occurring. Healthy soils and trees will keep nitrogen recycling.

Setting dormant season maintenance levels of nitrogen are dependent upon soil temperature, soil moisture levels, and root activity, but should be defined at an absolute minimum, if used at all. The dormant season (or more precisely, the portion of the year after leaf senescence begins until full leaf expansion is completed) is a time when nitrogen losses can be great.

Hitting Targets

It is difficult to determine if an application is reaching the targeted tree system. Dormant season applications without an active target organism to use any nitrogen provides many opportunities for erosional, denitrification, and off-site losses. General poor timing and dosing assure tree growth disruption, nitrogen waste, or both.

Life-stage planning, and a periodic sun-leaf tissue analysis program using fully expanded leaves, are needed for assurance of effectiveness and need for supplemental resource additions. Soil testing for nitrogen is fraught with problems and, away from toxicity and extreme deficiency, may have little meaning. Soil testing is critical for other essential elements, soil physical and chemical attributes, and soil organic matter determinations.

	Skin — Core Life Phase Multipliers in Trees (already multiplied into values)			
	(establishment)	1.0X (rapid growth)	0.83X (transition)	0.66X (mature)
% nitrogen in tissues	pounds N per 1000ft2 defined area	pounds N per 1000ft^2 defined area	pounds N per 1000ft^2 defined area	pounds N per1000ft^2 defined area
0.5 %N	0.2	0.4	0.3	0.25
1.0 %N	0.3	0.8	0.7	0.5
1.25 %N	0.4	1.0	0.85	0.65
1.5 %N	0.5	1.2	1.0	0.8
1.75 %N	0.55	1.4	1.2	0.9
2.0 %N	0.65	1.6	1.3	1.0
2.25 %N	0.7	1.8	1.5	1.2
2.5 %N	0.8	2.0	1.7	1.3
3.0 %N	1.0	2.4	2.0	1.6
3.5 %N	1.1	2.8	2.3	1.9
4.0 %N	1.3	3.2	2.7	2.1

Figure 43: Nitrogen enrichment amounts for trees based upon life phase. Maximum total pounds available nitrogen enriched annually per 1000 square feet of open soil surface. Values based upon tissue nitrogen content percentages (dry weight) and total living mass of tree throughout its four life phases.

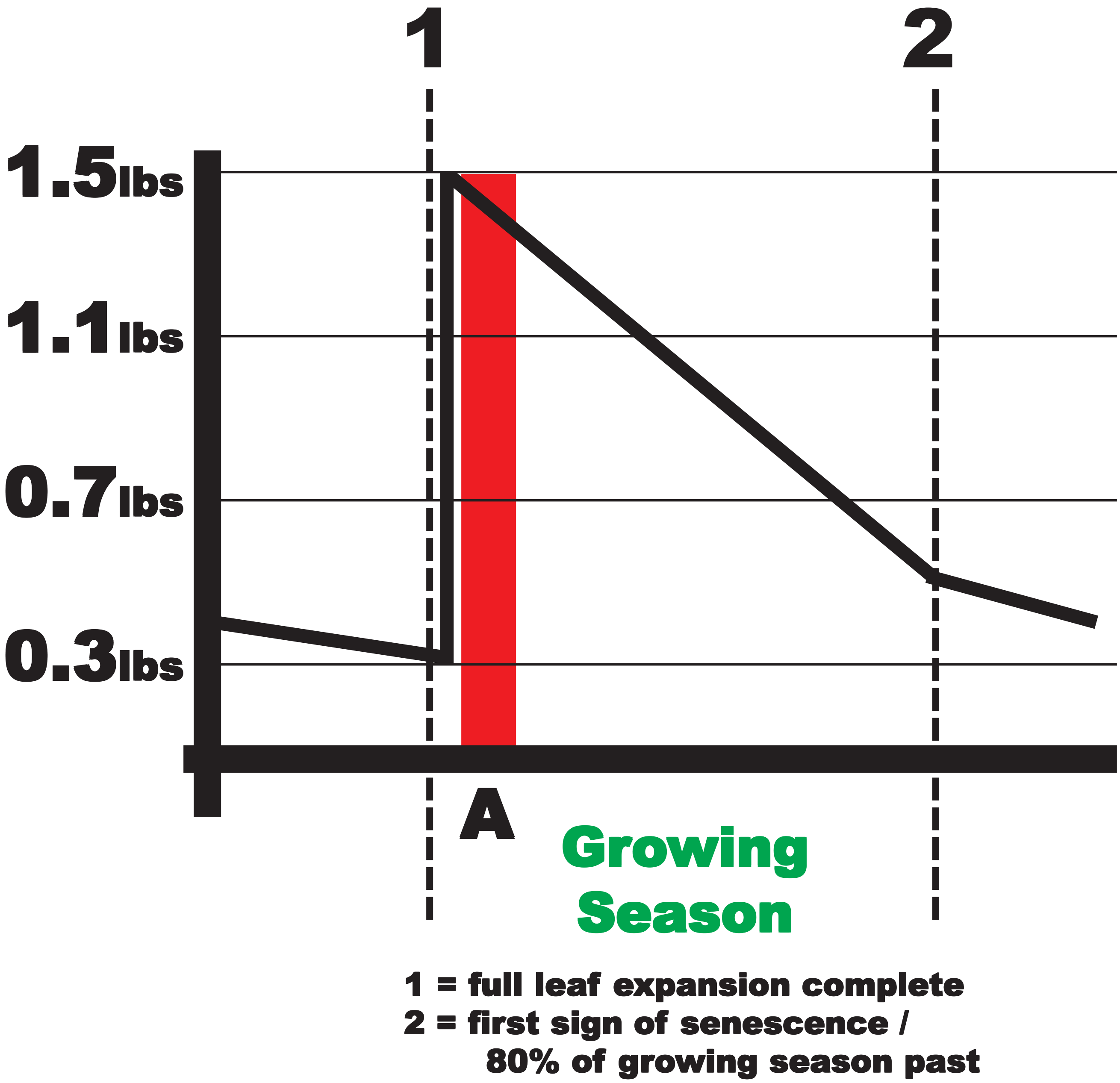


Figure 44: Example mature phase tree nitrogen enrichment with 1.5 lbs. N per 1000ft^2 per year prescribed in one application (A).

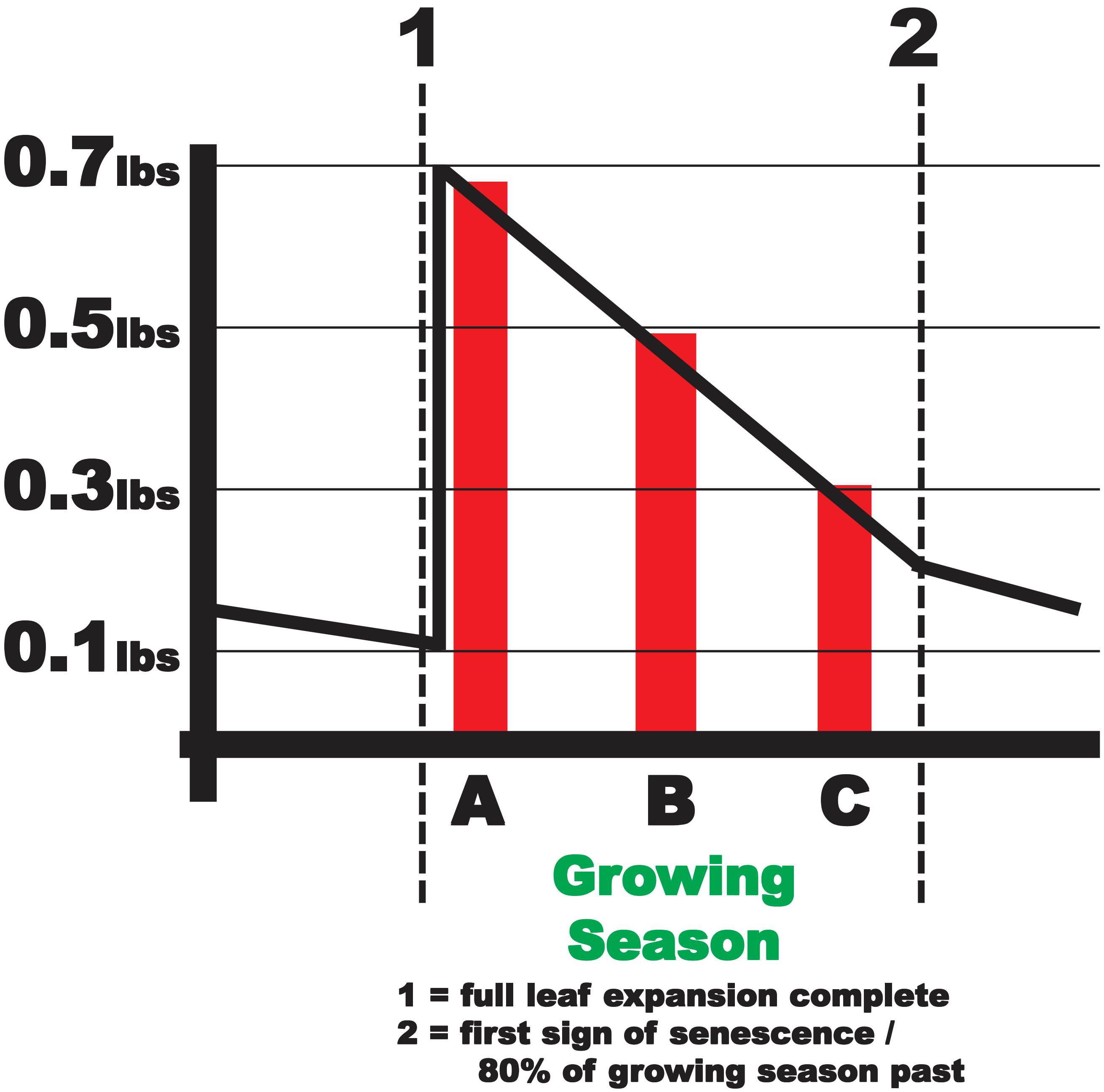


Figure 45: Example mature phase tree nitrogen enrichment with 1.5 lbs. N per 1000ft^2 per year prescribed in three applications (A + B + C).

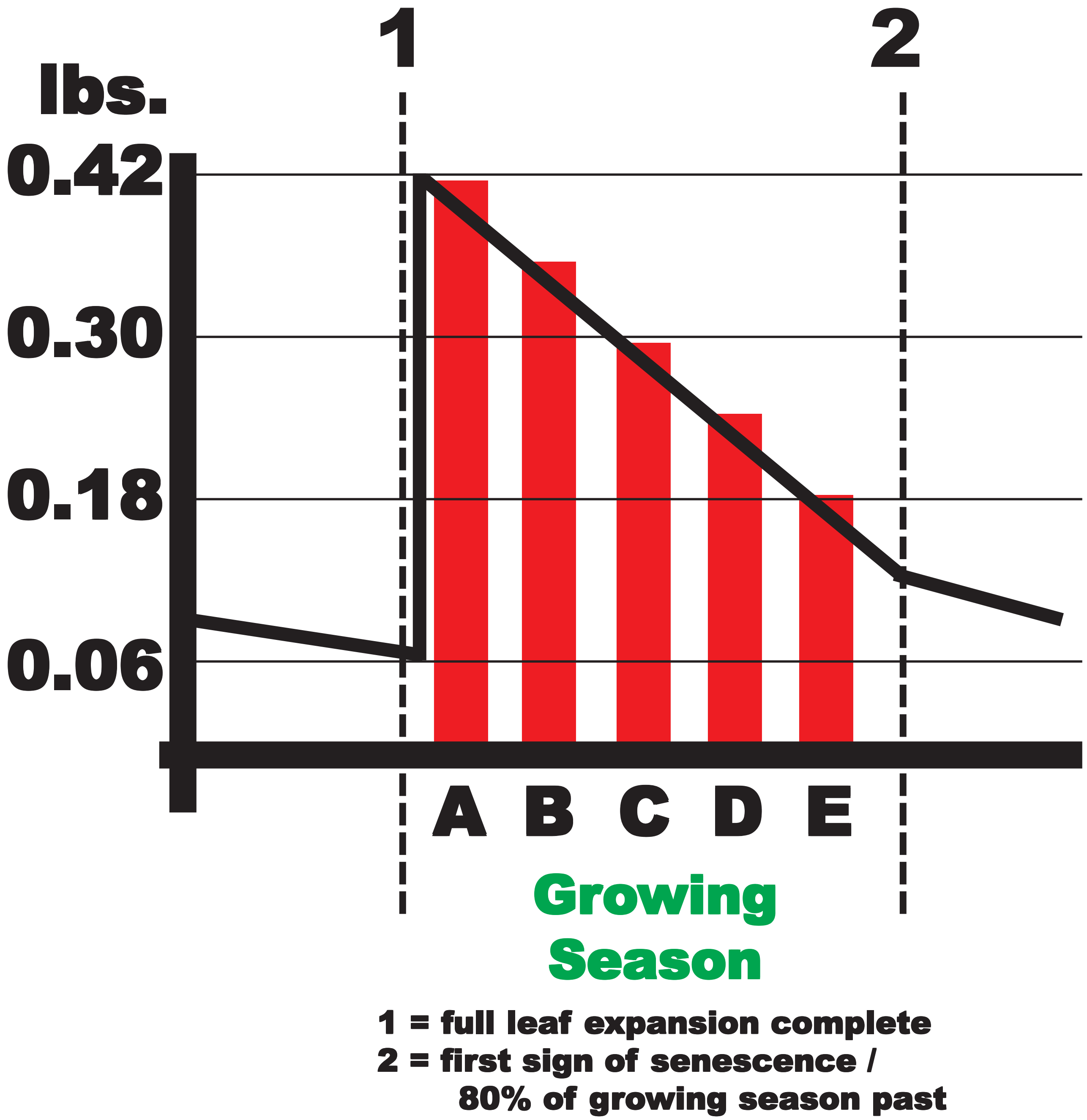
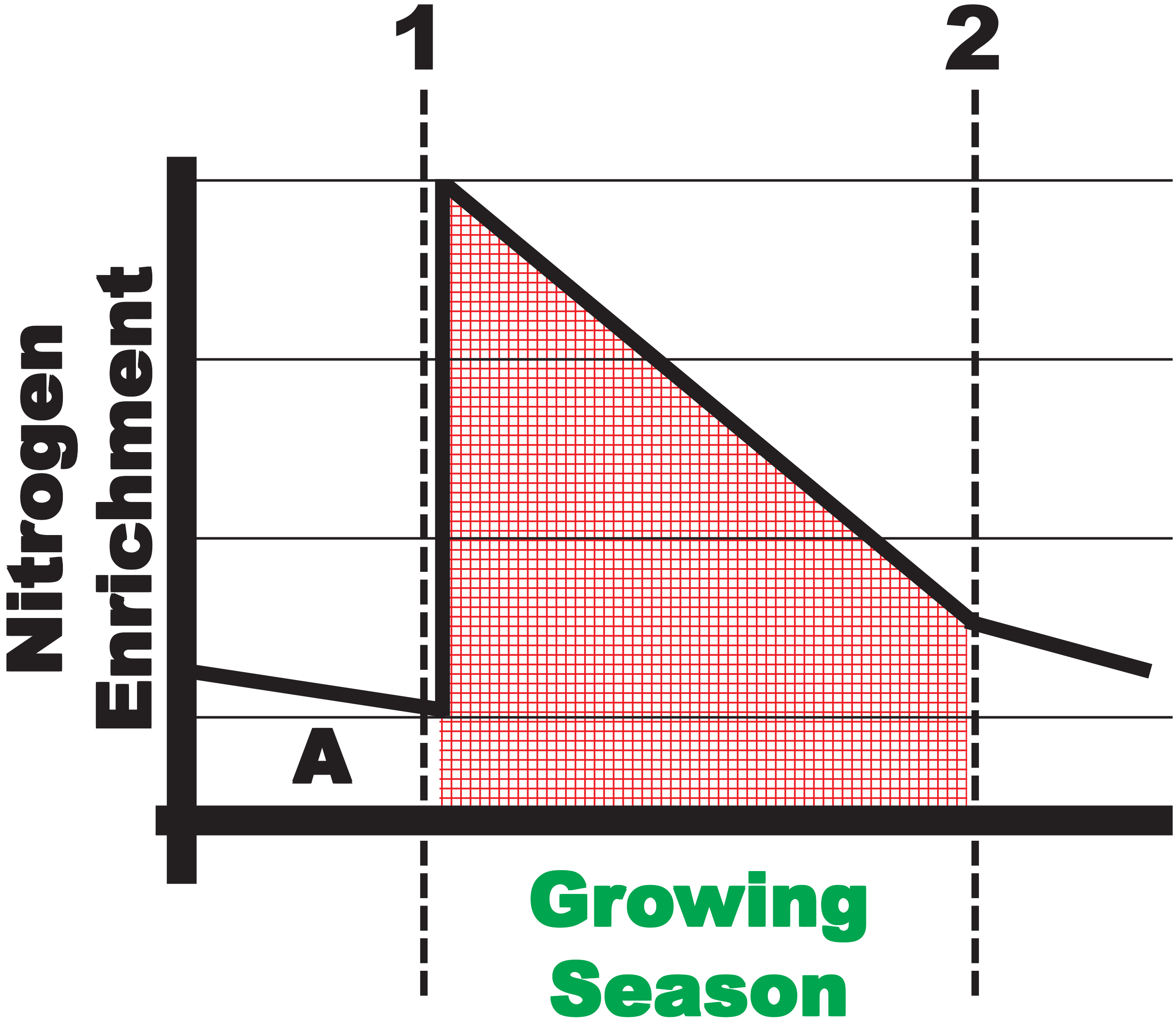
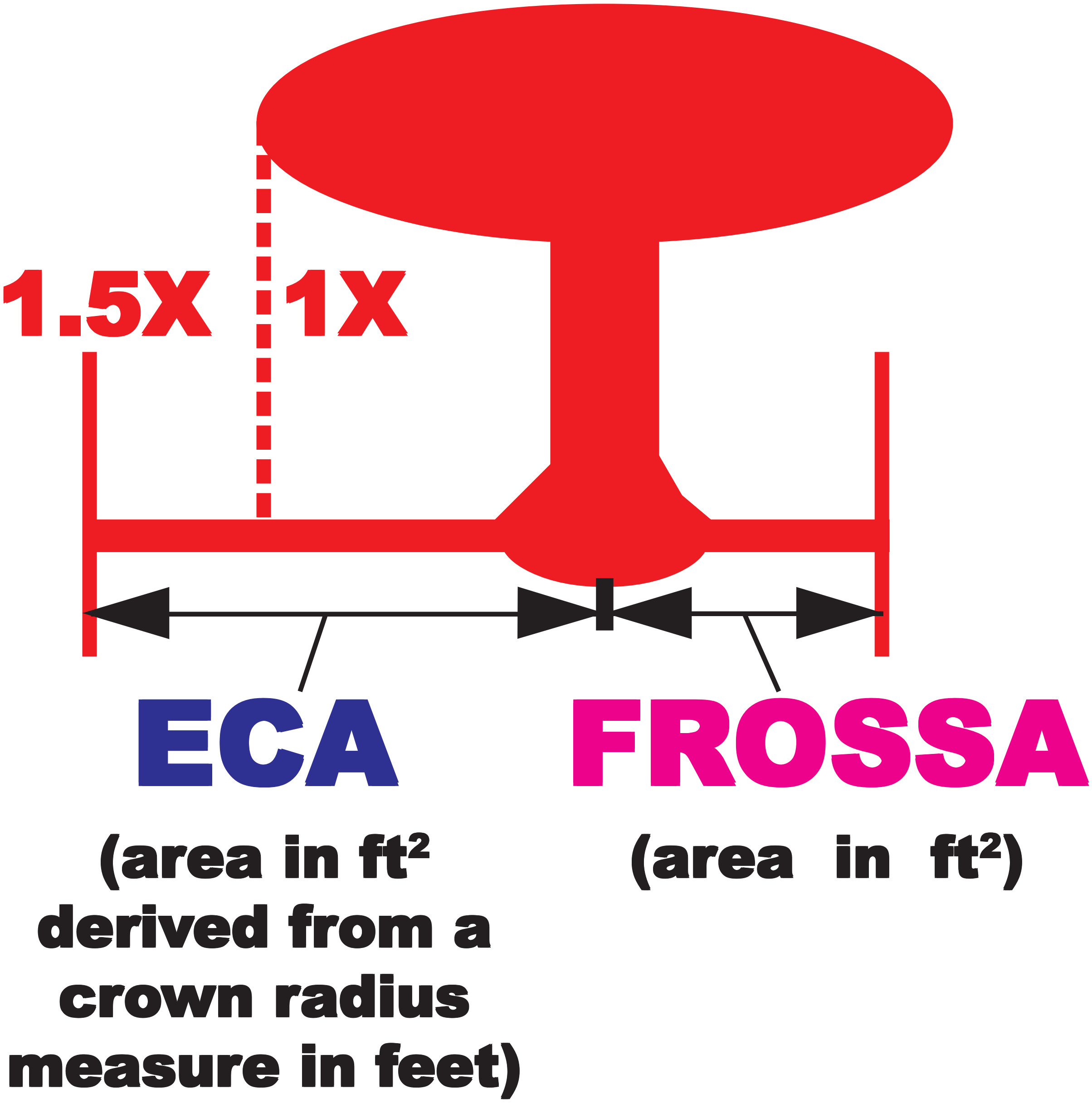


Figure 46: Example mature phase tree nitrogen enrichment with 1.5 lbs. N per 1000ft^2 per year prescribed in five applications (A + B + C + D + E).



1 = full leaf expansion complete
2 = first sign of senescence /
80% of growing season past

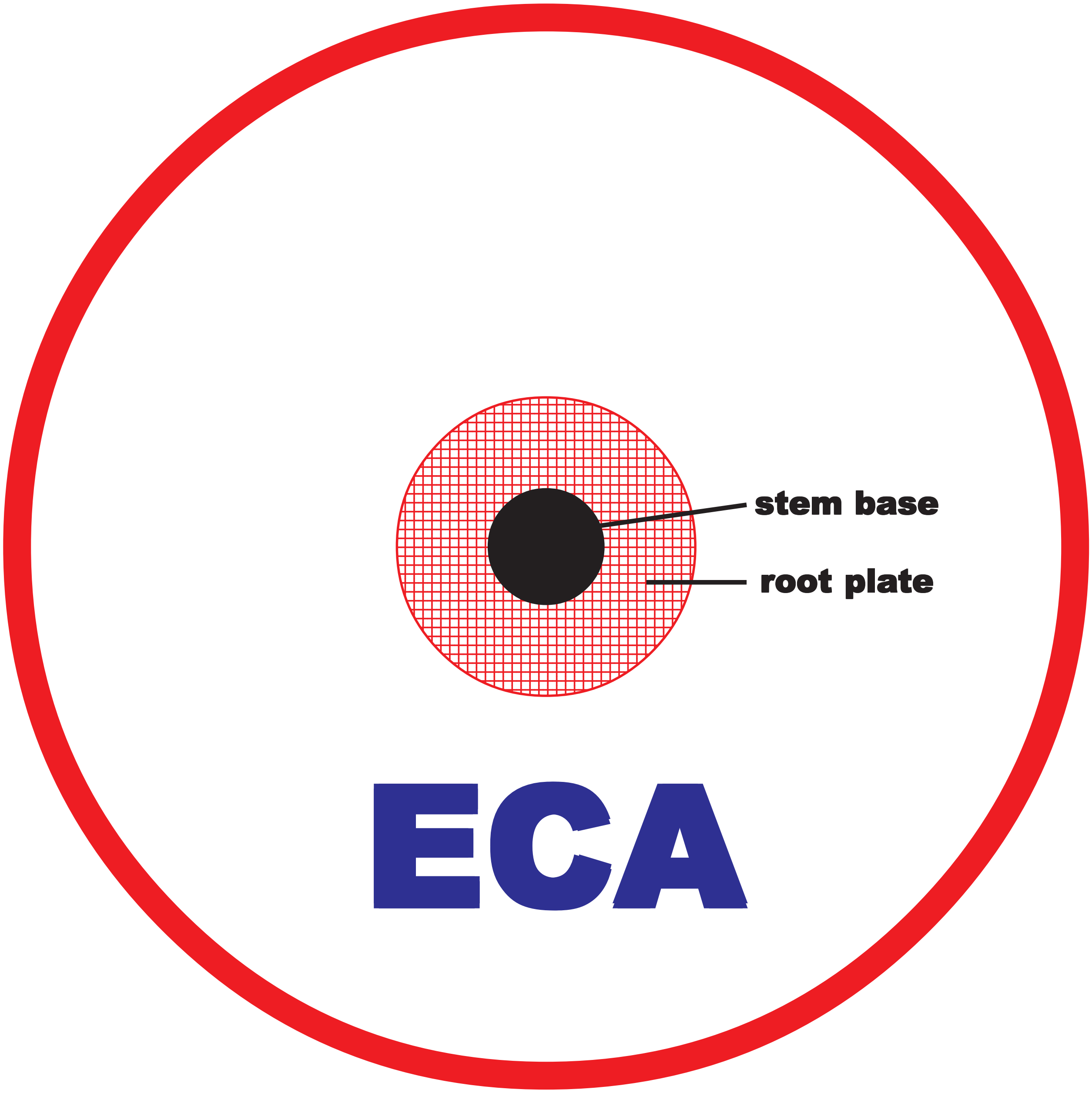
Figure 47: Example mature phase tree nitrogen enrichment with 1.5 lbs. N per 1000ft^2 per year prescribed for a single slow release / very slow release application (A). The shaded area beneath the mature tree curve represents the total prescribed dose for the season.



use smaller area (ft^2) of
ECA or FROSSA

Figure 48: Side view defining two means used for determining nitrogen enrichment application areas under a tree.

Nitrogen Enrichment Area



(exempt root plate area around stem base)

Figure 49: Top view of nitrogen enrichment application area extent under a tree where the open soil surface area is not limited and a crown-based area determination can be used.

Nitrogen Enrichment Area

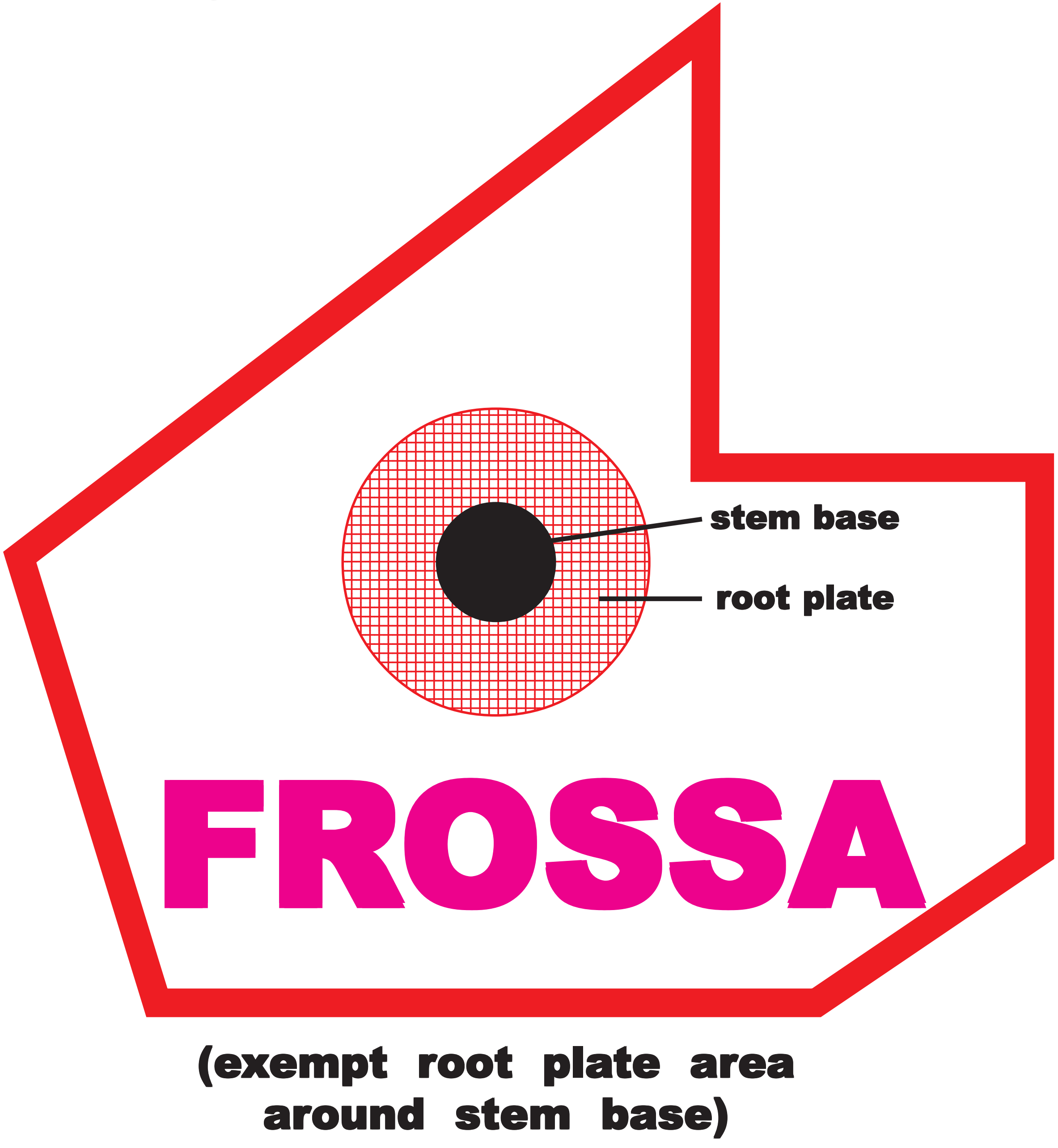


Figure 50: Top view of the extent of a nitrogen enrichment application area under a tree where open soil surface area is constrained in one or more directions and total open soil surface area available must be used.

How Much

For agronomic crops where a grain product is being removed each year, 5.7 pounds of nitrogen per 1000ft^2 of open soil surface area is considered a high enrichment rate, and 2.3 pounds of nitrogen per 1000ft^2 is considered a moderate enrichment rate. These levels of nitrogen enrichment do not make sense in shade and street tree culture. Figure 43 provides a rough estimate of supplemental nitrogen amounts that could be provided to trees at different life-stages and at different targeted leaf nitrogen percentages. The amount shown should be applied evenly over tree rooting areas on open soil surfaces where water flow and gas exchange to roots are not inhibited.

Soil limitations, rooting area / volume limits, and element holding capacity of soil are limitations to full applications. Smaller amounts of nitrogen in multiple applications may be an alternative. These calculated enrichment amounts include several assumptions provided by research including 60% of tree nitrogen (on average) is internally recycled each year, while only about 50% of the nitrogen applied to healthy soils may be eventually present in the target tree. Both of these conflicting / opposite results are usually treated as off-setting sums and not included in calculations.

Dosing Examples

Several figures provide examples of using a prescribed dose for mature trees. Note each enrichment curve corresponds to a mature tree's nitrogen utilization curve. Also note how the amount of nitrogen per application changes. Figure 44 shows a nitrogen enrichment of 1.5 pounds per 1000 square feet of open soil surface area all in one application just after full leaf expansion.

Figure 45 shows the same amount of nitrogen enrichment applied in three applications during the growing season. Figure 46 shows the same amount of nitrogen enrichment as before, but divided into five applications during the growing season. Figure 47 shows a early Spring application of a slow to very slow release nitrogen enrichment product designed to deliver a continuous supply of nitrogen over the growing season. Here the area under the curve (shaded in the figure) is equal to 1.5 pounds nitrogen per 1000 square feet.

Where

The location for application of nitrogen should be targeted at root concentration areas in healthy soil where nontarget organisms, erosion, and denitrification processes are minimized. Exempt the closest root plate area (3-5 feet radius around a medium-sized tree) from direct enrichment. Use any nitrogen designated for this stem base area across the rest of a site.

The tree and site provide two approximations to visualizing rooting areas and soil element containing locations. The two estimates for supplemental enrichment coverage area are ECA and FROSSA. The first is called the extended crown area (ECA) method based upon 1.5 times the average crown radius. The second is based upon the area where trees are free-to-root in soil whose surface is open to the atmosphere (FROSSA). Figure 48. Determine these area measures in square feet (ft^2) for your tree and site.

Just Enough

Figure 49 provides a top-view of the nitrogen enrichment area determined by ECA. Figure 50 provides a top-view of the nitrogen enrichment area determined by FROSSA. A calculation for measuring the enrichment area around a tree is presented in Figure 51 (steps 1 & 2 of 3) and in Figure 52 (step 3 of 3). This three step calculation of area available for nitrogen enrichment applications, where tree roots are most likely to derive the most benefit, assures effective and efficient nitrogen use while minimizing non-target losses. To prevent overdosing, this type of proportional area control is critical.

The smaller of the two calculated enrichment areas should always be used. In unlimited open soil surface areas, determining what proportion of a 1000 square feet are present makes it easy to determine nitrogen enrichment dosing. In places where many soil surface limitations occur, much more care is needed to determine accurately the available area for nitrogen enrichment. By examining both ECA and FROSSA, and by selecting the smaller of the two, proper dosing of nitrogen enrichment can occur. Figure 53.

To prevent too extensive of coverage away from the target tree, a calculation is presented in Figure 54 determining the radial distance away from the stem base for applications. In greatly misshapen and elongated open soil surface areas, care is needed to not enrich nitrogen too far away from the tree, which increases the chance of non-target use, loss and waste.

Stressed Out Trees

It is clear trees can be enriched with nitrogen products any time of the day or night, any season of the year, and with any type of preexisting conditions. A tree's defensive system is formidable, and with plenty of carbon in storage, can usually handle site disruptions, internal resource changes, and pest attacks brought about by nitrogen enrichment. This does not mean random large dumping is best for a tree, for a particular management objectives, or for the tree health care provider. Nitrogen additions can mask or overshadow other types of poor management practices. Nitrogen additions can change the balance of power between a tree, pest, and environment. Nitrogen additions can be used to initiate other problems requiring further treatment.

What is actually best for a tree can be different than what myth, tradition, and standard practices might suggest. In the past, ownership objectives and monetary income were top priorities for managers. Tree health was always a distant third under some management priorities. Nitrogen enrichment regimes can be purposely designed to damage and kill trees in established landscapes, especially if a tree is under stress and strain from other major environmental impacts. These types of purposeful designs are not formed out of maliciousness, but from ignorance and greed.

What Is Best

There are some management practices and nitrogen additions which are best for a tree. For many tree health care professionals, there is a growing recognition of what is best for a tree, is best for a tree owner, AND the professional. Survival of mythological practices and concepts remain a constant reminder of the value of professional development and growth. Tree/site resources management and an informed client require professional tree health care providers continue their education about tree nutrition and nitrogen interactions.

STEP 1

Measure average tree crown radius in feet (r).

$$4.7 \times (r)^2 = ECA$$

ECA =
expanded crown area (ft^2)

STEP 2

Measure contiguous area (ft^2) of open soil surface available to tree roots.

FROSSA =
free-to-root open soil surface area (ft^2)

Figure 51: Three step calculation determining open soil surface area around a tree for nitrogen enrichment applications. (here steps 1 & 2 of 3 are provided)

STEP 3

Proportional Area Control of Nitrogen Enrichment

A -- If ECA < FROSSA, use ECA for area.

OR

B -- If ECA > FROSSA, use FROSSA for area.

Figure 52: Final step (Step 3) in three step calculation determining open soil surface area around a tree for nitrogen enrichment applications. (here step 3 of 3 is provided)

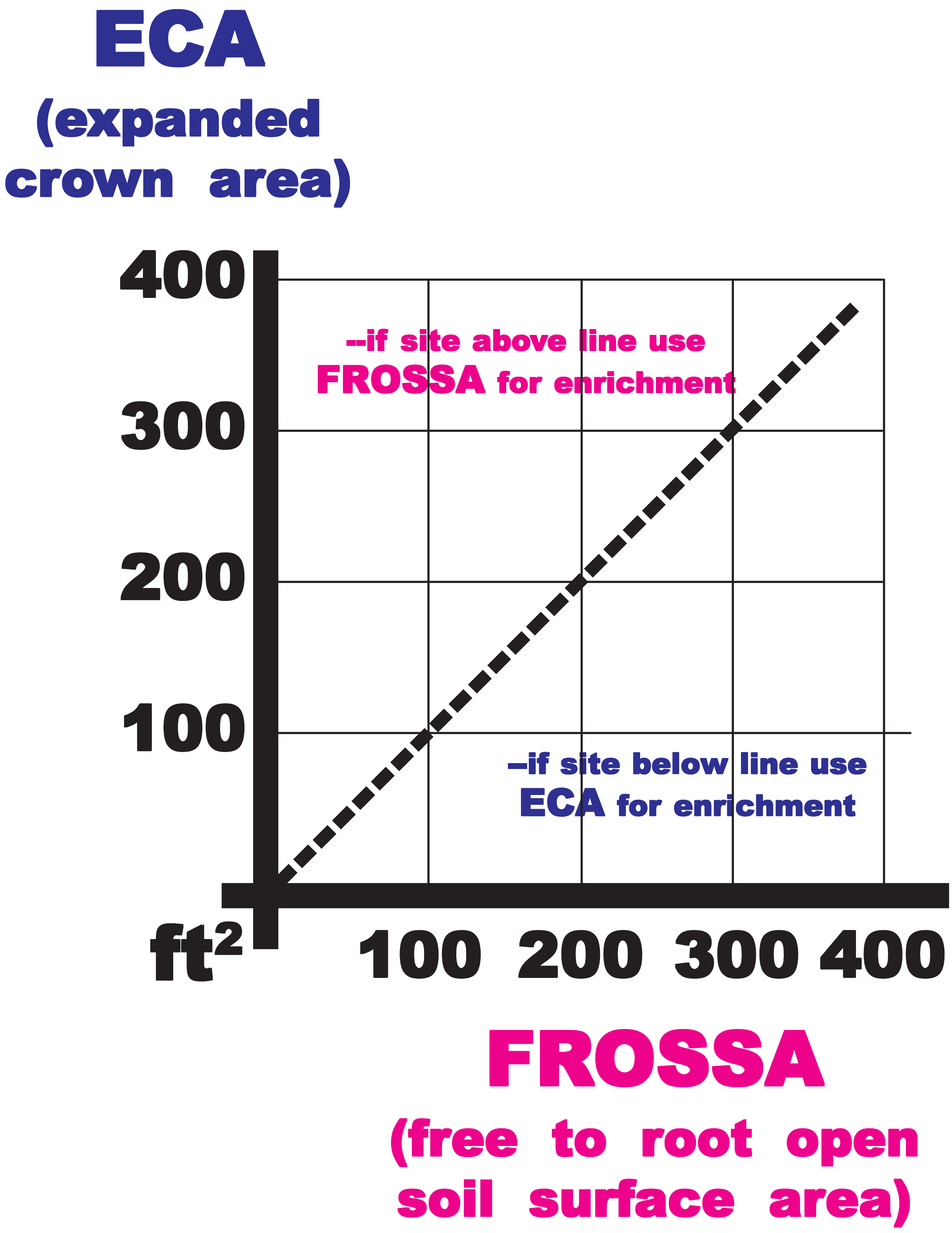


Figure 53: Selecting the smaller of two calculated areas (ft^2) for nitrogen enrichment applications under a tree.

Nitrogen Enrichment Area

$$\frac{\sqrt{\text{ECA or FROSSA}}}{3.14} =$$

Maximum Radial Distance From Stem Base In Feet For Nitrogen Enrichment

(exempt root plate area around stem base)

Figure 54: Determining the maximum distance (ft) from a tree stem for nitrogen enrichment applications.

Trees & Nitrogen

Conclusions

1) Know what you are doing ecologically.
2) Do not over-medicate or over-dose.
3) Prescription without testing is malpractice.

4) Cut through mists of turf nitrogen enrichment which can hide tree problems.
5) Use no general enrichment cookbooks without careful consideration.
6) Do not starve trees.

7) Do not blow away tree defenses.
8) Do not damage trees.
9) Ignorance is its own reward — education is key!