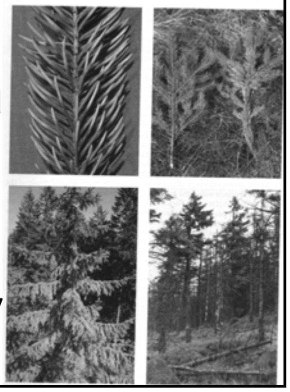
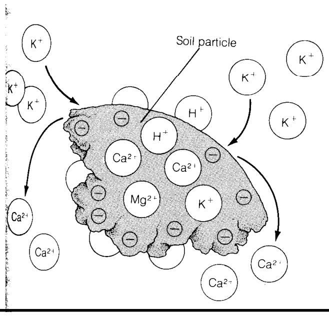
Mineral Nutrition

1. Which Nutrients are Used For What
2. **How Soils Hold and Release Nutrients**
3. **How plants obtain Nutrients**
4. **How efficiently they use them**



Many nutrient cations are held on and released from negatively charged soil particles



Cation Exchange Capacity

A measure of negative surface charge of soils – and hence its ability to hold and exchange nutrient cations (K, Ca, Mg, etc.)

Units:
moles (+)charge / kg soil

This is the size of the 'gas tank' – not necessarily how full it is.

% Base Saturation

How full the 'gas tank' is:

= $(Ca^{2+} + Mg^{2+} + K^{+} + Na^{+})/CEC \times 100$

Base saturation levels > 15% are considered to have 'buffering' capabilities against acid inputs.

Cation Exchange Capacity

Soils with high clay or organic matter content have the highest CEC. Sands have low CEC.

Clay particles carry (-) charge – both 'internally (isomorphous replacement)' and on the surface (dangling OH-s).

Organic matter is 'electron rich' and also has lots of dangling OH's.

Even within clays, CEC can vary dramatically – depends on surface area to volume

Equivalents = number of mol divided by valence state of substance.

e.g.,
1 mol Ca2+
=0.5 equivalents = 500 milliequivalents

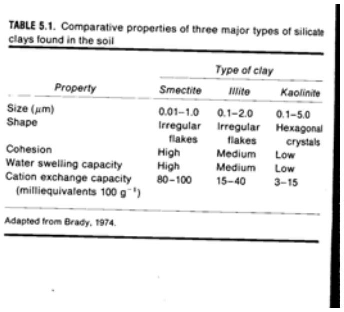


TABLE 5.1. Comparative properties of three major types of silicate clays found in the soil

	Type of clay		
Property	*Smectite*	*Illite*	*Kaolinite*
Size (μm)	0.01–1.0	0.1–2.0	0.1–5.0
Shape	Irregular flakes	Irregular flakes	Hexagonal crystals
Cohesion	High	Medium	Low
Water swelling capacity	High	Medium	Low
Cation exchange capacity (milliequivalents 100 g^{-1})	80–100	15–40	3–15

Adapted from Brady, 1974.

Adsorption strength depends on 2 factors:

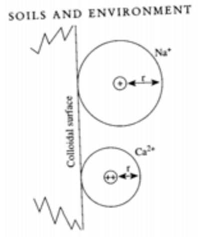


Figure 2.25 Factors influencing cation adsorption preference; r = radius of hydrati
(based on Foth 1990)

Valence state, and radius of hydration

Adsorption strength:

$Al^{3+}>H^{+}>Ca^{2+}>Mg^{2+}>K^{+}>NH^{4+}>Na^{+}$

Acid rain not only displaces good cations, but releases a very bad cation (Al^{3+})

"Liming" is an agricultural practice that swamps CE sites containing H^+ with Ca^{2+} - I.e. it reduces acidity and allows other cations to be held.

"Natural" liming also takes place due to atmospheric inputs and chemical weathering.

Soil pH strongly determines nutrient availability

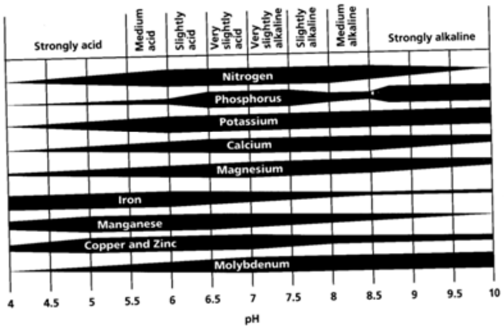


FIGURE 1. The availability of a number of ions in the soil as dependent on soil pH.

Here's an example of pH controls on P availability

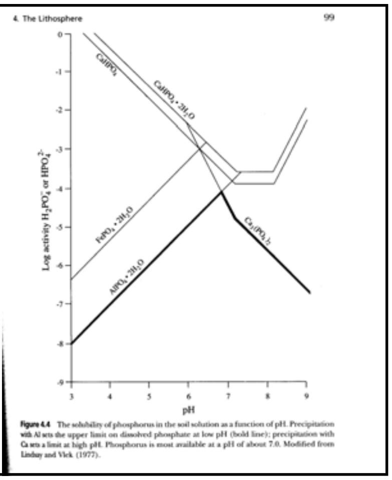
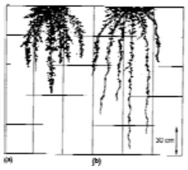


Figure 4.4 The solubility of phosphorus in the soil solution as a function of pH. Precipitation with Al sets the upper limit on dissolved phosphate at low pH (bold line); precipitation with Ca sets a limit at high pH. Phosphorus is most available at a pH of about 7.0. Modified from Lindsay and Vlek (1977).

So far, we've learned that storage and availability of key nutrients are determined largely by CEC and pH.



Now let's talk about how available nutrient ions move in soils to roots.

There are 3 main ways for roots to extract nutrients from soil:

1. Interception (root growth)
2. Mass flow (due to transpiration)
3. Diffusion

The amount of nutrients in roots often exceeds that intercepted

Thus, significant mass flow or diffusion must occur.

That is, roots do not generally go to the nutrients, but nutrients move toward roots.

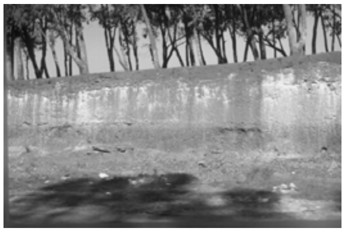
What's more important: Mass flow or Diffusion?

Either can be.

Depends on whether the concentration x mass flow rate of a nutrient exceeds the plant requirement for it.

If demand exceeds supply, a concentration gradient develops and diffusion may start to play a role.

For example, in desert soils Ca can be so abundant that passive mass movement with the transpiration stream is more than adequate for plants, and CaCO3 builds up around roots. Diffusion is negligible.



roadcut on the way from Casablanca to Rabat, Morocco, taken back in 1976. This Aridisol exposure contains caliche (calcium carbonate) deposits precipitated from the evaporation of water moving through in the soil.
raymondwiggers.homestead.com/SoilsGallery.html

Mass flow and diffusion together are described by the equation:

$$F = -D_e\ (dC/dr) + v\ C$$

Where F is nutrient flux into roots (mol $m^{-2}\ s^{-1}$)

D_e is the effective diffusion coefficient ($m^2 s^{-1}$)

dC/dr is the radial concentration gradient (mol m^{-4})

V is the inward flux of water ($m^3 m^{-2} s^{-1}$)

D_e is itself a function of soil water content (θ) and the tortuosity (f) of the pathlength to roots.

$D_e = \theta \times f \times D_o$

Where D_o is the diffusion coefficient of the nutrient in free solution.

θ= m^3water/m^3space
f = m path length/ m straight line distance

D_e can vary widely in soils, both within and among nutrients.

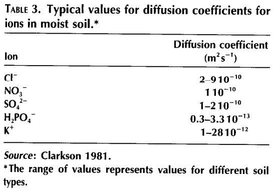


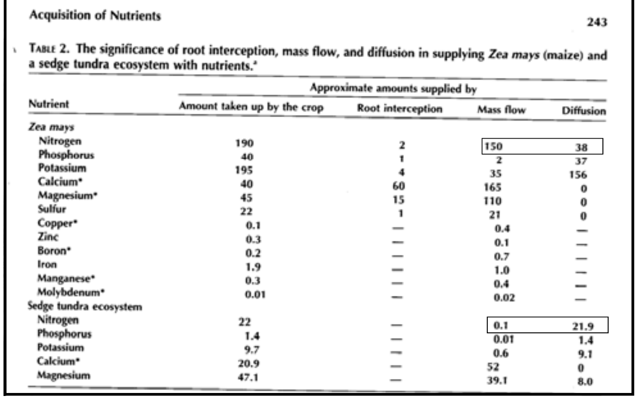
TABLE 3. Typical values for diffusion coefficients for ions in moist soil.*

Ion	Diffusion coefficient ($m^2 s^{-1}$)
Cl^-	$2–9\ 10^{-10}$
NO_3^-	$1\ 10^{-10}$
SO_4^{2-}	$1–2\ 10^{-10}$
$H_2PO_4^-$	$0.3–3.3\ 10^{-13}$
K^+	$1–28\ 10^{-12}$

Source: Clarkson 1981.
*The range of values represents values for different soil types.

In soils, at least 1 order of magnitude less than in free solution

Mass flow and diffusion usually dominate, relative %'s may differ widely

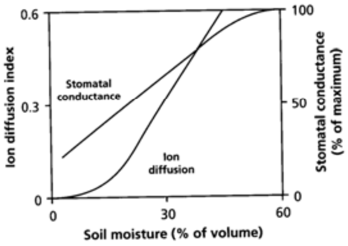


Acquisition of Nutrients 243

TABLE 2. The significance of root interception, mass flow, and diffusion in supplying *Zea mays* (maize) and a sedge tundra ecosystem with nutrients.ᵃ

Nutrient	Amount taken up by the crop	Approximate amounts supplied by		
		Root interception	Mass flow	Diffusion
Zea mays				
Nitrogen	190	2	150	38
Phosphorus	40	1	2	37
Potassium	195	4	35	156
Calcium*	40	60	165	0
Magnesium*	45	15	110	0
Sulfur	22	1	21	0
Copper*	0.1	—	0.4	—
Zinc	0.3	—	0.1	—
Boron*	0.2	—	0.7	—
Iron	1.9	—	1.0	—
Manganese*	0.3	—	0.4	—
Molybdenum*	0.01	—	0.02	—
Sedge tundra ecosystem				
Nitrogen	22	—	0.1	21.9
Phosphorus	1.4	—	0.01	1.4
Potassium	9.7	—	0.6	9.1
Calcium*	20.9	—	52	0
Magnesium	47.1	—	39.1	8.0

Higher soil moisture promotes both greater diffusion and mass flow



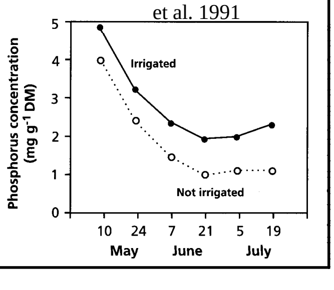
Thus, low soil water hurts plants in at least 2 distinct ways

We often think of water stress having a direct impact on plant growth, but low soil water also has big impacts on nutrient uptake, which also reduces growth.

Some desert annuals show greater growth response to nutrients than water!

Acquisition of Nutrients

Barley, Chapin et al. 1991

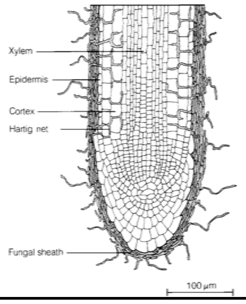


Now that we've talked about nutrient mobility in soils, what about root traits that promote nutrient acquisition?

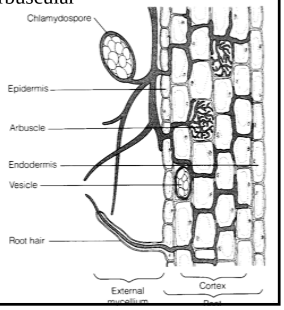
Not surprisingly, larger root mass and density lead to larger nutrient uptake, and nutrient stressed plants often show a greater root:shoot ratio, and a greater percentage of root hairs.

Additionally, nutrient uptake can be dramatically enhanced by fungal associations (e.g. phosphate 4X!)

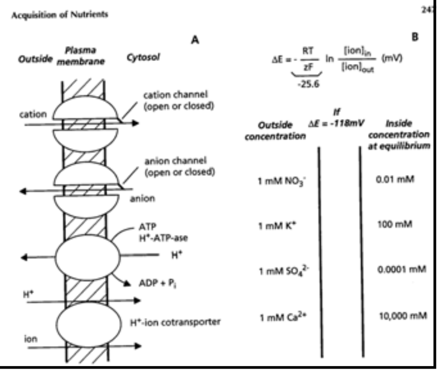
ecotrophic



arbuscular



Finally, nutrients can move into roots both by passive diffusion and by active pumping (ATP Proton Pump)



$$\Delta E = -\underbrace{\frac{RT}{zF}}_{-25.6} \ln \frac{[\text{ion}]_{in}}{[\text{ion}]_{out}} \text{ (mV)}$$

Outside concentration	*If $\Delta E = -118mV$*	*Inside concentration at equilibrium*
1 mM NO_3^-		0.01 mM
1 mM K^+		100 mM
1 mM SO_4^{2-}		0.0001 mM
1 mM Ca^{2+}		10,000 mM

Proton pumping to gain cations is in fact one of the main reasons why plants acidify soils.

It can be thought of as a 'double-edged sword' or a 'tragedy of the commons' where short term gain may compromise long term sustainability.

Nutrient Use Efficiency:

a useful indicator of how well plants grow/compete under nutrient scarcity or changing nutrient levels (in time or space).

Definition: Carbon gain/nutrients used (g/g)
Analogous to WUE (carbon gain/water used)

Nutrient Use Efficiency

- **Can be applied to leaves, harvestable organs, woody stems, or total plant.**
- **Can be defined instantaneously (PNUE) or longer term (daily, seasonal, lifetime)**
- **Can include nutrient losses as well**

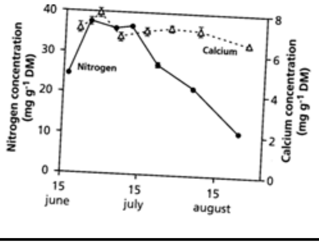
Thus, as in WUE, care must be taken in comparing numbers.

High apparent Nutrient Use Efficiency in crops or forests can be obtained with fertilization

but this can be a misleading measure of 'performance' if other losses are excluded.

Apparent Nutrient Use Efficiency at one time of year may also be very different from other times of the year, and the pattern may differ among nutrients

(salix, willow)



In natural ecosystems, plants are usually efficient in recycling of nutrients, but this is not often considered in NUE calculations

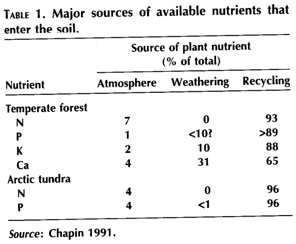
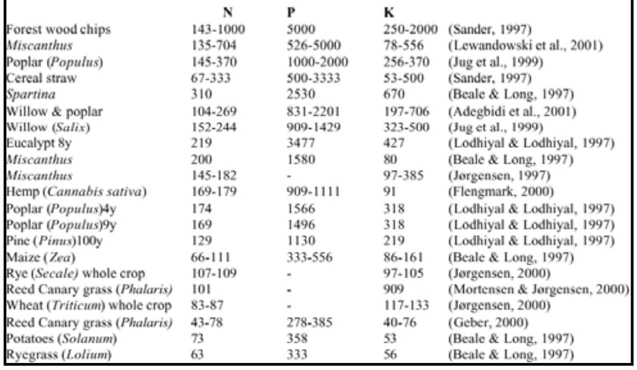


TABLE 1. Major sources of available nutrients that enter the soil.

Nutrient	Source of plant nutrient (% of total)		
	Atmosphere	Weathering	Recycling
Temperate forest			
N	7	0	93
P	1	<10?	>89
K	2	10	88
Ca	4	31	65
Arctic tundra			
N	4	0	96
P	4	<1	96

Source: Chapin 1991.

Crops generally have much lower NUE than natural vegetation (Table from Jorgensen and Schelde (2001)



	N	P	K	
Forest wood chips	143-1000	5000	250-2000	(Sander, 1997)
Miscanthus	135-704	526-5000	78-556	(Lewandowski et al., 2001)
Poplar (*Populus*)	145-370	1000-2000	256-370	(Jug et al., 1999)
Cereal straw	67-333	500-3333	53-500	(Sander, 1997)
Spartina	310	2530	670	(Beale & Long, 1997)
Willow & poplar	104-269	831-2201	197-706	(Adegbidi et al., 2001)
Willow (*Salix*)	152-244	909-1429	323-500	(Jug et al., 1999)
Eucalypt 8y	219	3477	427	(Lodhiyal & Lodhiyal, 1997)
Miscanthus	200	1580	80	(Beale & Long, 1997)
Miscanthus	145-182	-	97-385	(Jørgensen, 1997)
Hemp (*Cannabis sativa*)	169-179	909-1111	91	(Flengmark, 2000)
Poplar (*Populus*)4y	174	1566	318	(Lodhiyal & Lodhiyal, 1997)
Poplar (*Populus*)9y	169	1496	318	(Lodhiyal & Lodhiyal, 1997)
Pine (*Pinus*)100y	129	1130	219	(Lodhiyal & Lodhiyal, 1997)
Maize (*Zea*)	66-111	333-556	86-161	(Beale & Long, 1997)
Rye (*Secale*) whole crop	107-109	-	97-105	(Jørgensen, 2000)
Reed Canary grass (*Phalaris*)	101	-	909	(Mortensen & Jørgensen, 2000)
Wheat (*Triticum*) whole crop	83-87	-	117-133	(Jørgensen, 2000)
Reed Canary grass (*Phalaris*)	43-78	278-385	40-76	(Geber, 2000)
Potatoes (*Solanum*)	73	358	53	(Beale & Long, 1997)
Ryegrass (*Lolium*)	63	333	56	(Beale & Long, 1997)

NUE tends to decline with more nutrient availability, due to both acclimation and adaptation (or lack thereof)

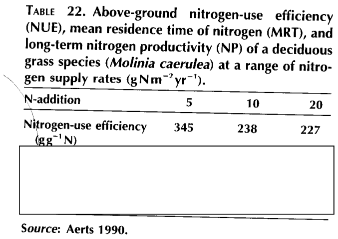


TABLE 22. Above-ground nitrogen-use efficiency (NUE), mean residence time of nitrogen (MRT), and long-term nitrogen productivity (NP) of a deciduous grass species (*Molinia caerulea*) at a range of nitrogen supply rates ($g N m^{-2} yr^{-1}$).

N-addition	5	10	20
Nitrogen-use efficiency ($g g^{-1} N$)	345	238	227

Source: Aerts 1990.

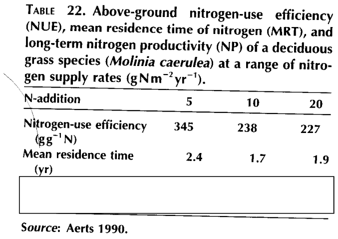
However, the decreased NUE could be driven by different causes:

1. Plant growth rate plateaus – more nutrients cannot indefinitely support faster growth. Nutrients are taken up and stored, but not used to support further growth.
2. Plants might lose nutrients more readily in litterfall (less efficient translocation).

Both these factors involve the variable of TIME, which is not a dimension explicitly contained in NUE

Molinia caerulea
Purple Moor Grass

The decrease in NUE is often partially due to a decrease in mean residence time of nutrients (greater leaf turnover, herbivory, root death)



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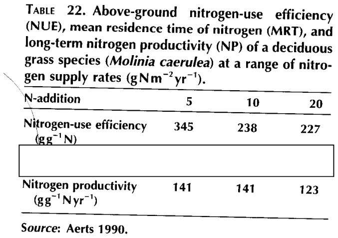
N-addition	5	10	20
Nitrogen-use efficiency ($g g^{-1} N$)	345	238	227
Mean residence time (yr)	2.4	1.7	1.9

Source: Aerts 1990.

And partially due to reduction in a variable called 'nutrient productivity'.



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N-addition	5	10	20
Nitrogen-use efficiency ($g g^{-1} N$)	345	238	227
Nitrogen productivity ($g g^{-1} N yr^{-1}$)	141	141	123

Source: Aerts 1990.

Nutrient Productivity:

a measure of growth performance over a time interval per unit of nutrient investment,
a kind of time-based Nutrient Use Efficiency

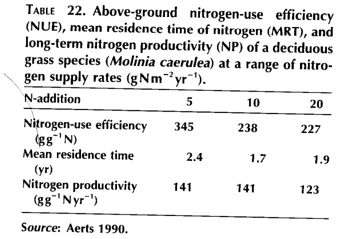
NP = relative growth rate/ Nutrient concentration.

Relative growth rate =
rate of biomass accrual per unit existing biomass (mg g^{-1} d^{-1}). Roughly in economic terms, "Interest/Capital".

NUE is the product of NP and MRT

$NUE\ (gC/gN) = NP\ (gC/(\cancel{gC}\ \cancel{d}))/(gN/\cancel{gC}) \times MRT\ (\cancel{d})$

Both factors play a role in the decrease in NUE of this grass species.



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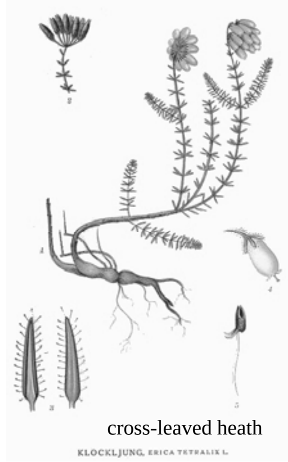
Google earth.



cross-leaved heath

Heather (Calluna vulgaris)

By the same token, NUE can be very similar between species or ecosystems, but for different reasons.

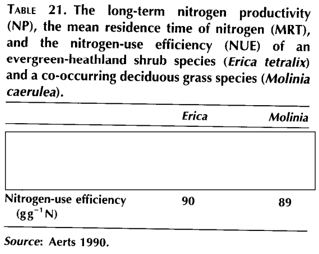
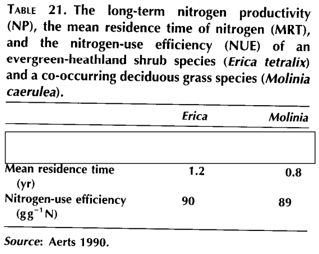


TABLE 21. The long-term nitrogen productivity (NP), the mean residence time of nitrogen (MRT), and the nitrogen-use efficiency (NUE) of an evergreen-heathland shrub species (*Erica tetralix*) and a co-occurring deciduous grass species (*Molinia caerulea*).

	Erica	*Molinia*
Nitrogen-use efficiency (gg^{-1}N)	90	89

Source: Aerts 1990.

The evergreen species holds onto leaves substantially longer than the deciduous species.



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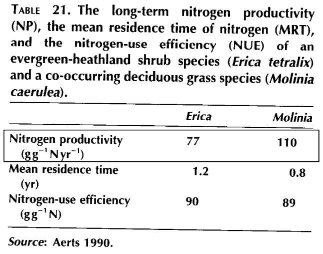
	Erica	*Molinia*
Mean residence time (yr)	1.2	0.8
Nitrogen-use efficiency (gg^{-1}N)	90	89

Source: Aerts 1990.

But had less Nitrogen productivity.



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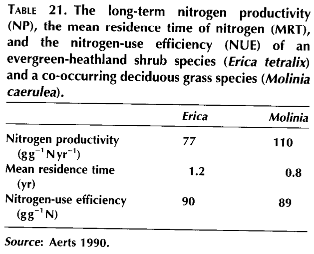
	Erica	*Molinia*
Nitrogen productivity (gg^{-1}Nyr^{-1})	77	110
Mean residence time (yr)	1.2	0.8
Nitrogen-use efficiency (gg^{-1}N)	90	89

Source: Aerts 1990.

So who's the competitive winner here?

It depends…



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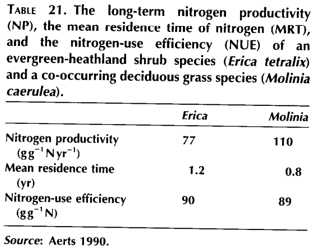
Source: Aerts 1990.

Aerts (1990) showed that in high nutrient soils, the grass (high NP) outcompeted the evergreen shrub (low NP), but in infertile sites, the greater longevity of evergreen leaves made the shrub outcompete the grass.

(rabbit vs. turtle)



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Source: Aerts 1990.

Conclusions on NUE:

NUE is a useful indicator of plant performance in relation to nutrient resource availability.

Plants/species on infertile sites generally show greater NUE.

However, it must be used with care, as it masks possible underlying dynamics of nutrient use and retention.

A broader view of multiple nutrient use and limitations in plants:

Nutritional Disharmony (Oren and Schulze 1989)

Nutrient saturation (Aber 1989)