Nutrient Cycling on Land

1. Basic Stoichiometry of Organisms
2. Autotrophic (Plants) Transformation
    - Uptake
    - Mutualistic associations(e..g, Rhizobia & Mycorrhizae)
3. Nutrient Allocation and Budgets
4. Nutrient Cycling in the Soil
    - Microorganisms and Decomposition
    - Nitrogen Transformation
    - Fixation and Mobilization of Phosphorus
    - Sulfur Transformation
5. Fire and Nutrient Cycling
6. Food Web Interactions and Nutrient Cycling
7. Scaling up temporally and spatially

A Question of Basic Stoichiometry:
Do all living things require a balanced nutrition?

Cell Elemental Composition

Element	Dry Weight, %
Carbon	50
Oxygen	20
Nitrogen	14
Hydrogen	8
Phosphorus	3
Sulfur	1
Potassium	1
Sodium	1
Calcium	0.5
Magnesium	0.5
Chlorine	0.5
Iron	0.2
All others	0.3

Source: Stanier et al 1976. The Microbial World. 4th ed. Prentice-Hall, Englewood Cliffs, NJ.
These number varies depending on species and conditions, such as granules (phosphorus, sulfur, etc.), but the C, O, H, N are much stable.
Porges et al. 1956 determined that the ratio of a heterogeneous microbial population: $C_5H_7NO_2$

A Question of Basic Stoichiometry:

Do all living things require a balanced nutrition?

Table 6.5 Biomass and Element Accumulation in Biomass of Mature Forests[a]

Forest biome	Number of stands	Total biomass (t/ha)	Percent of total biomass				Mass ratio		
			Leaf	Branch	Bole	Roots	C/N	C/P	N/P
Northern/subalpine conifer	12	233	4.5	10.2	62.8	22.6	143	1246	8.71
Temperate broadleaf deciduous	13	286	1.1	16.2	63.1	19.5	165	1384	8.40
Giant temperate conifer	5	624	2.5	10.2	66.4	20.8	158	1345	8.53
Temperate broadleaf evergreen	15	315	2.7	14.7	66.2	16.5	159	1383	8.73
Tropical/subtropical closed forest	13	494	1.9	21.8	59.8	16.4	161	1394	8.65
Tropical/subtropical woodland and savanna	13	107	3.6	19.1	60.4	16.9	147	1290	8.80

[a] From Vitousek et al. (1988).

Nutrient Cycling on Land

1. Basic Stoichiometry of Organisms

2. Autotrophic (Plants) Transformation

Uptake: How and where do plants get their nutrients?

Mutualistic associations(e..g, Rhizobia & Mycorrhizae)

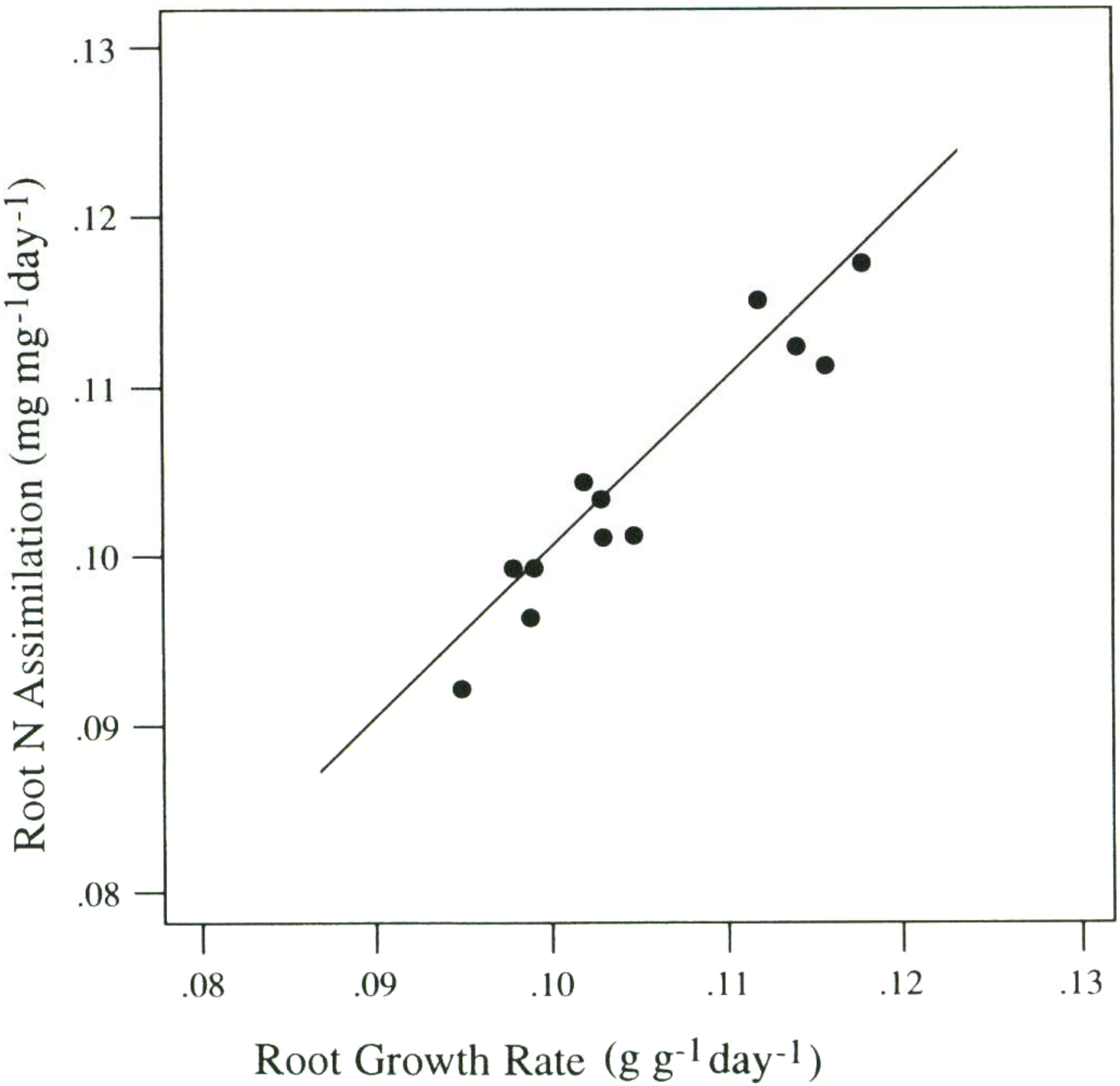

Figure 6.2 The rate of N uptake in tobacco as a function of the relative growth rate of roots. From Raper et al. (1978).

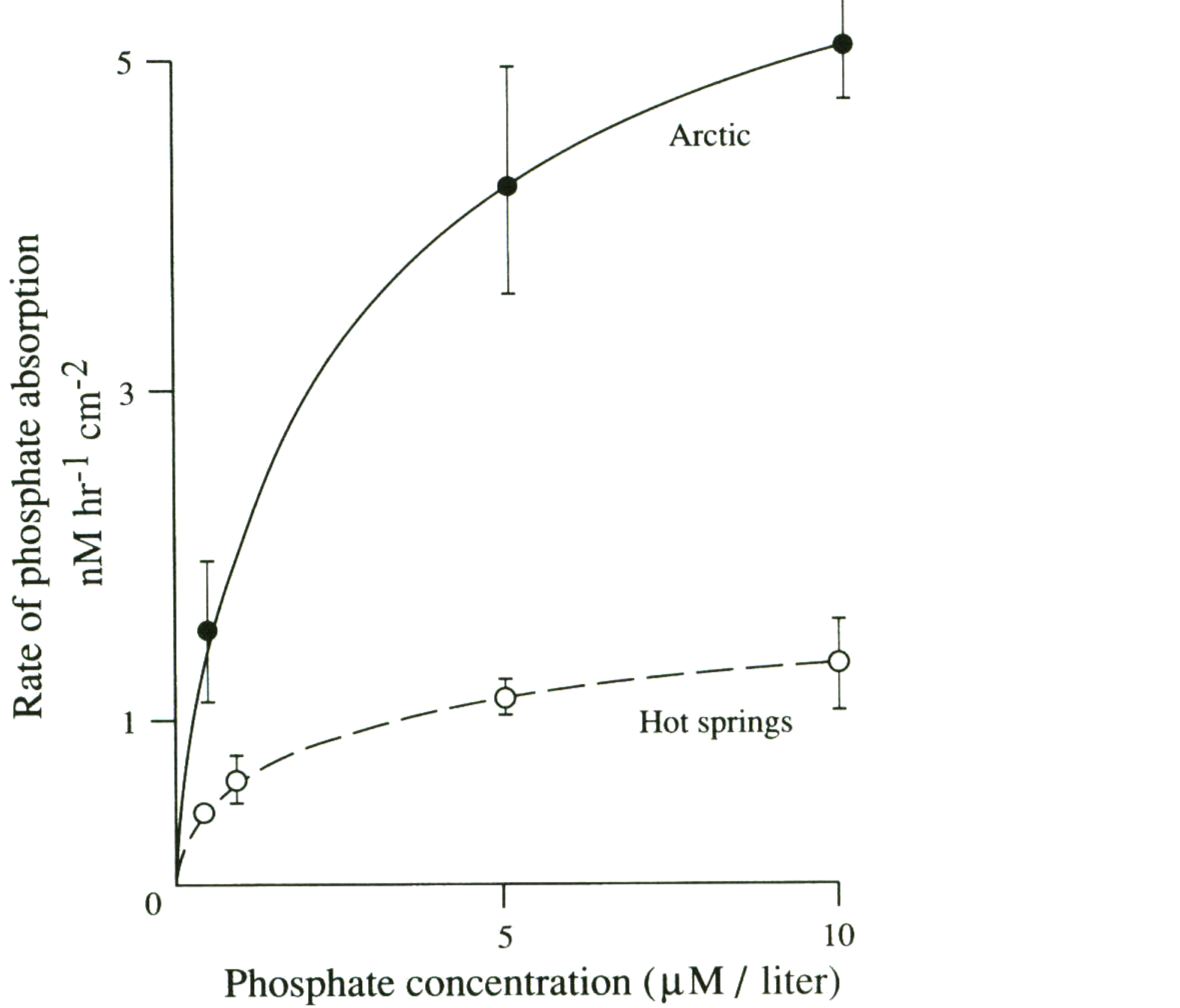

Figure 6.1 Rate of phosphate absorption per unit of root surface area in populations of *Carex aquatilis* from cold (Arctic) and warm (Hot Springs) habitats measured at 5°C. From Chapin (1974).

Nutrient Cycling on Land

1. Basic Stoichiometry of Organisms

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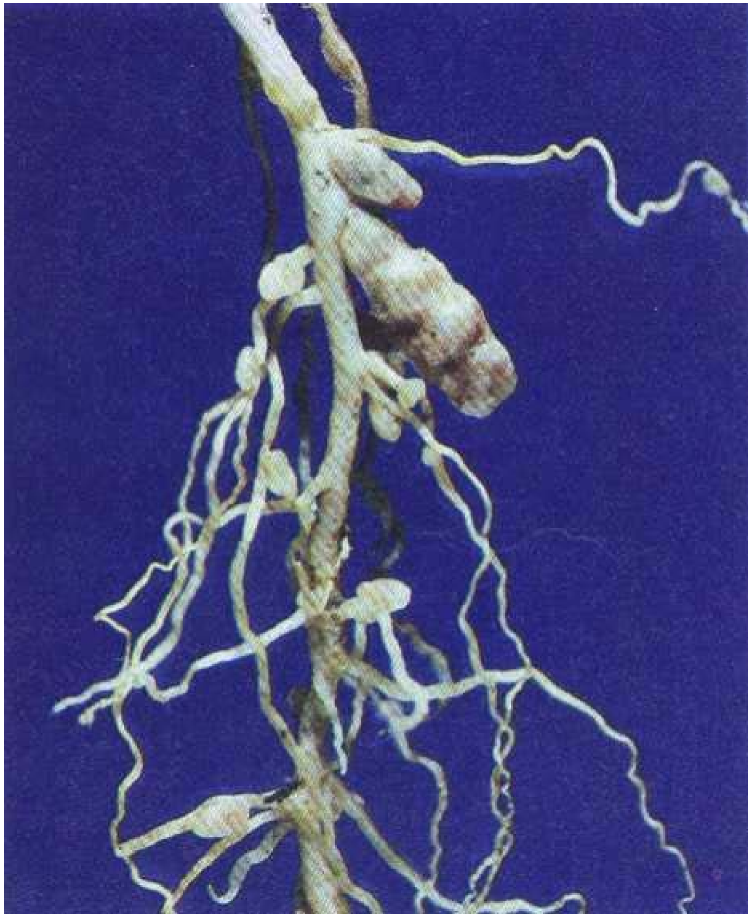
Uptake

Mutualistic associations (e..g, Rhizobia & Mycorrhizae):

Facing nutrient scarcity, do plants turn to others for help?

Help from symbiotic N_2-fixing Bacteria

Nodules on Clover



Rhizobial Nodules
in Leguminosae

Nodules on Alder

'Frankia' (actinomycetes) Nodules

Help from asymbiotic bacteria

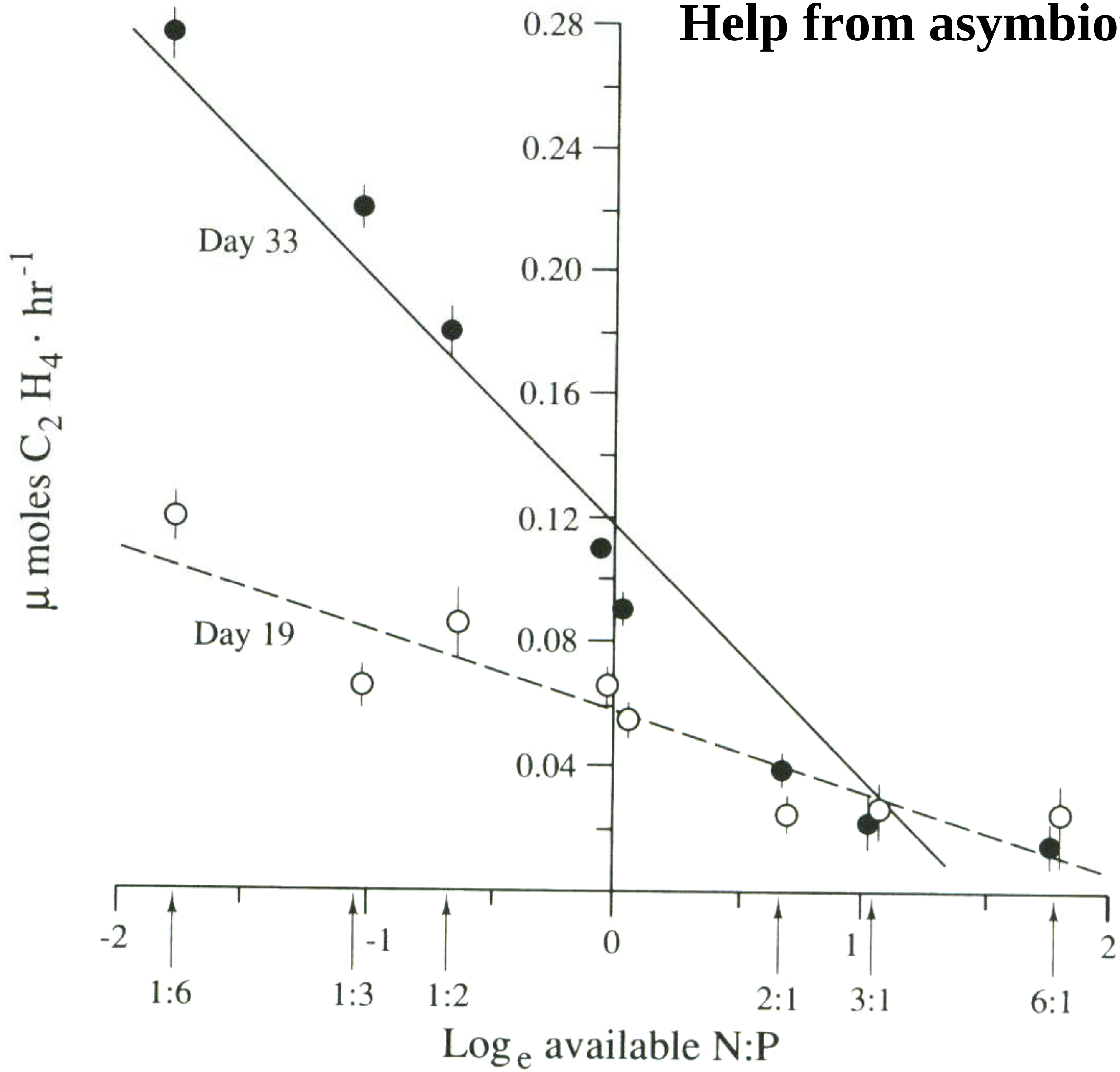


FIGURE 6.4 Acetylene reduction, an index of nitrogen fixation by asymbiotic N-fixing bacteria, as a function of the N : P ratio in soil. From Eisele et al. (1989).

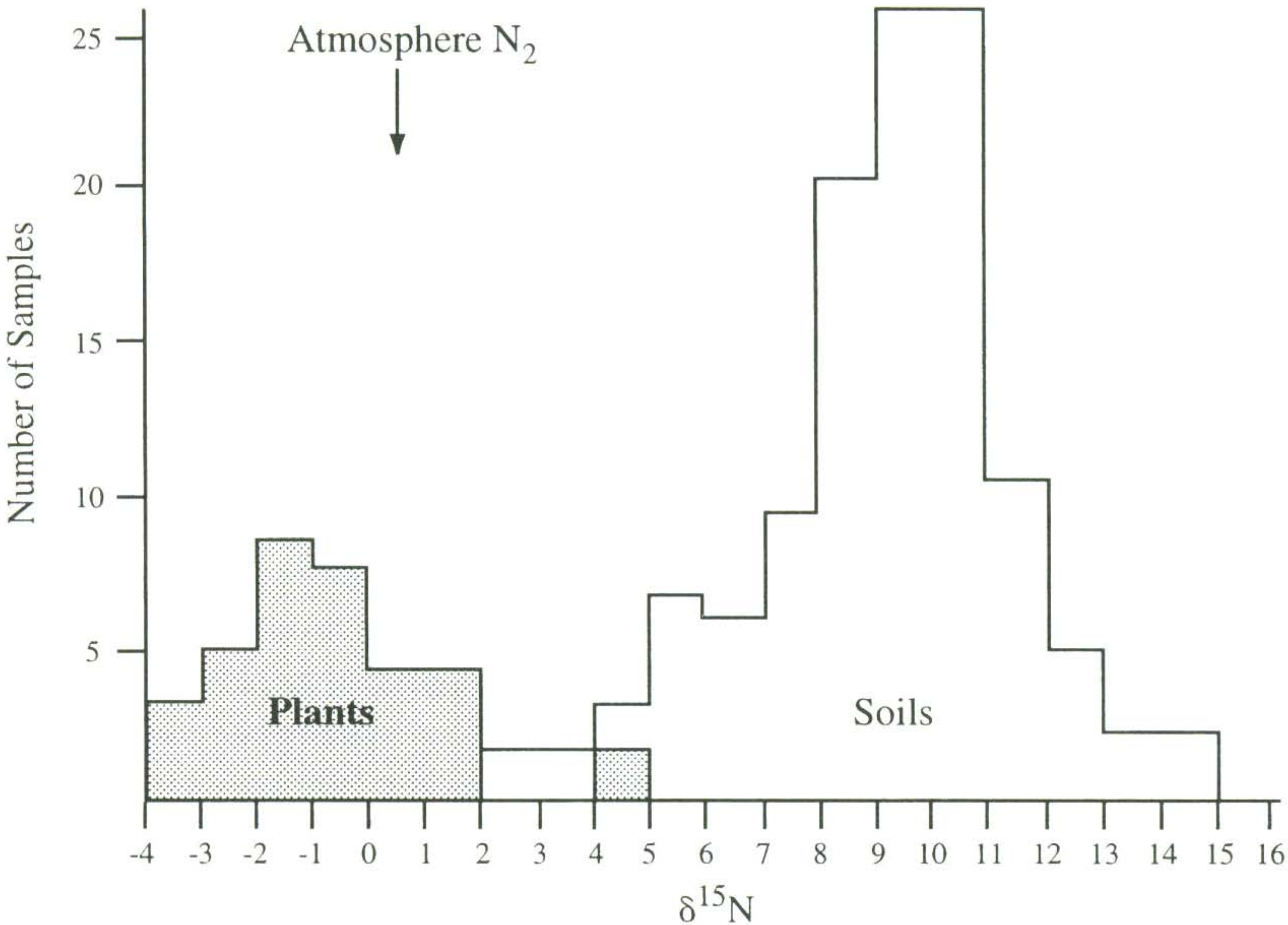


FIGURE 6.5 Frequency distribution of $\delta^{15}N$ in the tissues of 34 nitrogen-fixing plants and in the organic matter of 124 soils from throughout the United States. Plotted using data from Shearer and Kohl (1988, 1989).

Help from symbiotic fungi for P, N, and H_2O

Ectomycorrhiza on Douglas fir

Key Features;
(1) only penetrate the spaces between cells of the cortex;
(2) may form sheath around the host root;
(3) Change fine root morphology

Key Features:
(1) Penetrate and grow into host cells;
(2) Some form vesicular-arbuscular structures (VAM);
(3) Does not change fine root morphology.

Endomycorrhizal root system showing the intact network with external hyphae (arrow) with spores (S) produced by *Glomus mosseae*.

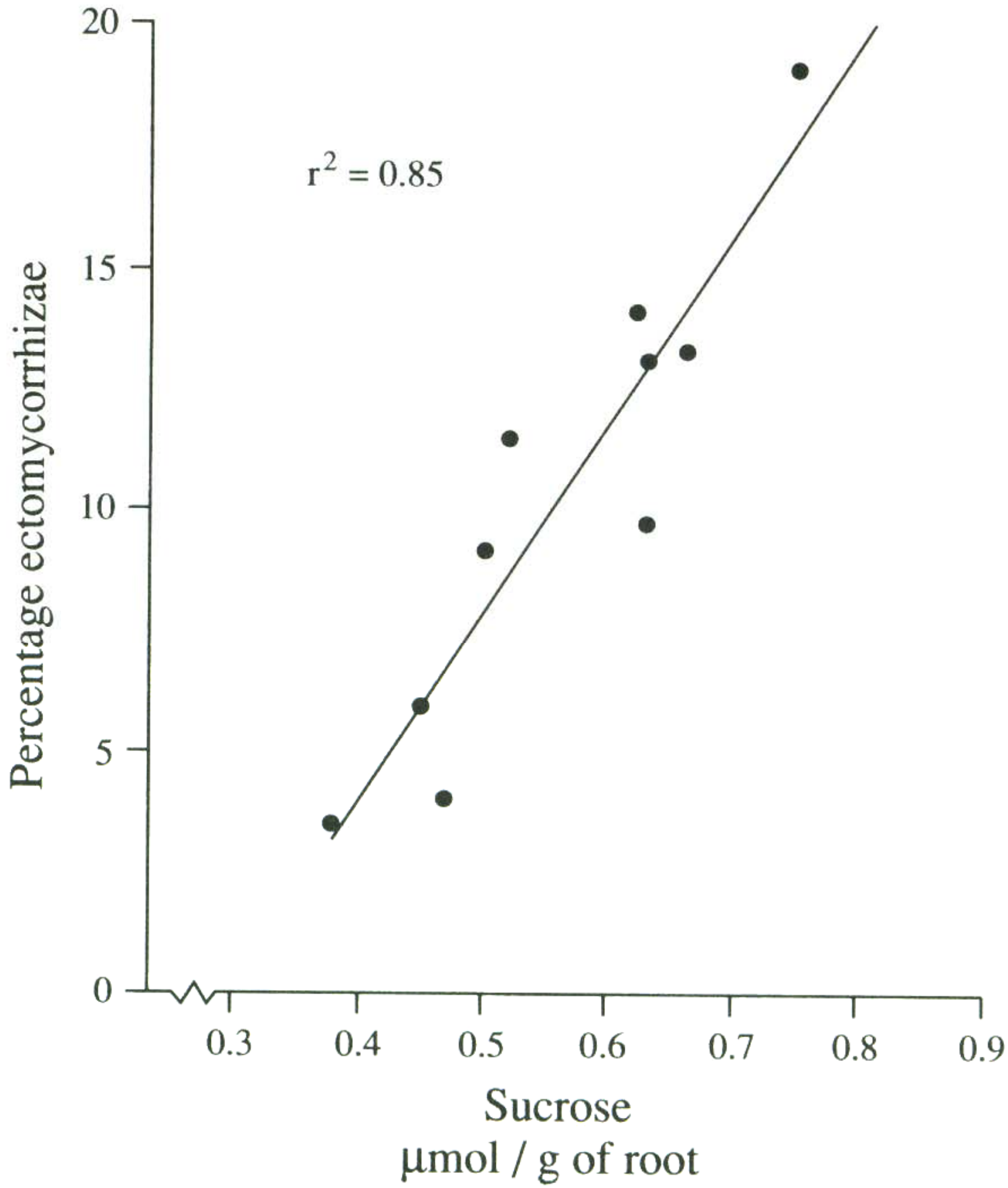


Figure 6.6 Relationship between infection of the roots of loblolly pine by ectomycorrhizal fungi and the sucrose concentration in the root. From Marx et al. (1977).

Table 6.3 Effects of Mycorrhizae and N-Fixing Nodules on Growth and Nitrogen Fixation in *Ceanothus velutinus* Seedlings[a]

	Control	+Mycorrhizae	+Nodules	+Mycorrhizae and nodules
Mean shoot dry weight (mg)	72.8	84.4	392.9	1028.8
Mean root dry weight (mg)	166.4	183.4	285.0	904.4
Root/shoot	2.29	2.17	0.73	0.88
Nodules per plant	0	0	3	5
Mean nodule weight (mg)	0	0	10.5	44.6
Acetylene reduction (mg/nodule/hr)	0	0	27.85	40.46
Percent mycorrhizal colonization	0	45	0	80
Nutrient concentration (in shoot, %)				
N	0.32	0.30	1.24	1.31
P	0.08	0.07	0.25	0.25
Ca			1.07	1.15

[a] From Rose and Youngberg (1981).

Nutrient Cycling on Land

1. Basic Stoichiometry of Organisms
2. Autotrophic (Plants) Transformation
   Uptake
   Mutualistic associations(e..g, Rhizobia & Mycorrhizae)
3. **Nutrient Allocation and Budgets:**
   Where do nutrients come from, stay in, and go to?

Key points:

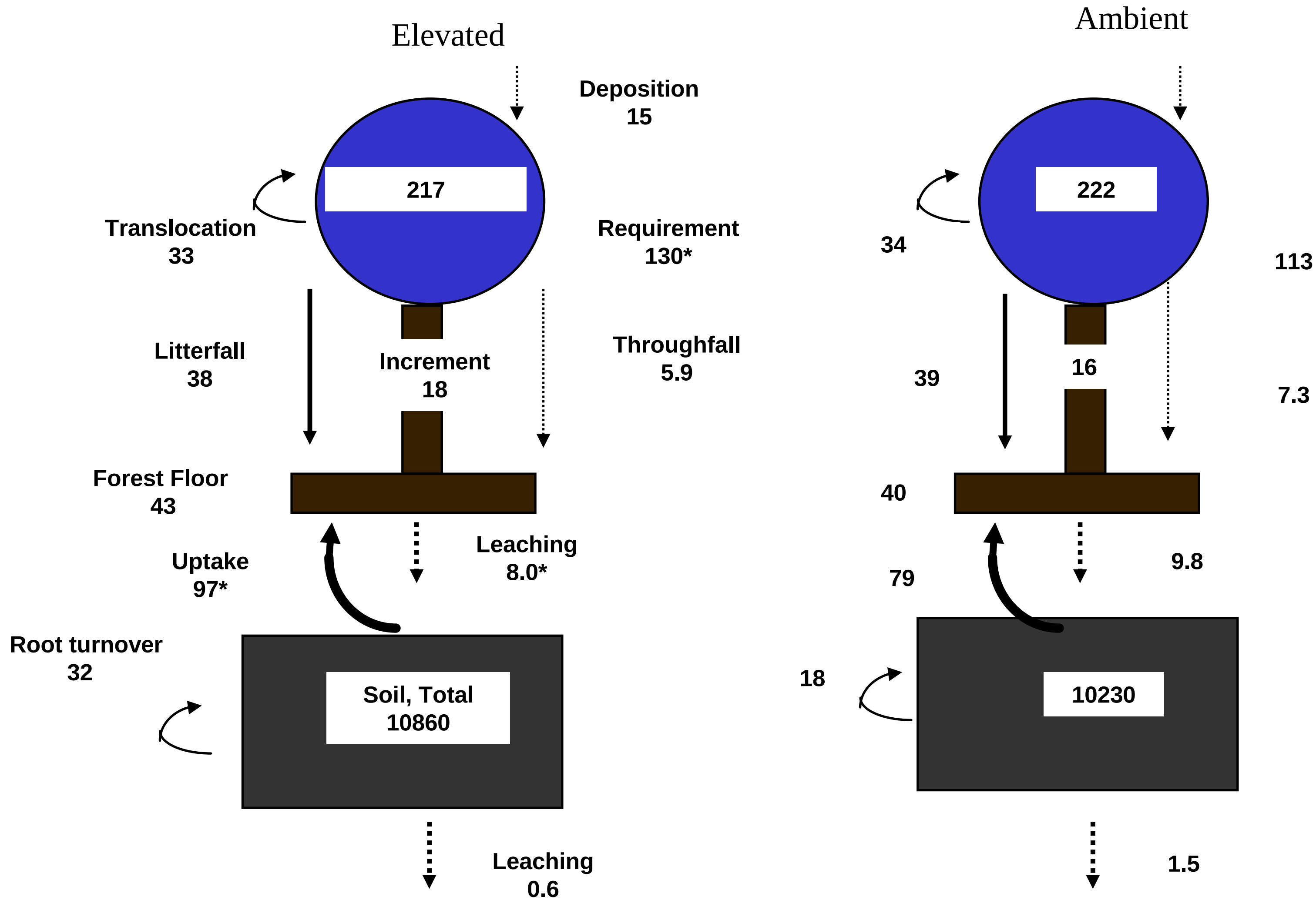
uptake = retained + returned

requirement = uptake + retranslocation

NUE is controlled by functions of leaves, functions of roots, recycling, and retention/leaching.

Nitrogen Cycling

kg ha^{-1} or kg $^{-1}$ ha $^{-1}$ yr $^{-1}$



From: Johnson et al. 2004

Table 6.6 Net Primary Production (kg ha^{-1} yr^{-1}) per Unit of Nutrient Uptake Used as an Index of Nutrient-Use Efficiency to Compare Deciduous and Coniferous Forests[a]

	Production per unit nutrient uptake				
Forest type	N	P	K	Ca	Mg
Deciduous	143	1859	216	130	915
Coniferous	194	1519	354	217	1559

[a] From Cole and Rapp (1981).

Nutrient Cycling on Land

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4. **Nutrient Cycling in the Soil**
   - Microorganisms and Decomposition
   - Nitrogen Transformation
   - Fixation and Mobilization of Phosphorus
   - Sulfur Transformation

Microorganisms and Decomposition

Decomposition:

A general term for the breakdown of organic matter either from complex forms to simpler forms or from simpler forms to inorganic forms. Although decomposition may involves both biotic processes and abiotic processes, soil microorganisms do most of the work.

Mineralization:

A term refers to processes that release carbon as CO_2 and other nutrients in inorganic forms. Mineralization involves mostly biotic processes.

Immobilization refers to the accumulation of nutrients in soil microbial biomass resulted from microbial growth or assimilation.

Stoichiomstry of soil microbial biomass

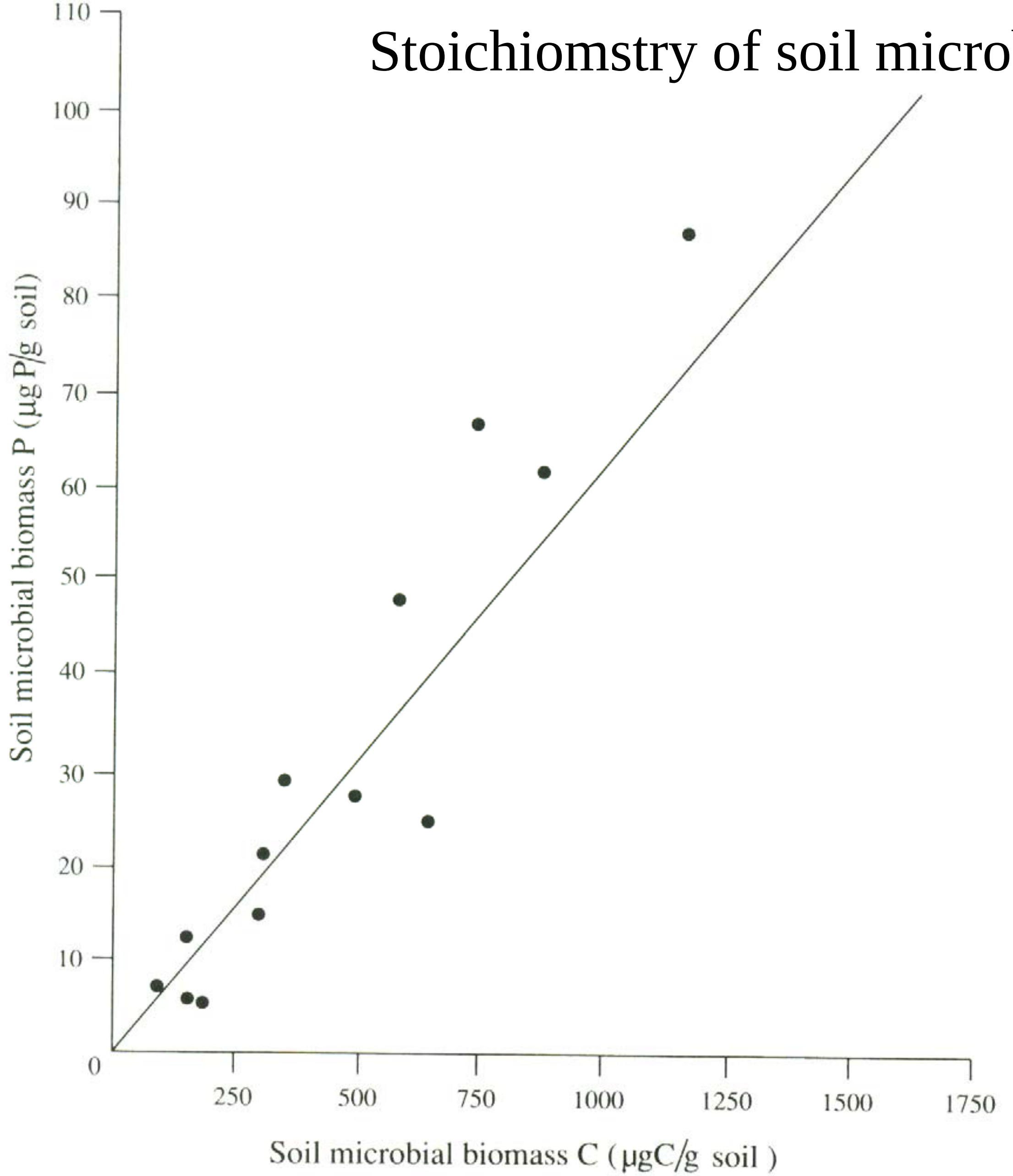
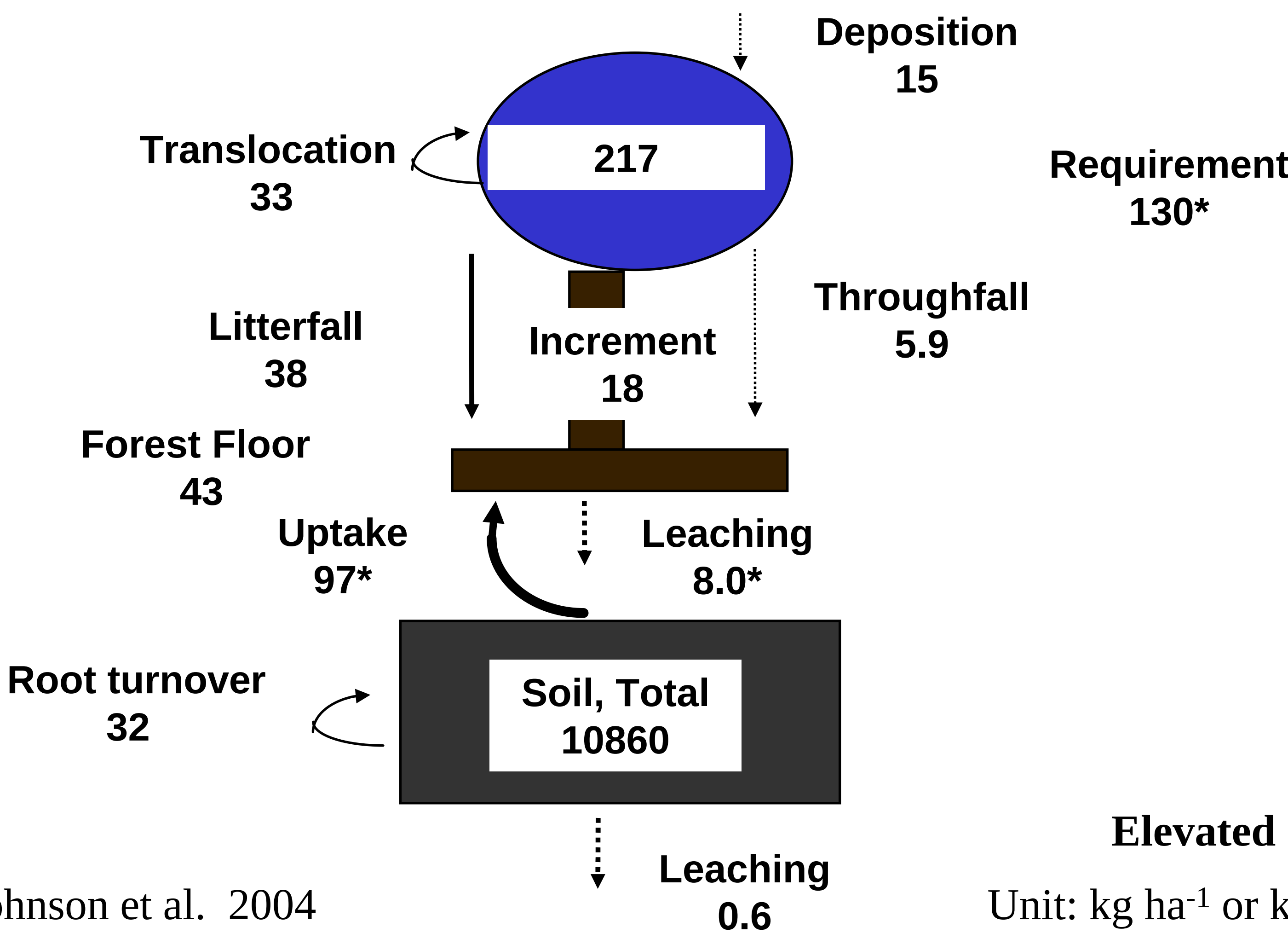


FIGURE 6.9 Relationship between the phosphorus and carbon contained in the microbial biomass of 14 soils. From Brooks et al. (1984).

Decomposition and mineralization are linked to plant production because most plants take up inorganic nitrogen only.



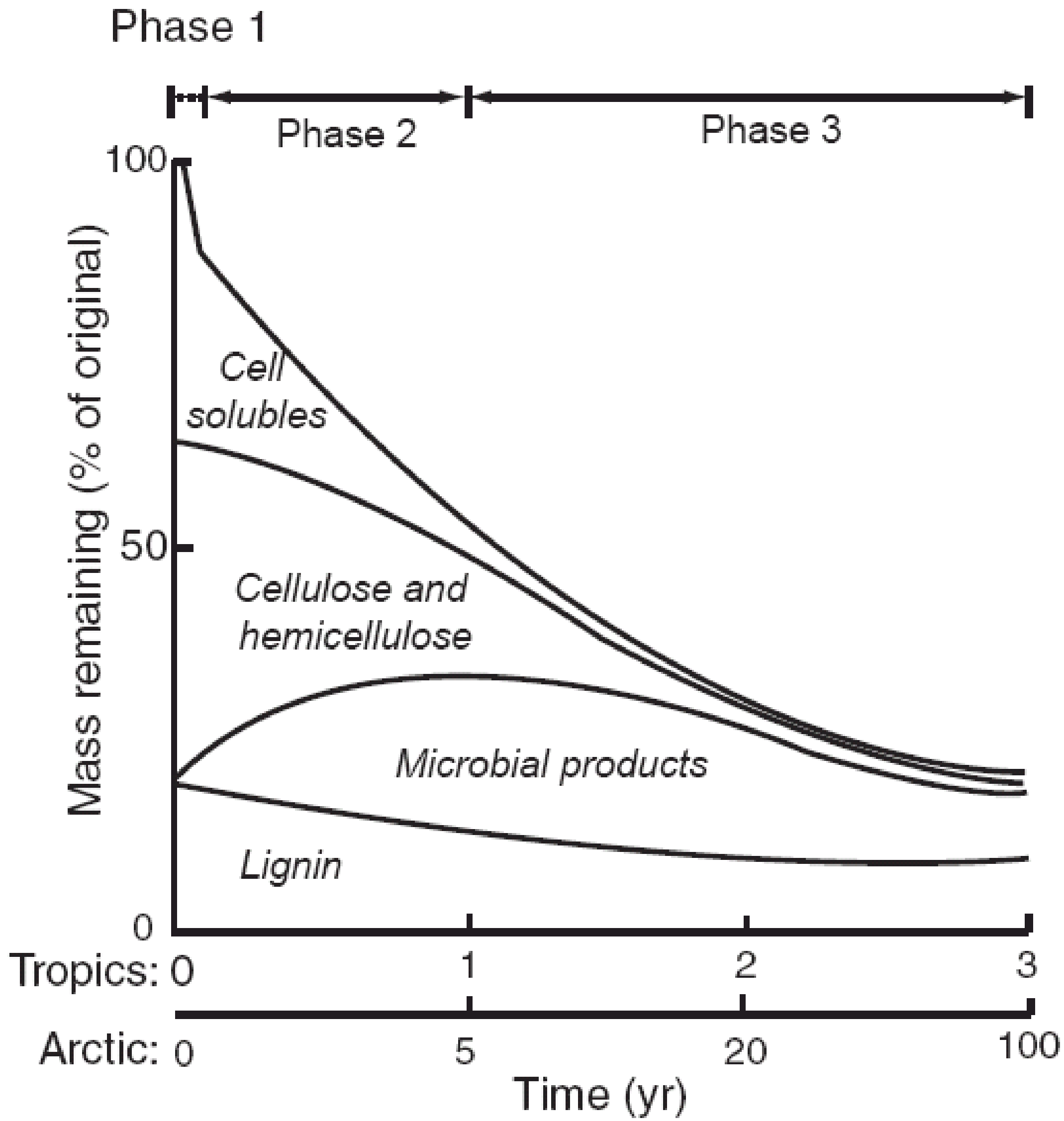
Elevated CO_2

From: Johnson et al. 2004

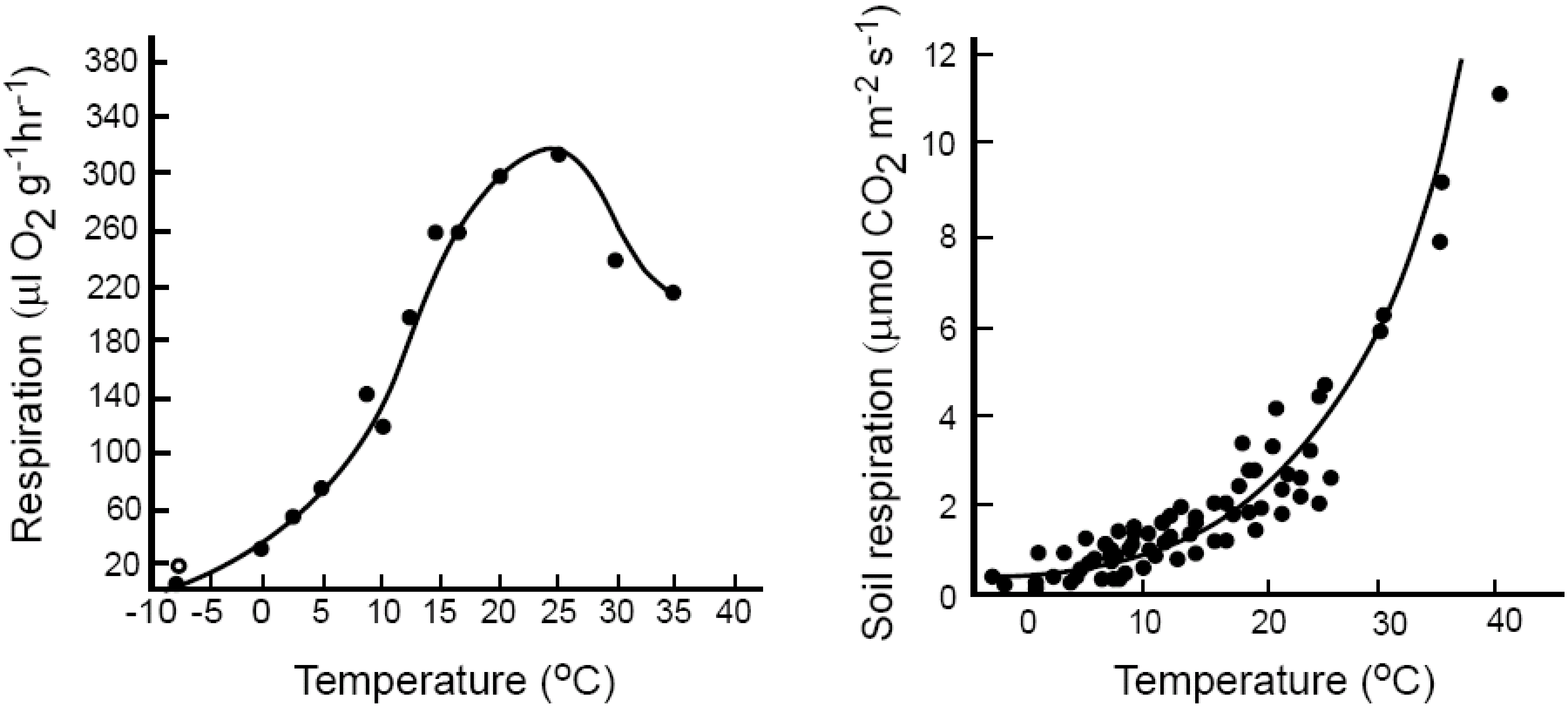
Unit: kg ha^{-1} or kg $^{-1}$ ha $^{-1}$ yr $^{-1}$

Nitrogen Cycling in a Sweetgum Plantation Near Oak Ridge National Lab.

Decomposition of Plant Litter

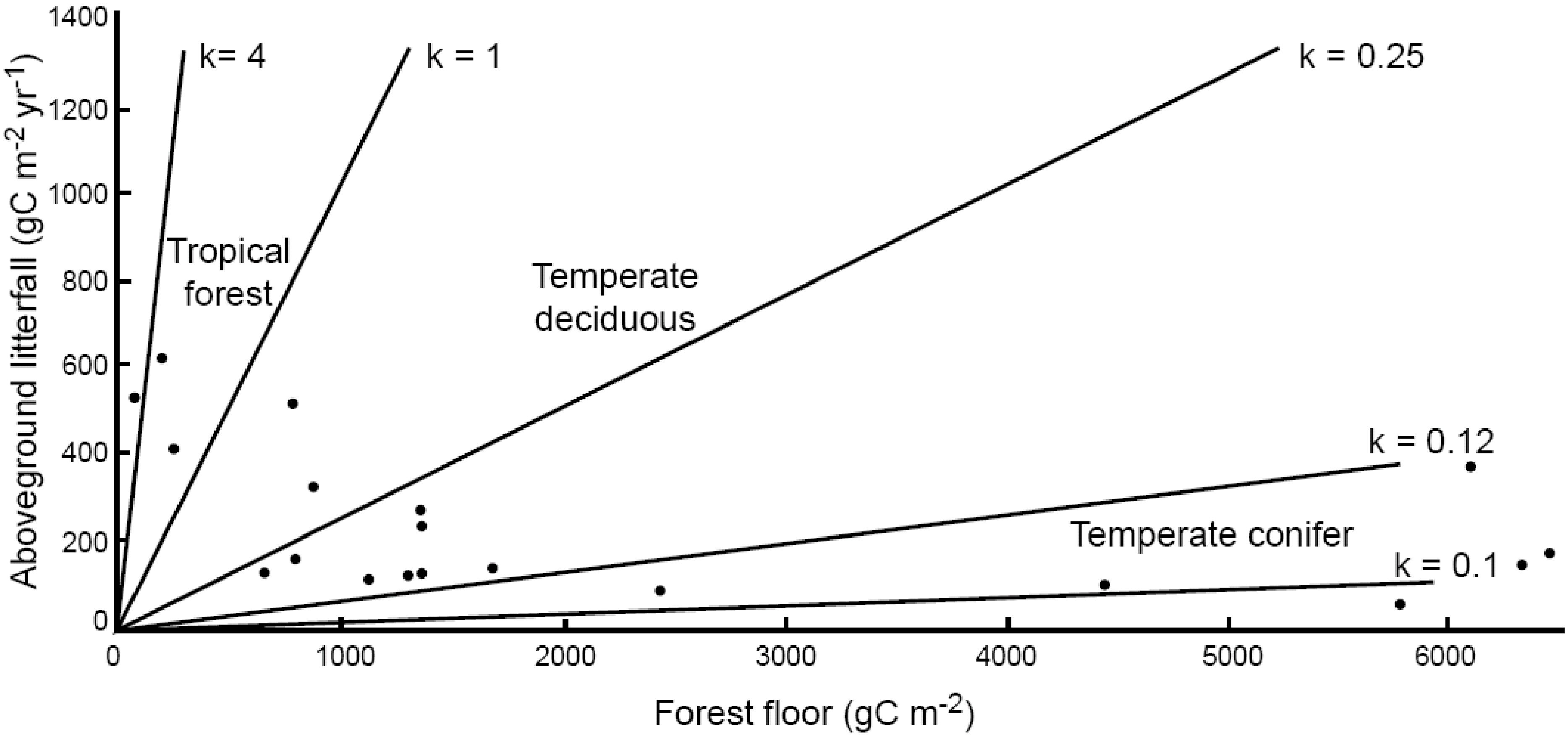


Representative time course of leaf-litter decomposition, showing the major chemical constituents (cell solubles, cellulose and hemicellulose, lignin, and microbial products), the three major phases of litter decomposition, and the time scales commonly found in warm (tropical) and cold (arctic) environments. (Chapin et al. 2002)



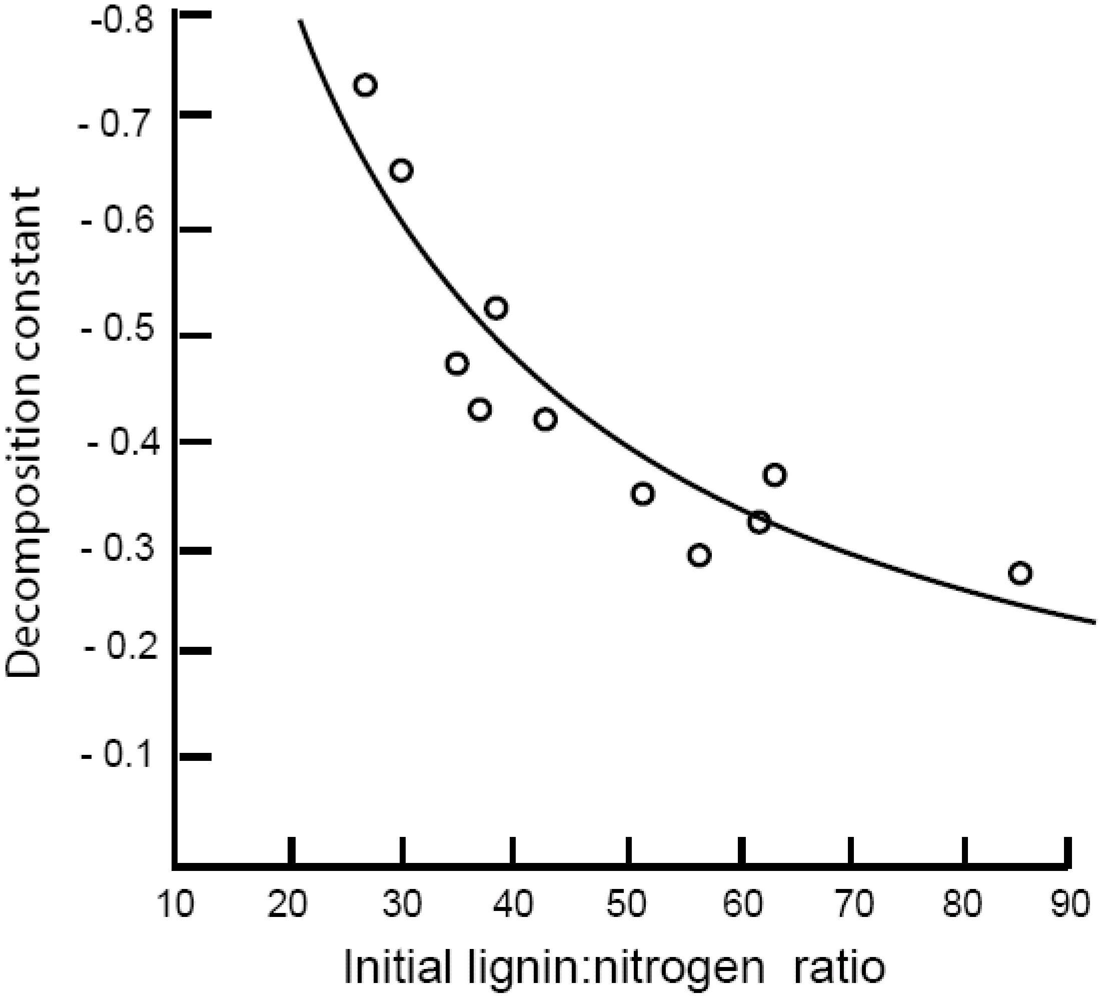
Relationship between temperature and soil respiration in (left) laboratory incubations of tundra soils (Flanagan and Veum 1974) and (right) field measurements of soil respiration in 15 studies, where data have been fitted to have the same respiration rate at 10°C (Lloyd and Taylor 1994).

The "k' is from this equation: $M_t = M_0 e^{-kt}$

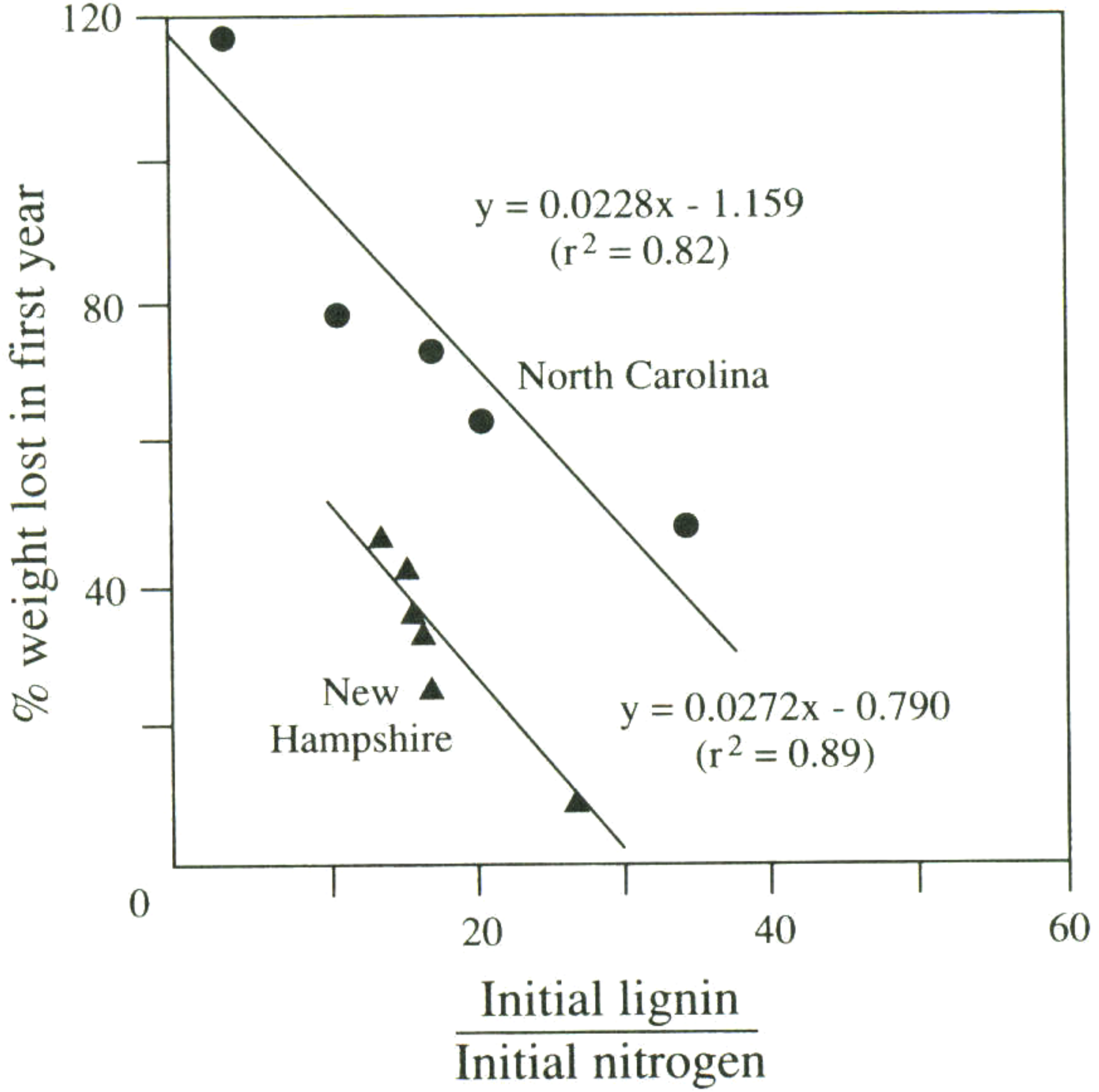


Forest-floor biomass and aboveground litter inputs for selected evergreen forests (Olsen 1963). Lines show the decomposition constants for the forest floor, calculated from these data.

Litter decomposition rate is negatively correlated to initial lignin:nitrogen ratio.

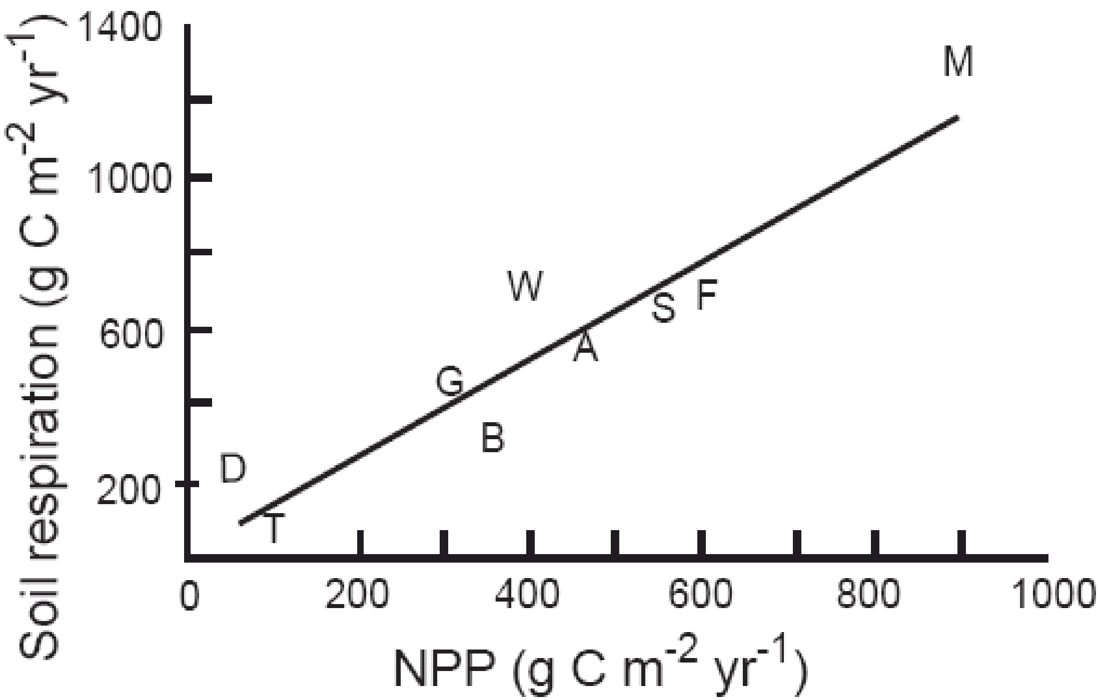


Relationship between the decomposition constant and the lignin:nitrogen ratio of litter (Melillo et al. 1982).

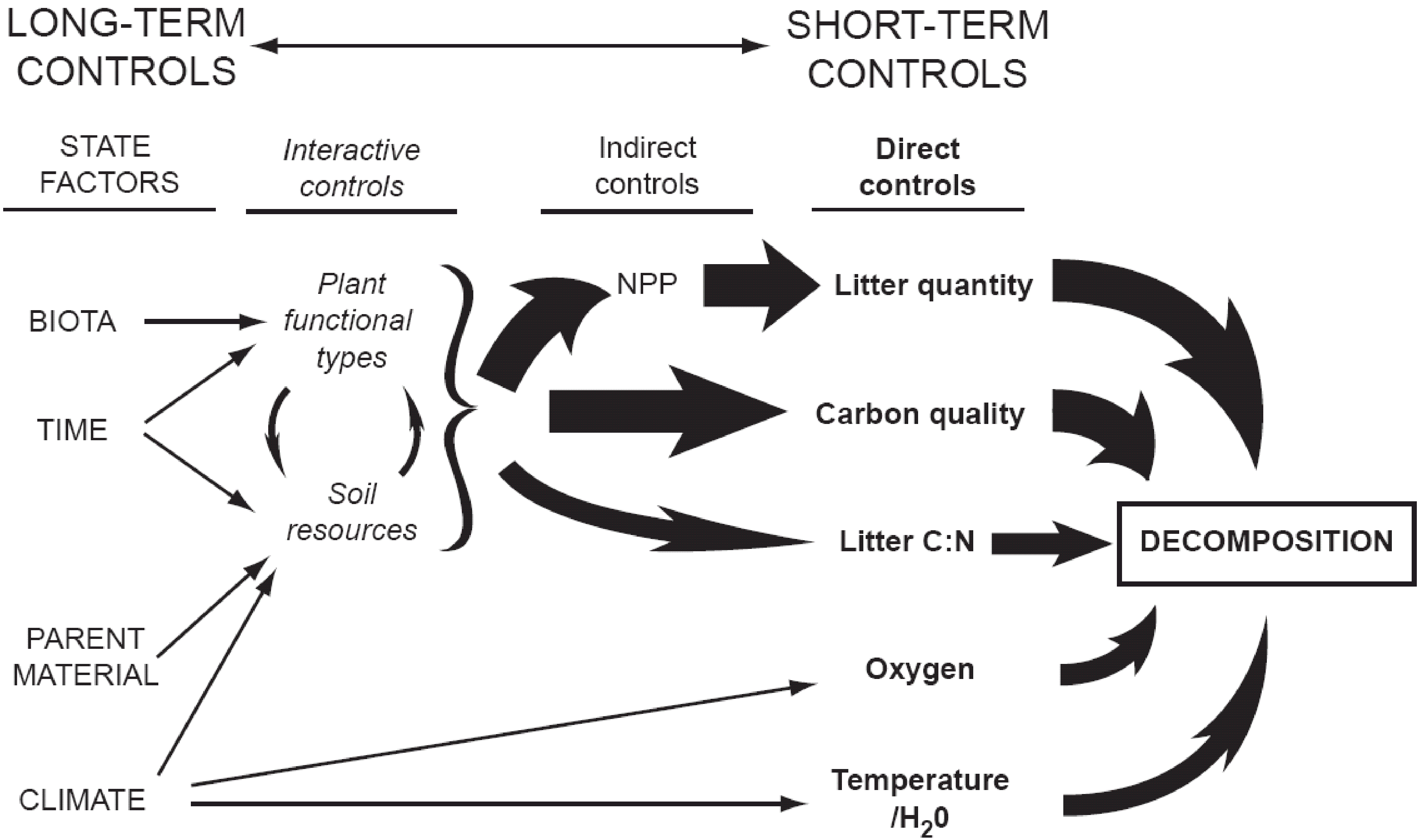


Also see **Figure 6.11** in Schlesinger and Bernhardt

Soil respiration or the rate of CO_2 release is often used as a measure of soil organic matter decomposition.



Relationship between mean annual soil respiration rate and mean annual NPP for Earth's major biomes (Raich and Schlesinger 1992). Ecosystem types are agricultural lands (A), boreal forest and woodland (B), desert scrub (D), temperate forest (F), temperate grassland (G), moist tropical forest (M), tropical savanna and dry forest (S), tundra (T), and mediterranean woodland and heath (W).



The major factors governing decomposition at the ecosystem scale. These controls range from proximate controls that determine the seasonal variations in decomposition to the state factors and interactive controls that are the ultimate causes of ecosystem differences in decomposition. Thickness of the arrows indicates the strength of the effect. The factors that account for most of the variation in decomposition among ecosystems are the quantity and carbon quality of litter inputs, which are ultimately determined by the interacting effects of soil resources, climate, vegetation, and disturbance regime. (Chapin et al. 2002)

Nitrogen transformation:
(conversions among different forms of nitrogen)

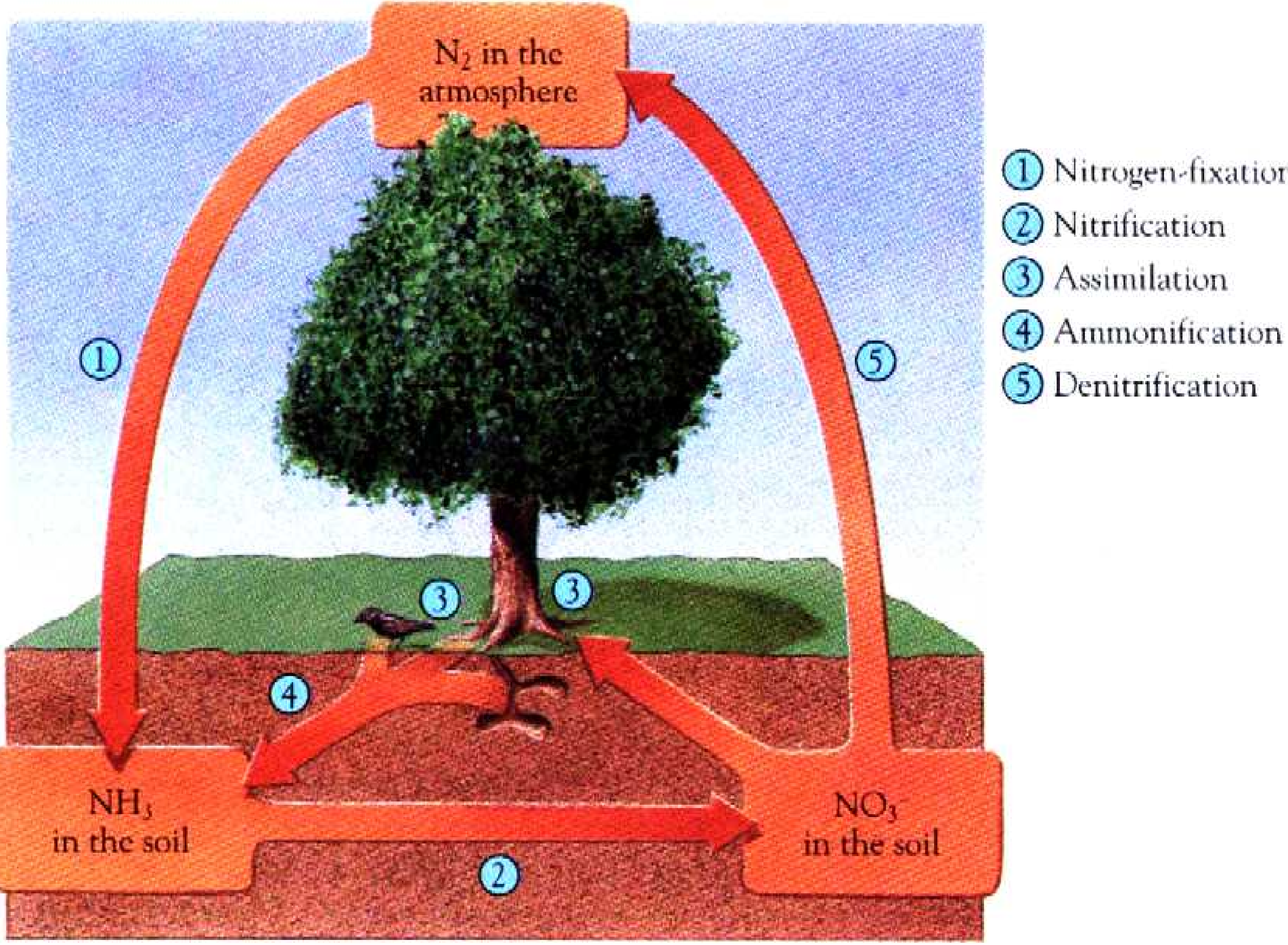
Nitrogen fixation: N_2 ----> R-NH_2 (or NH_3,NH_4^+, NO_x)

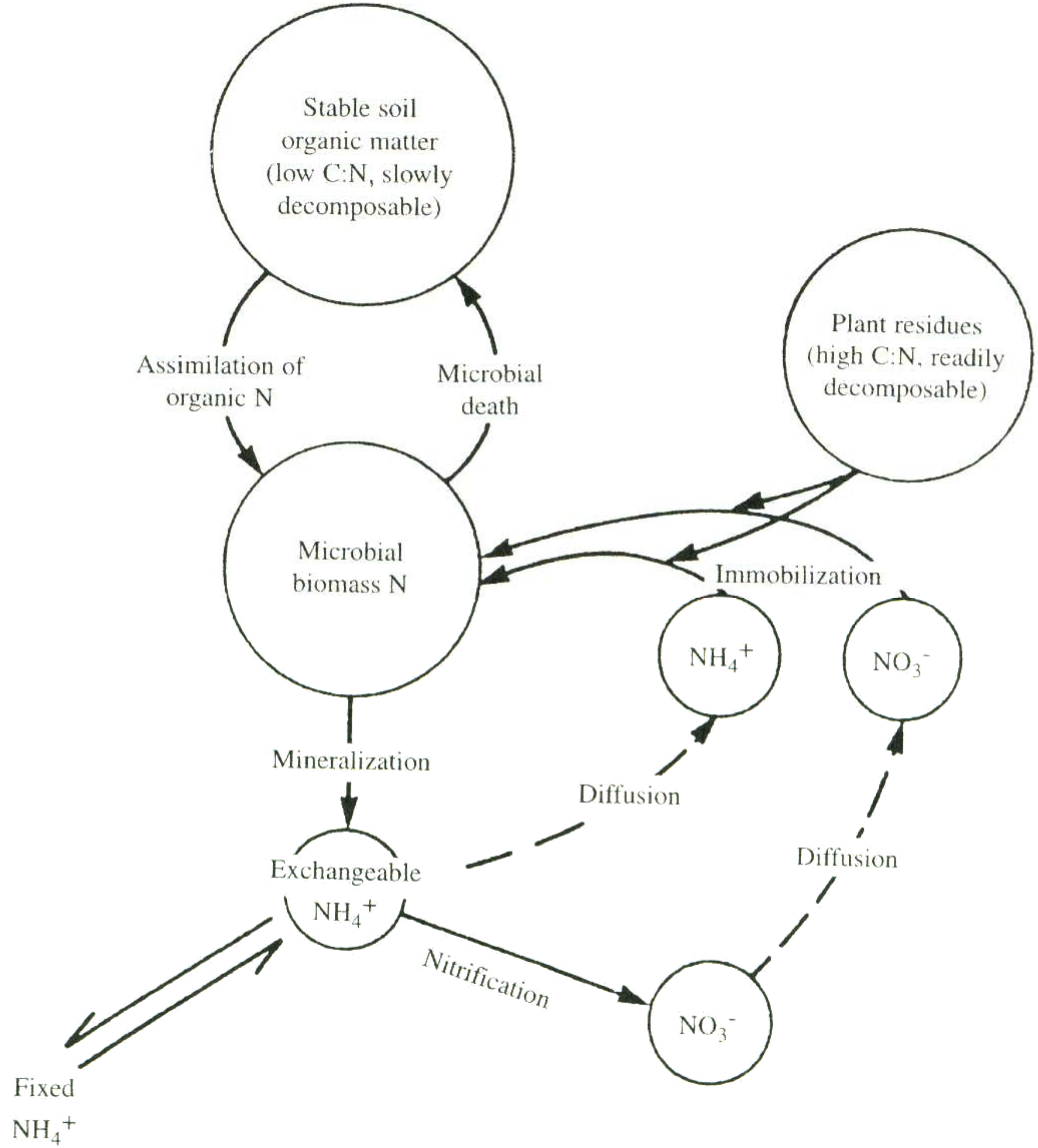
Ammonification: R-NH_2 ----> NH_3 (NH_4^+)

Assimilation: NO_3 (NH_4^+) ----> R-NH_2

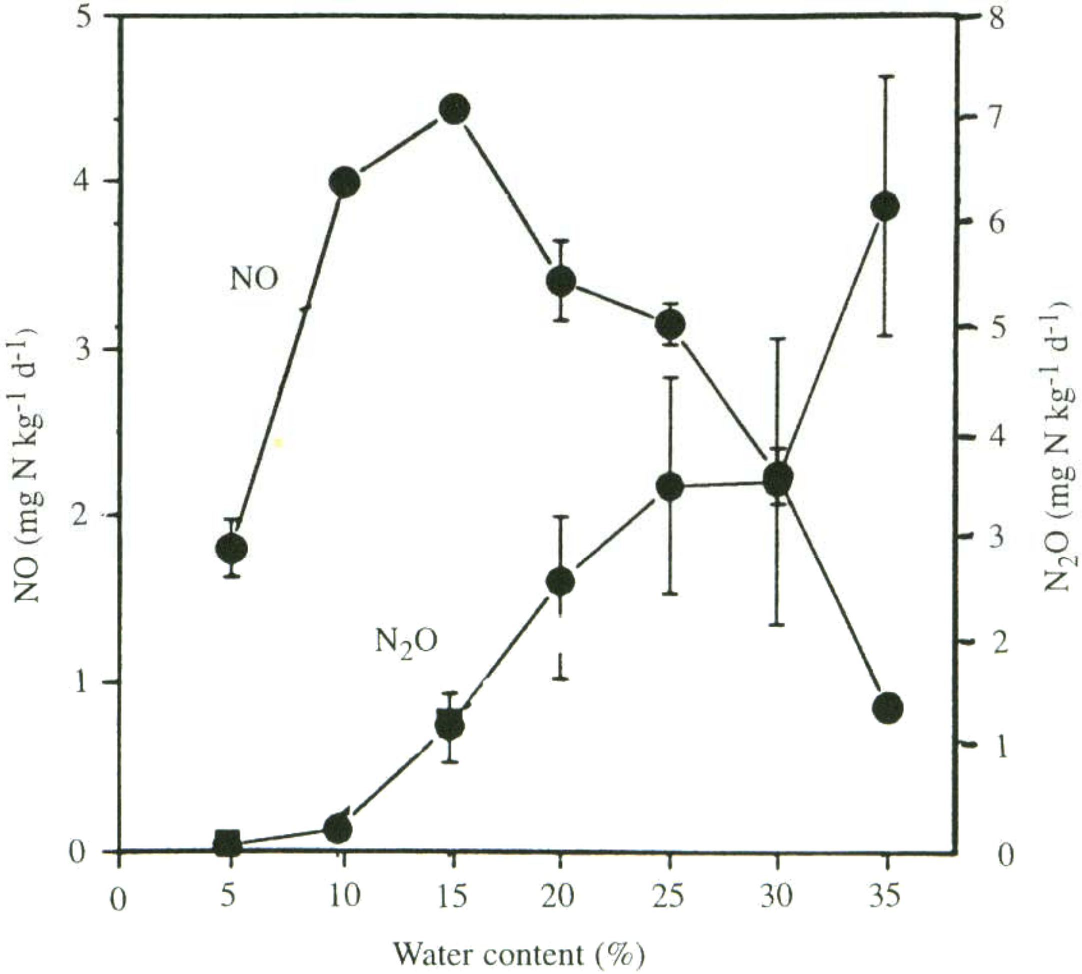
Nitrification: NH_4^+ ----> NO_2^- ---->NO_3^-

Denitrification: NO_3^- ----> NO_2^- ----> (NO_x) ----> N_2O----> N_2

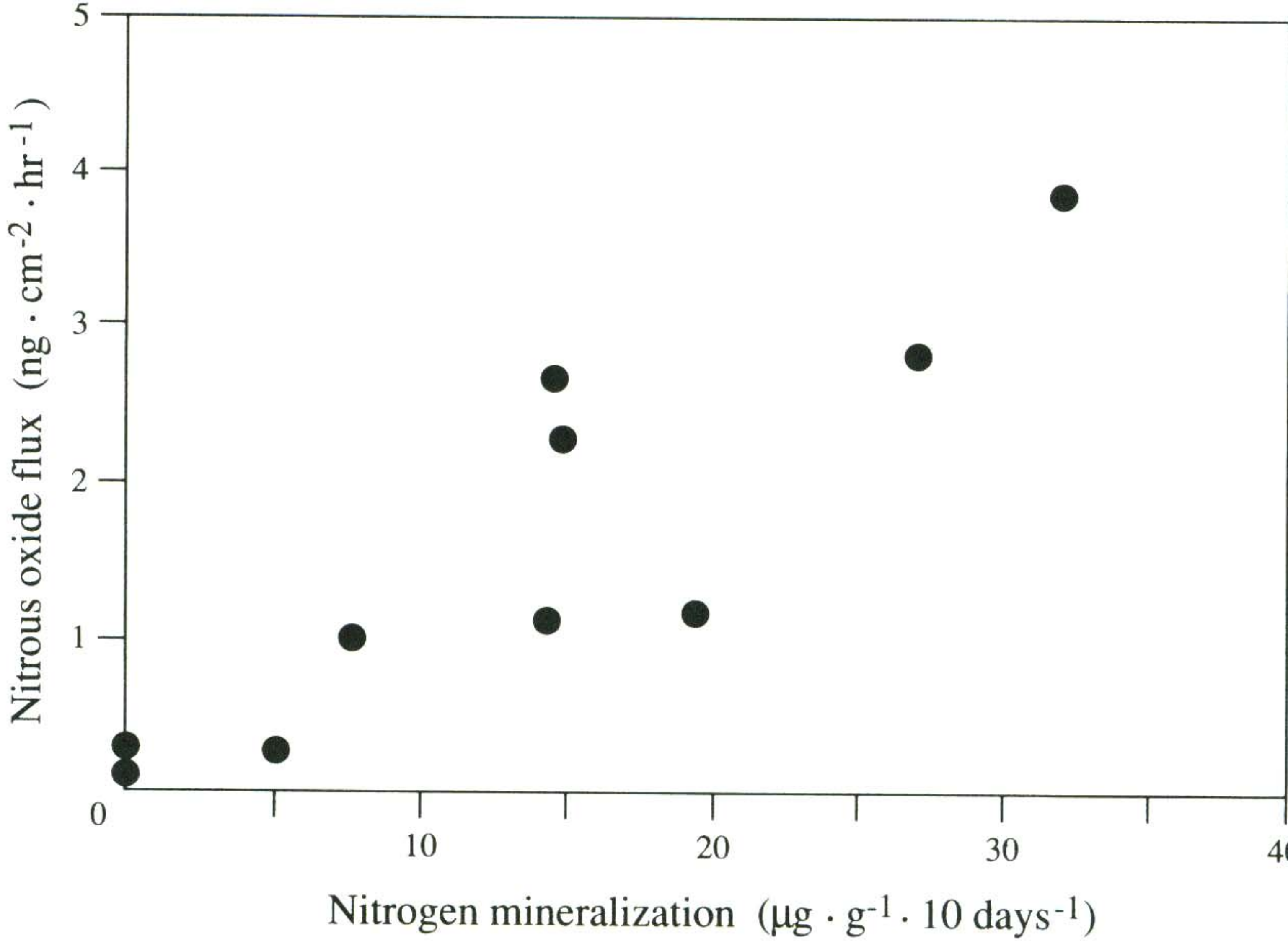

N_2 in the atmosphere
1
5
3
3
4
NH_3 in the soil
NO_3^- in the soil
2
1 Nitrogen-fixation
2 Nitrification
3 Assimilation
4 Ammonification
5 Denitrification



A conceptual model of the soil nitrogen cycle. From Drury et al. (1991).



Flux of NO and N_2O from denitrification in a clay-loam soil as a function of soil water content under anoxic conditions. Modified from Drury et al. (1992).



Relationship between nitrogen mineralization measured in laboratory incubations and the loss of N_2O from 10 tropical forest soils. From Matson and Vitousek (1987).

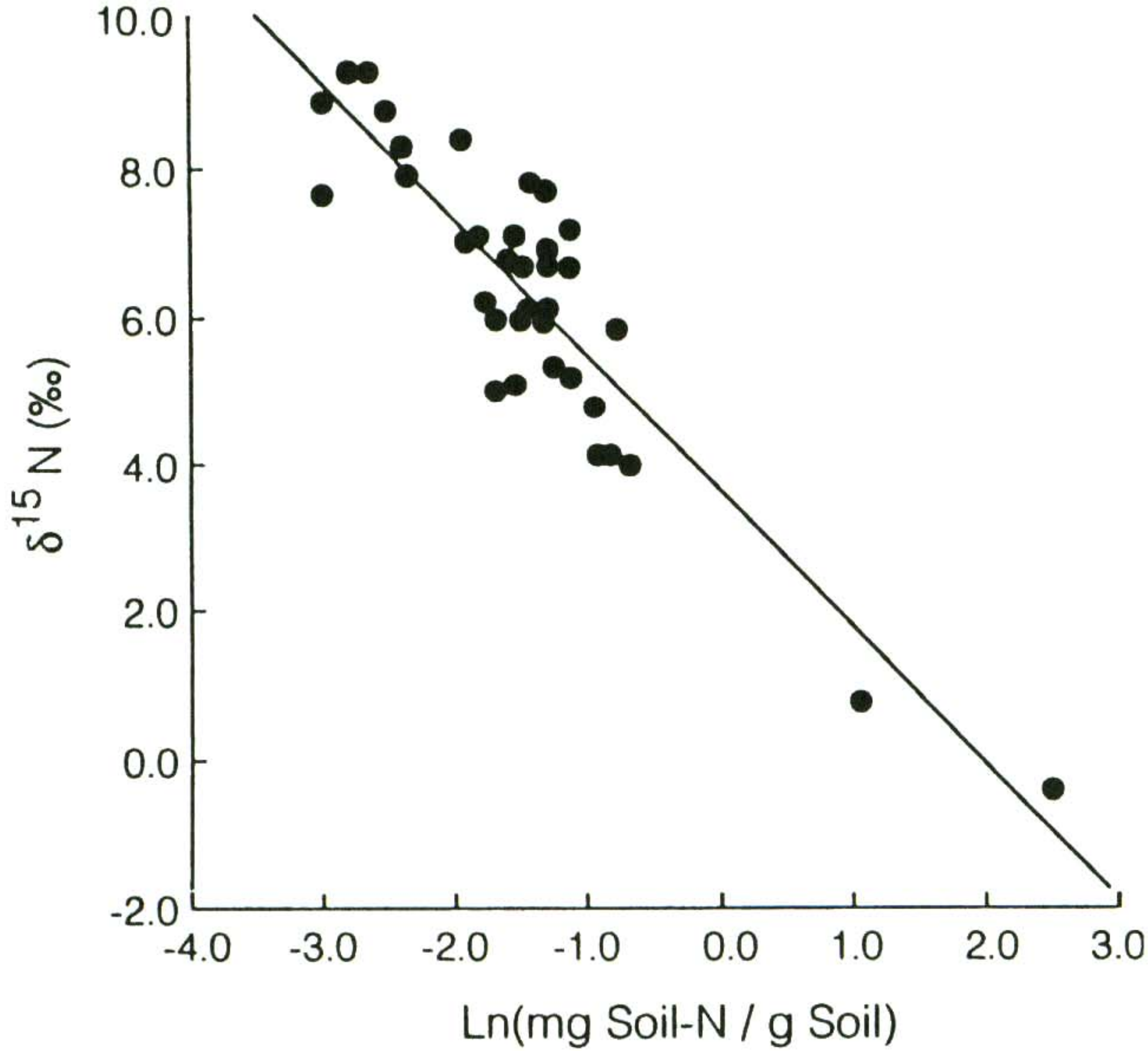


Figure 6.18 $\delta^{15}N$ of soil organic matter as a function of the total N content in soils of juniper woodlands of Utah (USA). From Evans and Ehleringer (1993).

Mean Residence Time (yr) for Organic Matter and Nutrients in the Surface Litter of Forest and Woodland Ecosystems[a]

Region	Mean residence time (yr)					
	Organic matter	N	P	K	Ca	Mg
Boreal forest	353	230	324	94	149	455
Temperate forest						
Coniferous	17	17.9	15.3	2.2	5.9	12.9
Deciduous	4	5.5	5.8	1.3	3.0	3.4
Mediterranean	3.8	4.2	3.6	1.4	5.0	2.8
Tropical rainforest	0.4	2.0	1.6	0.7	1.5	1.1

[a] Values are calculated by dividing the forest floor mass by the mean annual litterfall. Boreal and temperate values are from Cole and Rapp (1981), tropical values are from Edwards and Grubb (1982) and Edwards (1977, 1982), and Mediterranean values are from Gray and Schlesinger (1981).

Fixation and Mobilization of Phosphorus

Phosphorus is easily fixed by chemical reactions with Ca^{2+}, Mg^{2+}, Fe^{2+} ,Al^{3+} etc. Phosphorus fixation is pH-dependent, and is the process that removes P from active pools. Both too high and too low of pH values can resulted in P fixation, for example:

$$2PO_4^{3+} + 3Ca^{2+} \text{ (or } Mg^{2+}, Fe^{2+} \text{ etc) --> } Ca_3(PO_4)_2$$

This is solely a chemical process.

Although the total P content of soils is large, in most soils only a small fraction is available to biota, primarily because of chemical fixation.

Microbes play a crucial role in the transforming process from organic P to inorganic P, and in mobilizing chemically-fixed P (mycorrhizal roots and other rhizosphere activities).

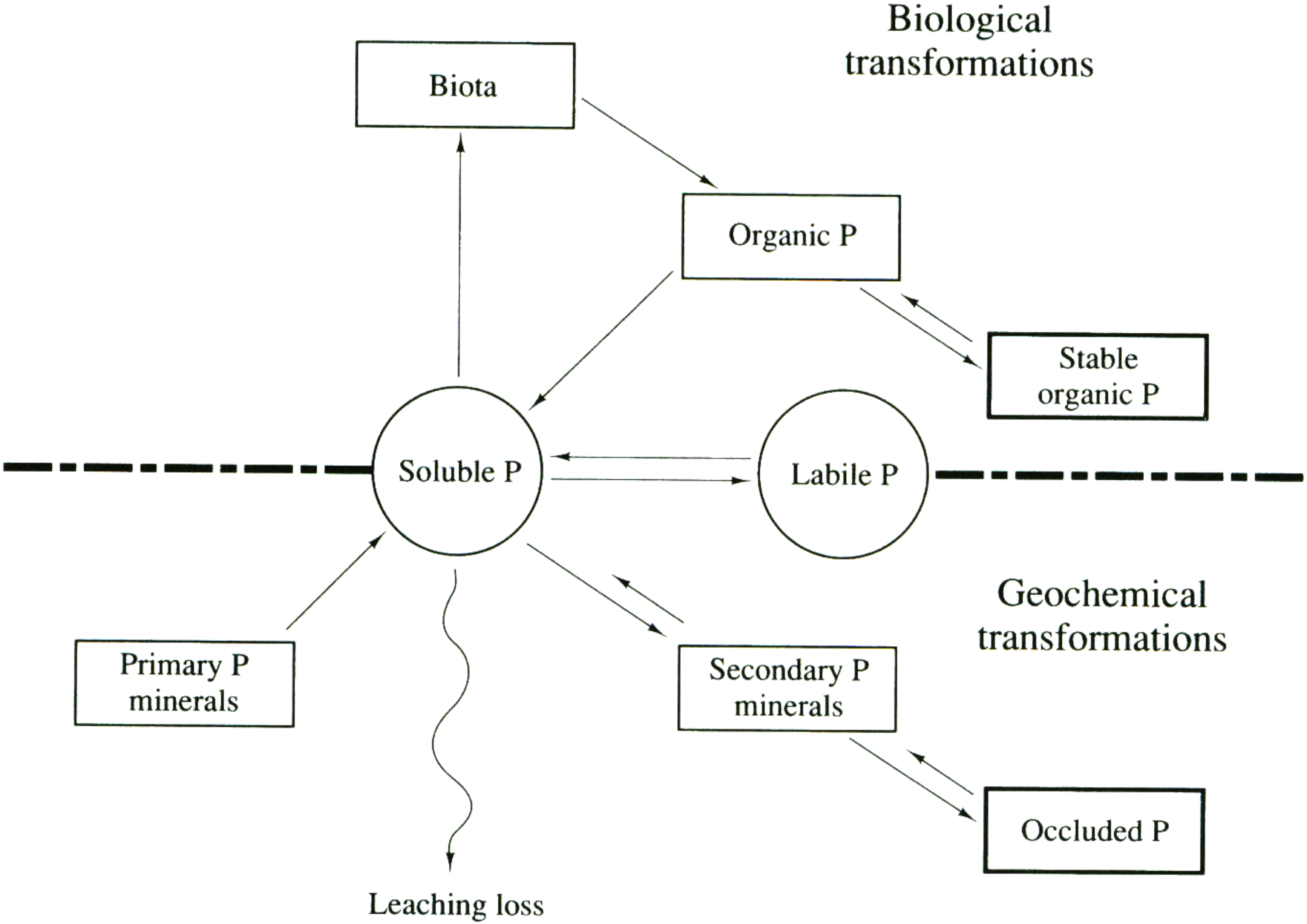


Figure 6.19 Phosphorus transformations in the soil. From Smeck (1985).

Sulfur Transformation in Soils

Oxidative transformations:

$H_2S + O_2$ --> S^0 + O_2 ---> H_2SO_4

Sulfur oxidation produces acids.

Reductive sulfur transformations:

$SO_4^{=}$ ---> $SO_3^{=}$ ---> S^0 ---> H_2S

Sulfate reduction occurs at wide range of pH values, pressure, temperature and salinity. Sulfate reduction is inhibited by oxygen, nitrate, ferric ions. H_2S is very toxic to aerobes and plant roots. Assimilatory sulfate reduction happen in many organisms.

Desulfuration (analogous to ammonification):

R-SH+ H_2O --→RH + H_2S

Fires and nutrient cycling on land

Fires were a natural part of the environment before human intervention.

While 10-50% of the N and S in plant canopy and litter can be lost from one fire event, ash and heat from fires can increase soil nutrient availability.

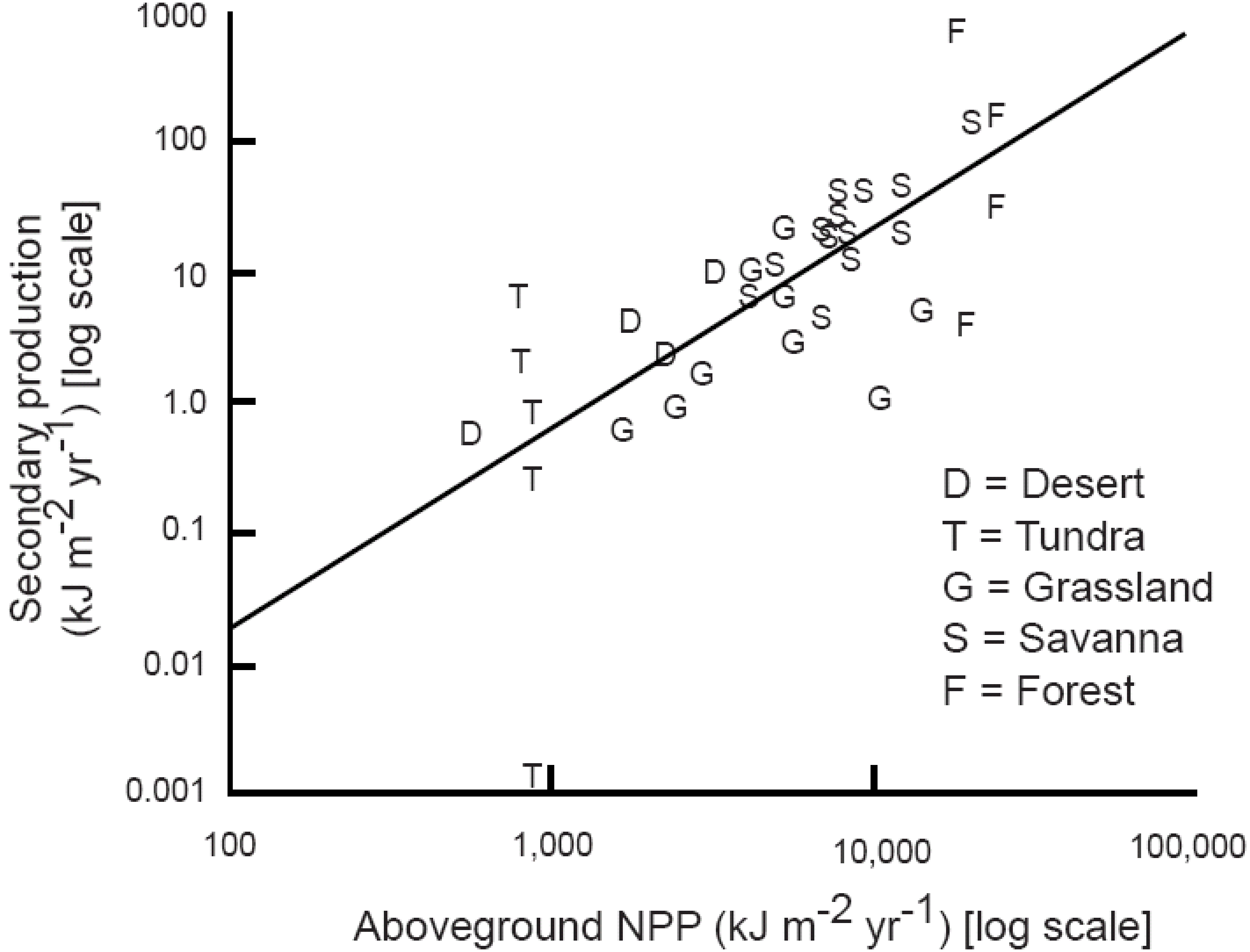
Fires can also cause large pulses of nutrient loss due to erosion from runoffs.

There are ecosystems that adapted to frequent fires, e.g., most grasslands, and semi-arid shrub lands.

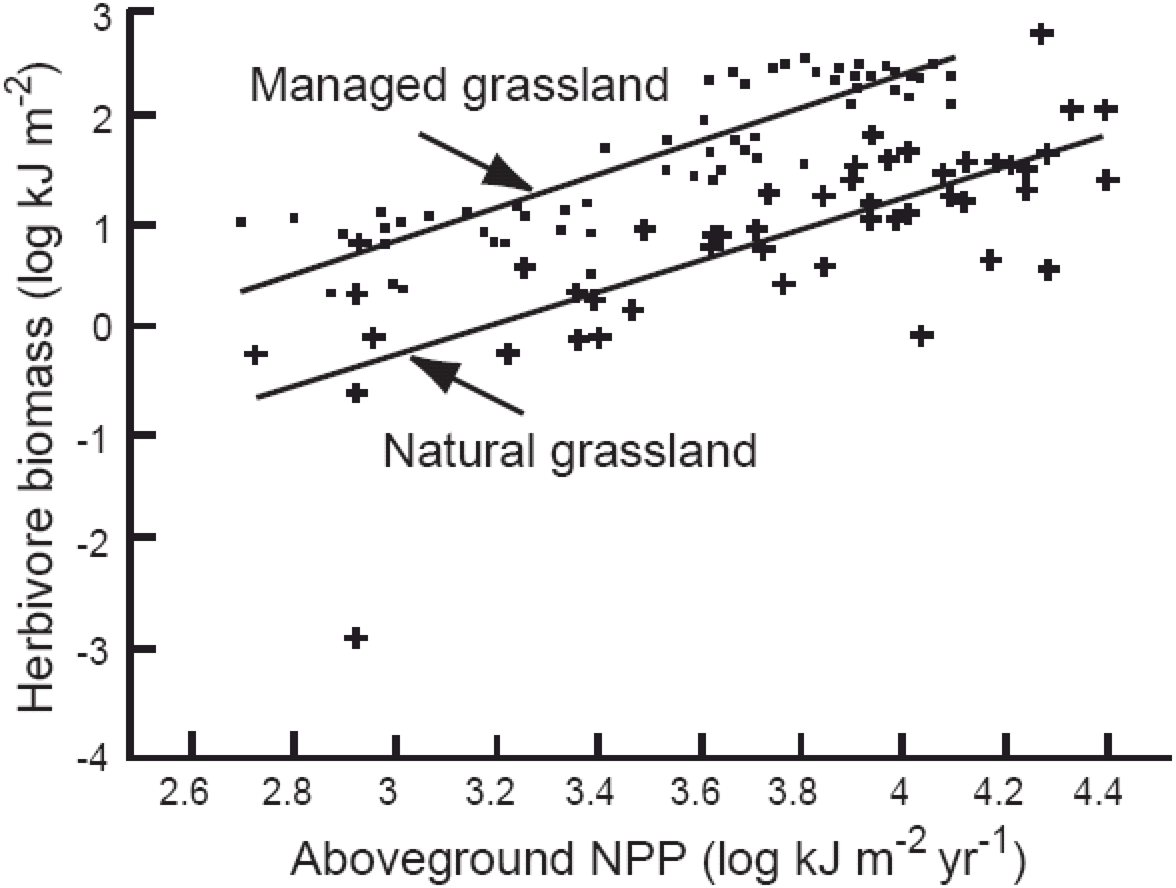
Fires and nutrient cycling on land

Food Web Interactions and Nutrient Cycling

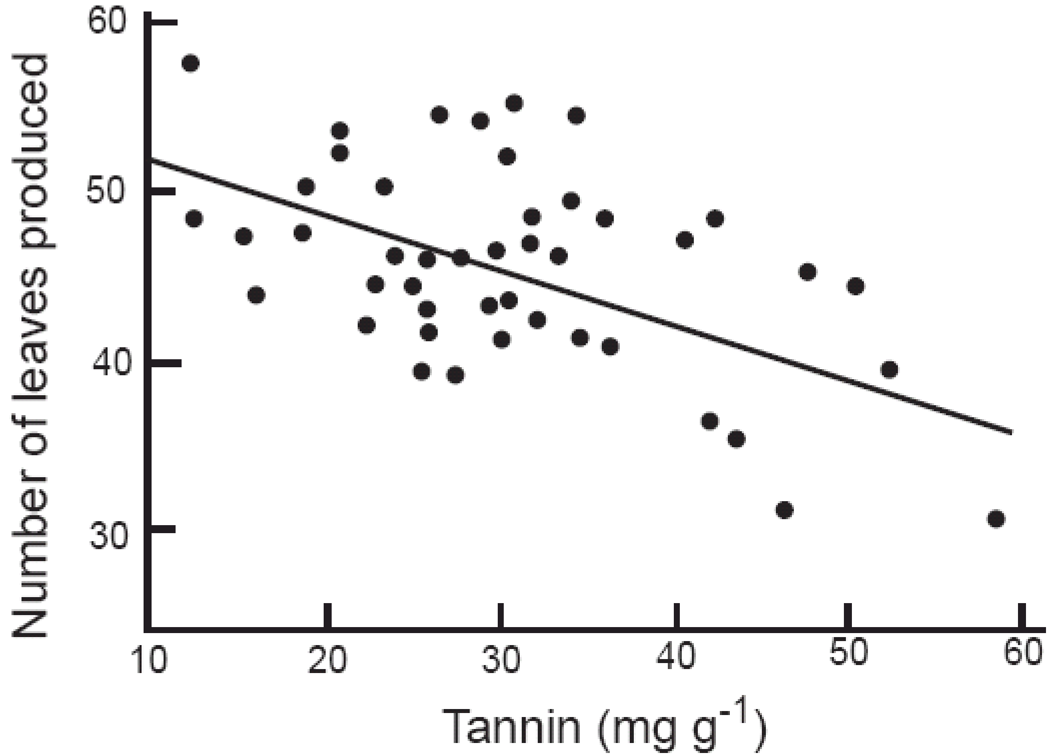
Statement: Biotic systems are regulated directly or indirectly by Food web interactions.



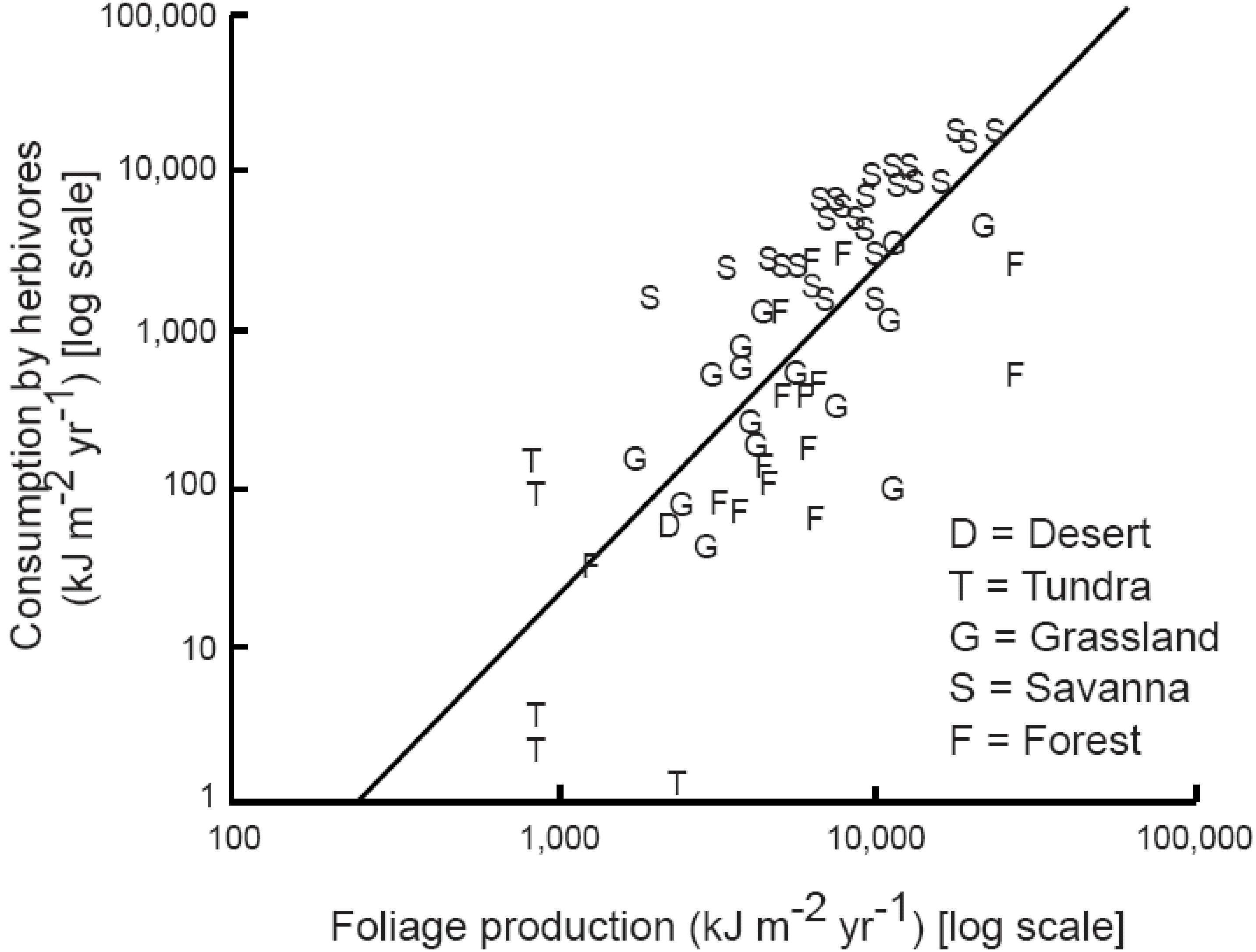
Log-log relationship between aboveground net primary production (NPP) and herbivore production (McNaughton et al. 1989). One gram of ash-free biomass is equivalent to 20 kJ of energy. Production of aboveground herbivores correlates with aboveground NPP across a wide range of ecosystems.



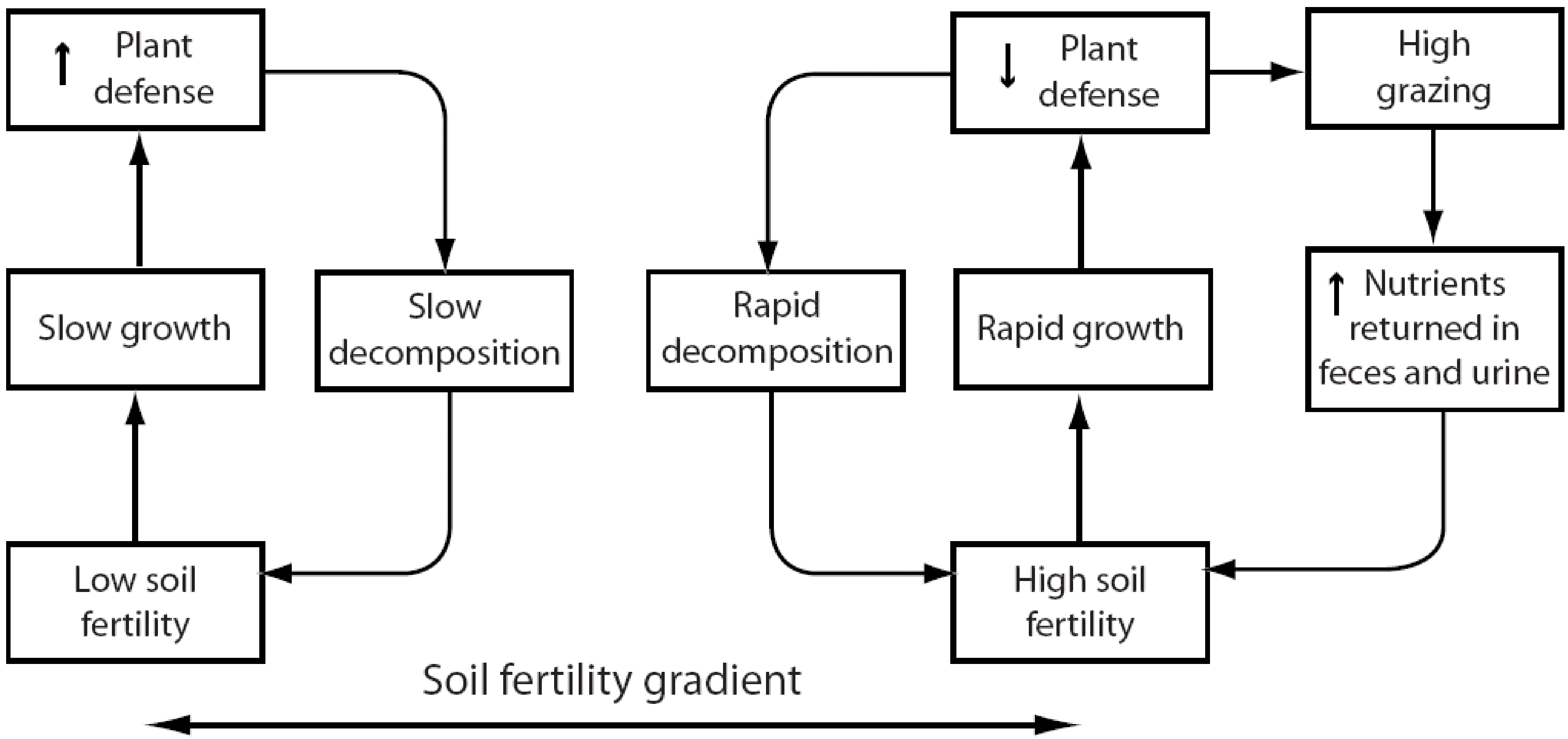
Log-log relationship between mammalian herbivore biomass and aboveground plant production in natural and managed grazing systems of South America (Osterheld et al. 1992). Herbivore biomass increased with increasing NPP. Animal biomass on the managed grassland was 10-fold greater than on the natural grassland at a given level of plant production, because managers control predation, parasitism, and disease and provide supplemental drinking water and minerals in managed systems. This difference in herbivore biomass between managed and unmanaged systems indicates that NPP is not the only constraint on animal production.



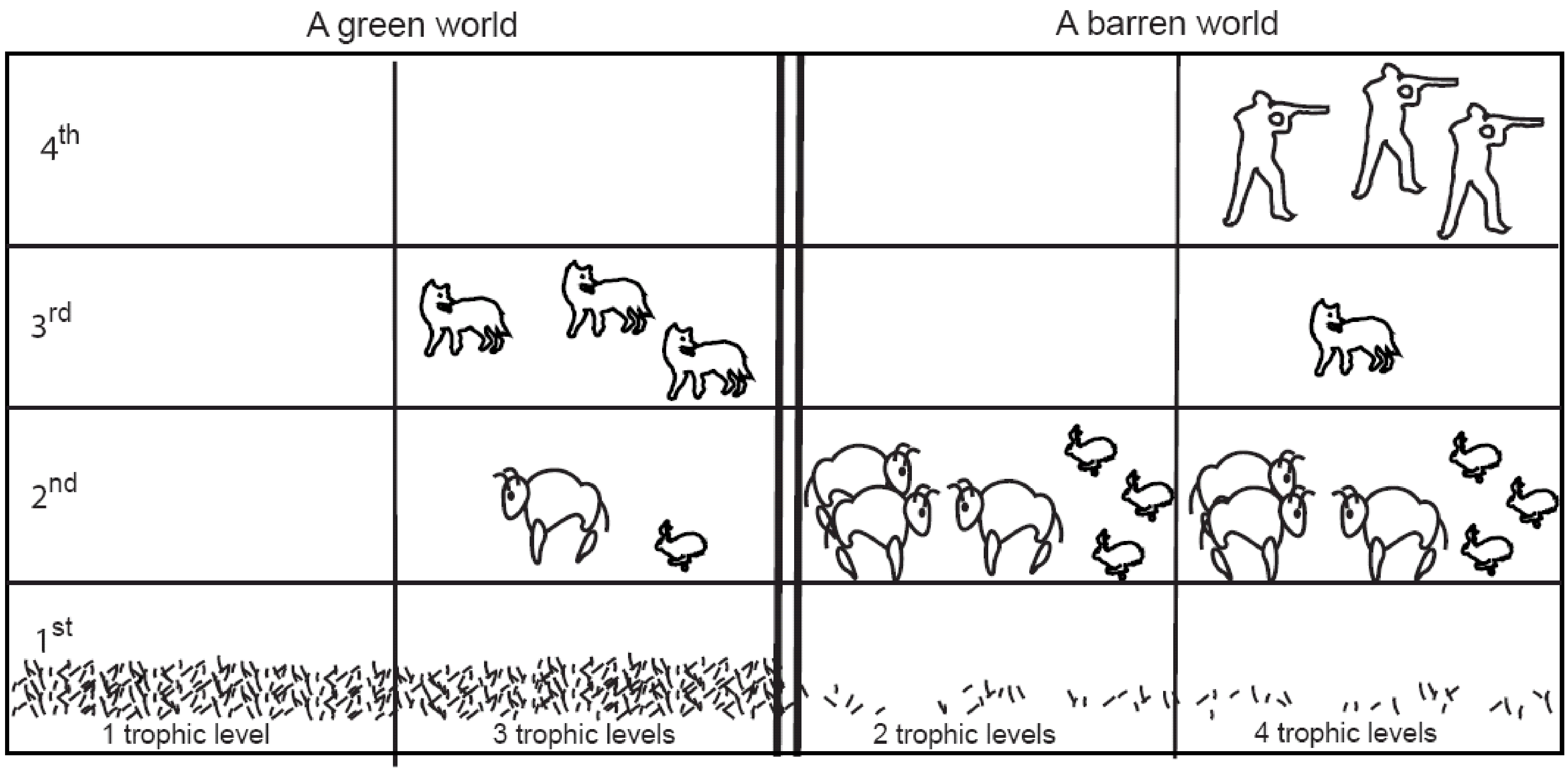
Relationship between rate of leaf production (an index of growth rate) and leaf tannin concentration in the tropical tree *Cecropia peltata* (Coley 1986). The graph shows a negative relationship between investment in defense and growth rate.

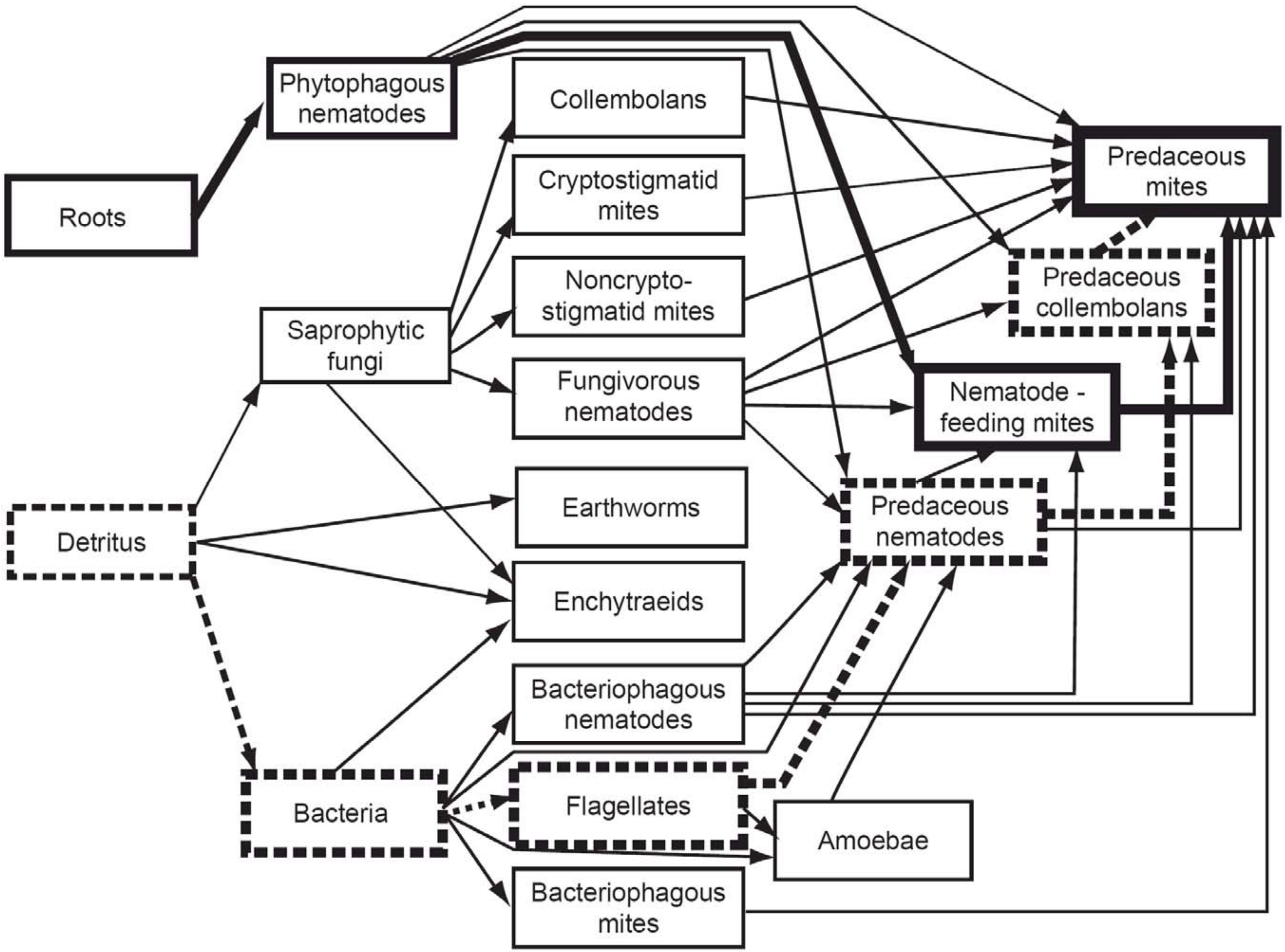


Log-log relationship between foliage production and consumption by herbivores (McNaughton et al. 1989). One gram of ash-free biomass is equivalent to 20 kJ of energy. Consumption by herbivores is more closely related to foliage production that to total aboveground NPP.



Feedbacks by which grazing and plant defense magnify differences among sites in soil fertility (Chapin 1991). In infertile soils herbivory selects for plant defenses, which reduce litter quality, decomposition, and nutrient supply rate. In fertile soils, herbivory speeds the return of available nutrients to the soil.


A green world
A barren world
4th
3rd
2nd
1st
1 trophic level
3 trophic levels
2 trophic levels
4 trophic levels


Roots
Phytophagous nematodes
Collembolans
Cryptostigmatid mites
Noncrypto-stigmatid mites
Saprophytic fungi
Fungivorous nematodes
Detritus
Earthworms
Enchytraeids
Bacteriophagous nematodes
Bacteria
Flagellates
Amoebae
Bacteriophagous mites
Predaceous mites
Predaceous collembolans
Nematode - feeding mites
Predaceous nematodes

Scaling up temporally and spatially

Statement: Nutrient cycling occurs at various temporal and spatial scales with patterns and mechanisms imbedded within scales and between scales.

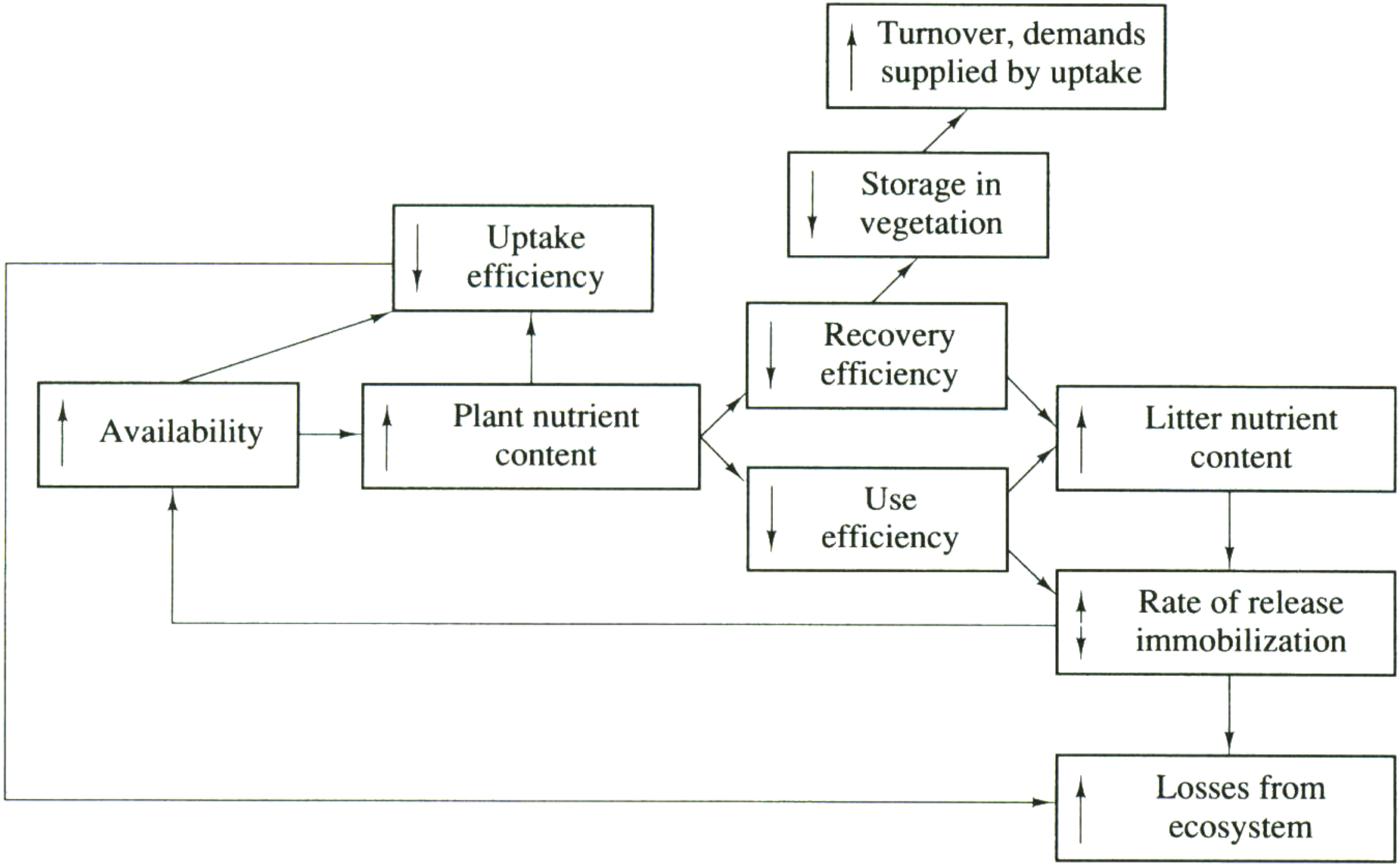


Figure 6.22 Changes in internal nutrient cycling that are expected with changes in nutrient availability. From Shaver and Melillo (1984).

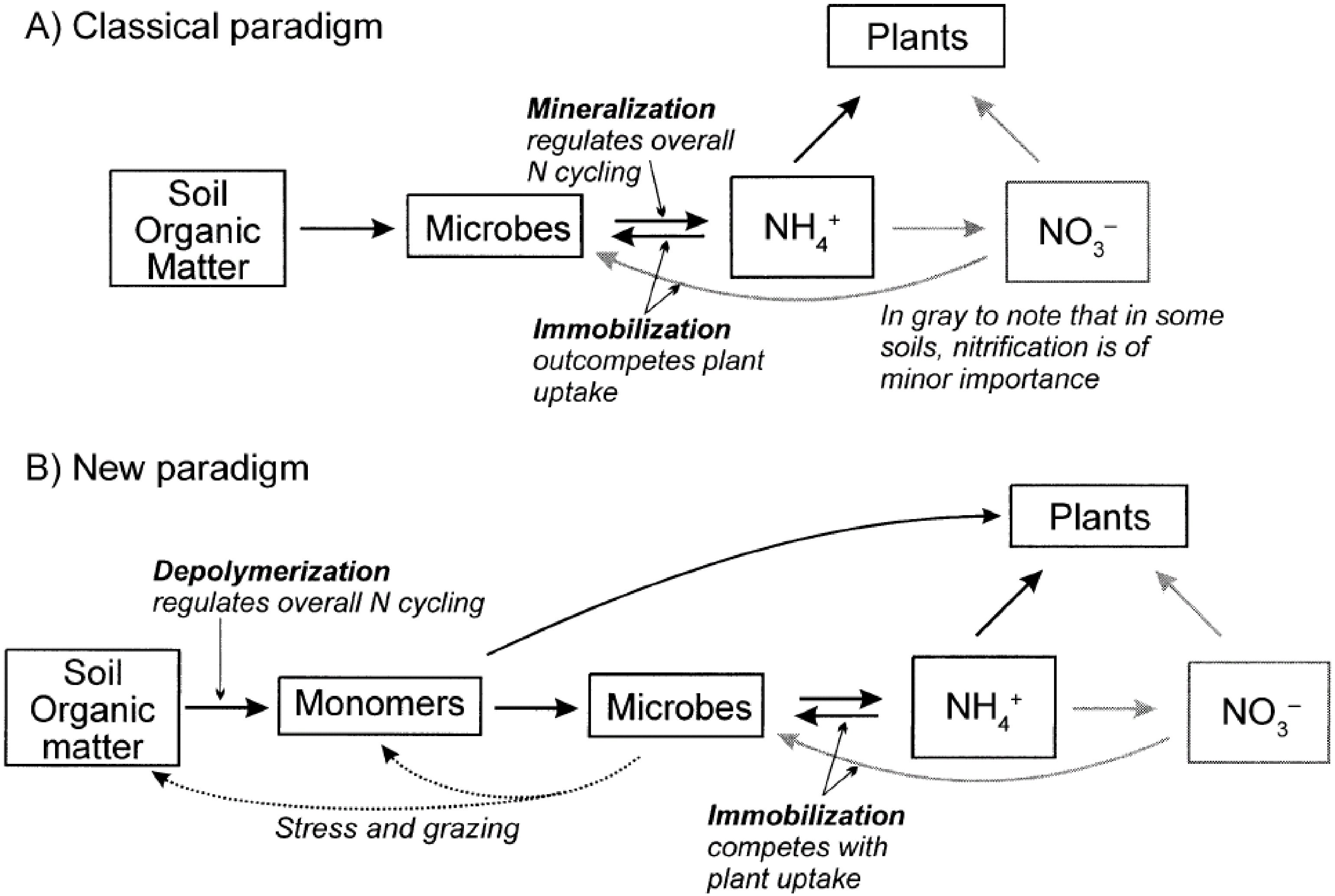
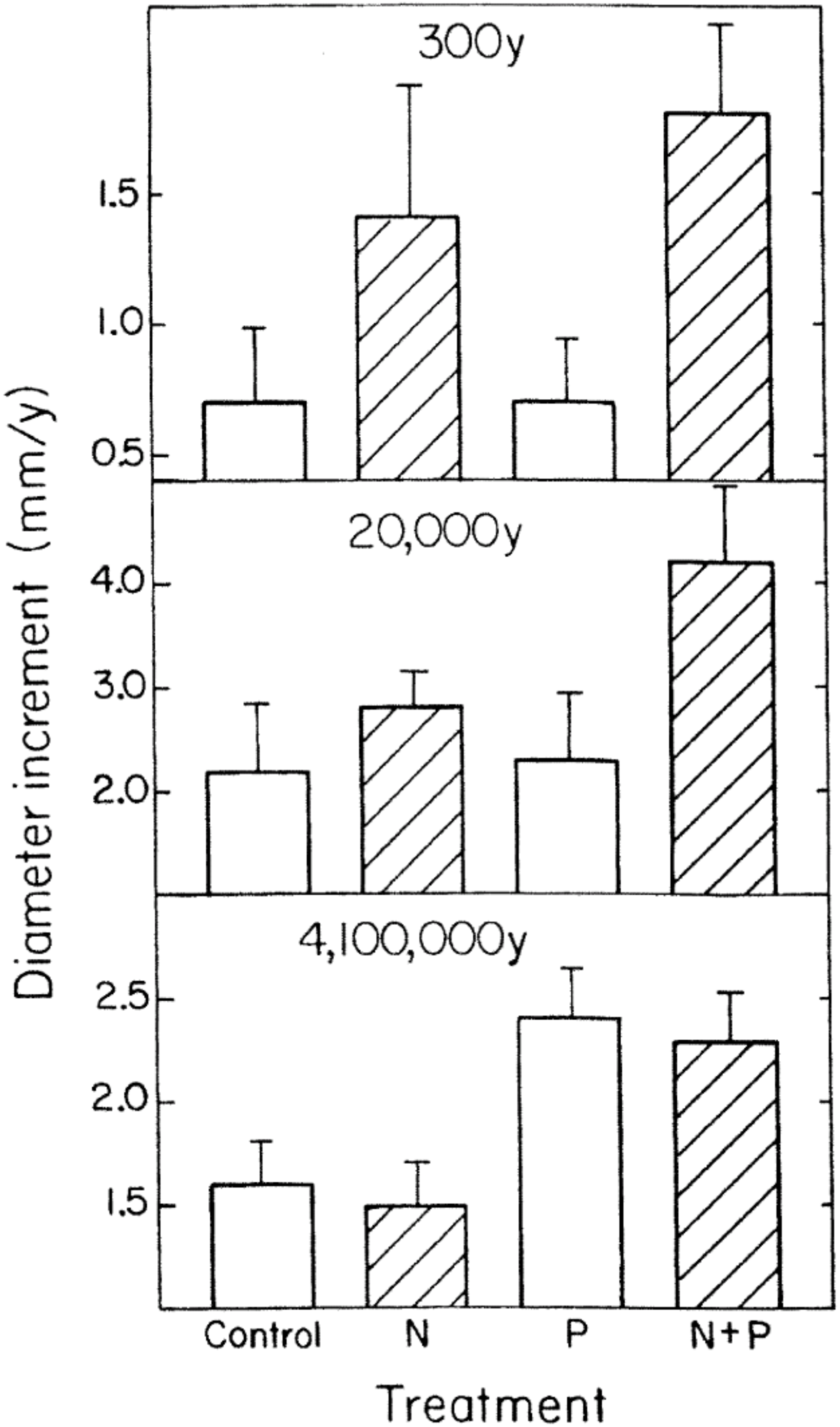


FIG. 1. The changing paradigm of the soil N cycle. (A) The dominant paradigm of N cycling up through the middle 1990s. (B) The paradigm as it developed in the late 1990s.



Vitousek & Farrington 1997