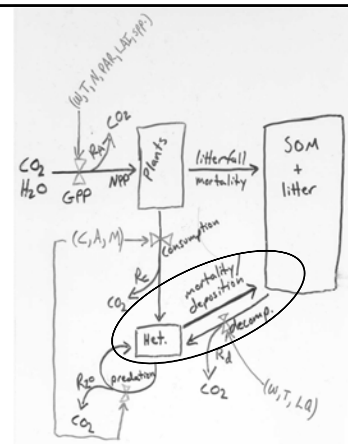
Terrestrial Decomposition (Ch. 7)

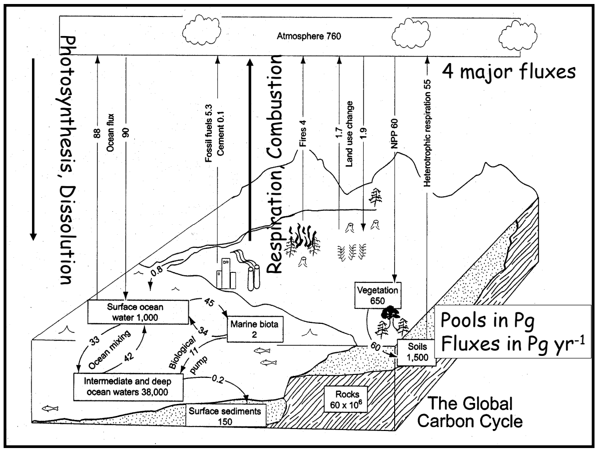
H.D. Thoreau - "Shall I not have intelligence with the earth? Am I not partly leaves and vegetable mould myself?"

I. What is it?
   A. Overview
   B. Stages
II. Who does it?
   A. Bacteria & Fungi: chemical breakdown
   B. Microfauna: nutrient regeneration
   C. Mesofauna: fragmentation
   D. Macrofauna: fragmentation, soil modification
III. Temporal patterns
   A. Exponential decay
   B. Phases of decomposition
IV. Controls on decomp (Phase 2)
   A. Physical Environment: temp, moisture, soils, disturbance
   B. Substrate Quality
   C. Microbial community
   D. Humus formation
V. Decomposition at the ecosystem scale

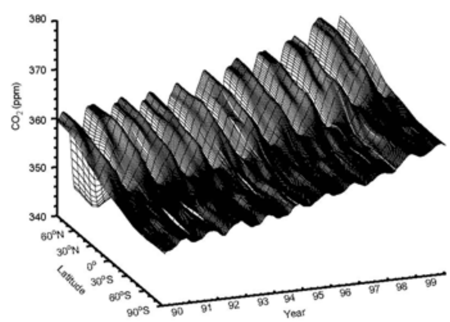
Powerpoint modified from Harte & Hungate (http://www2.for.nau.edu/courses/hart/for479/notes.htm) and Chapin (http://www.faculty.uaf.edu/fffsc/)

C-cycle: the role of decomposition





Atmospheric evidence of large carbon exchanges by the biosphere



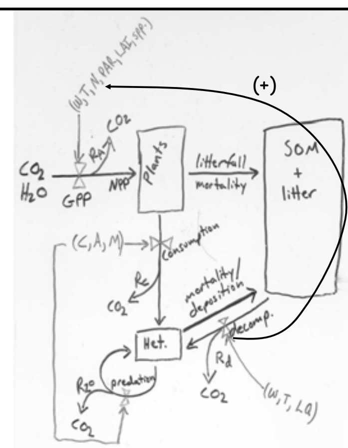
6.11

I. What is it?

A. Decomposition is physical and chemical breakdown of dead organic matter

- Provides energy for microbial growth (draw)
- Not all C can be metabolized: leftovers enter SOM pool, which influences ecosystem carbon storage (and therefore climate).
- Releases nutrients for plant uptake

C-cycle: the role of decomposition



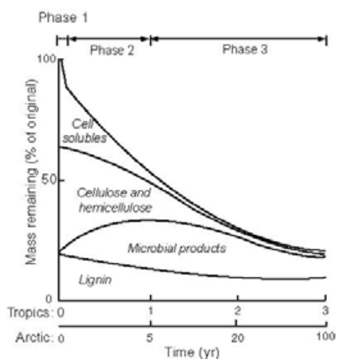
B. Decomposition consists of three processes occurring simultaneously

- 1. Leaching by water
  - Transfers soluble materials
- 2. Fragmentation by soil animals
  - Increases surface area for microbial attack
- 3. Chemical alteration
  - Available C metabolized
  - Changes chemical composition of remaining detritus

Leaching

- Moves water-soluble compounds away from decomposing material
- Begins while leaves are still on plant
- Most important early in decomposition

Leaching can remove ~5% of litter mass in first 24 hrs in wet climates.



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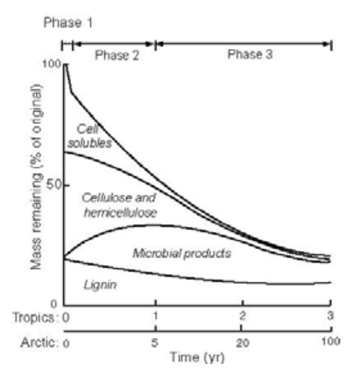
Fragmentation

- Fresh litter is protected from microbial attack
  - Bark, epidermis or skin on exterior
  - Plant cells protected by lignin in cell walls
- Carried out mainly by soil animals
- Increases surface area for microbial attack
- Important in aquatic and terrestrial ecosystems

Chemical alteration

- Breaks down organic matter to CO_2 and nutrients
- Forms complex recalcitrant compounds

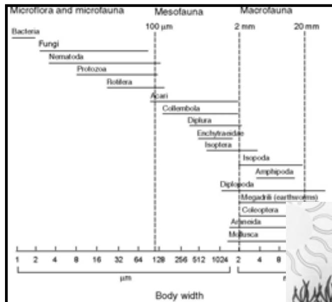
Phase 2 – consumption of available C, such that by Phase 3, most of the remaining is recalcitrant (→ SOM).



7.2

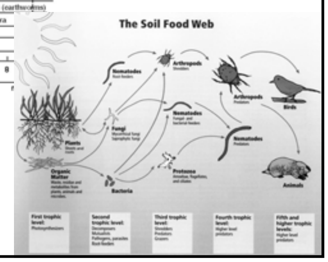
II. Who are the decomposers and <u>why</u> do they do it?

- Decomposer organisms are subject to natural selection
- Decomposition is result of their feeding activity and population dynamics
- NOT a community service to the carbon cycle
  - They don't care about whether their activity promotes nutrient cycling and productivity of ecosystems



- Bacteria & fungi – chemical breakdown & metabolism
- Microfauna – nutrient regen.
- Mesofauna – fragmentation
- Macrofauna – fragmentation, soil "engineering"

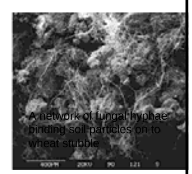
7.1 Who are the major players in decomposition?



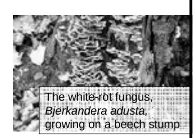
A. Chemical alteration by bacteria & fungi

1. Chemical Alteration by Fungi

- **Fungi** are the main initial decomposers of terrestrial dead plant material and, together with bacteria, account for 80-90% of the total decomposer biomass and respiration
- Fungi have networks of **hyphae** (i.e., filaments that enable them to grow into new substrates and transport materials through the soil over distances of cm to m)
- Hyphal networks enable fungi to acquire their carbon in one place and their N in another
- **White-rot fungi** decompose lignin to get at N



A network of fungal hyphae binding soil particles on to wheat stubble



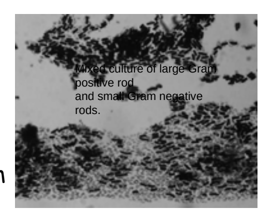
The white-rot fungus, *Bjerkandera adusta*, growing on a beech stump

Fungi (cont'd)

- Fungi account for 60-90% of the microbial biomass in forest soils, where litter frequently has a high lignin and low N concentration
- They have a competitive advantage at low pH, which is also common in forest soils
- Fungi make up about half the microbial biomass in grassland soils where pH is higher, and wood is absent
- Most fungi lack a capacity for anaerobic metabolism and therefore absent from or dormant in anaerobic soils and aquatic sediments

2. Chemical Alteration by Bacteria

- Grow rapidly
- Specialize on labile substrates
- Some bacteria function anaerobically
- Dependent on substrates that diffuse to bacterium (not like fungi)
- Diffusion gradient caused by
  - Production of soluble substrates (enzymes)
  - Uptake of substrates by bacterium



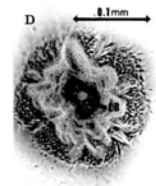
Mixed culture of large Gram positive rod and small Gram negative rods.

Bacteria (contd)

- Spatial specialists
  - Rhizosphere, macropores, interior of aggregates
  - form biofilms on particle surfaces
- Chemical specialists
  - Different bacteria produce different enzymes (consortia)

Bacteria (contd)

- Become inactive when substrate is exhausted
  - 50 to 80% of soil bacteria inactive
- Activated by presence of substrate
  - e.g., when root grows past



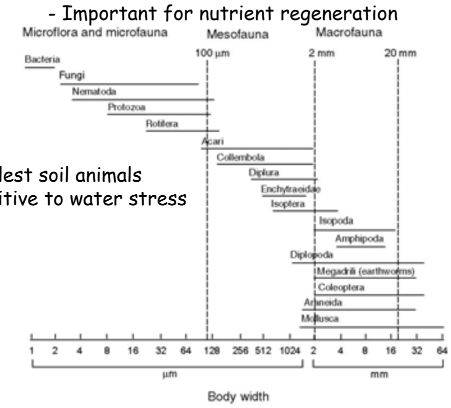
Soil animals

- Account for only 5-10% of soil respiration
- Major impacts on decomposition are indirect
  - Alter soil environment
  - Graze bacteria and fungi
  - Excrete nitrogen and phosphorus

B. Soil animals: Microfauna

- Important for nutrient regeneration

- Smallest soil animals
- Sensitive to water stress

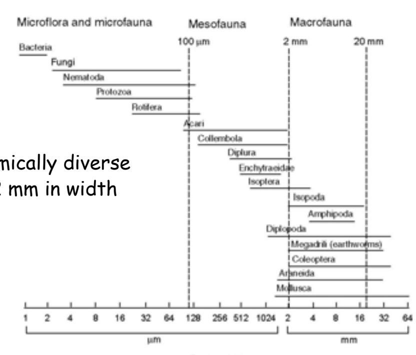


7.1

Soil animals: microfauna

- Protozoans (ciliates, amoebae)
  - Aquatic, mobile
  - Bacterial predators (phagocytosis)
  - Rhizosphere specialists
- Nematodes (many trophic roles)
  - Extremely abundant
  - Trophically diverse (root herbivores/parasites, bacterial & fungal grazers, predators
  - Often eat as much as aboveground grazers
- Mites (many trophic roles)

C. Soil animals: Mesofauna



- taxonomically diverse
- 0.1 to 2 mm in width

7.1

Soil animals: mesofauna

- Animals with greatest effect on decomposition
- Fragment litter
- Ingest litter particles and digest the microbial jam
- Produce large amounts of fecal material with a greater surface area and moisture-holding capacity than the original litter

Soil Animals (Mesofauna)

- **Springtails** (**Collembola**) are small insects that feed primarily on fungi
- Collembolans are important mesofauna in northern soils

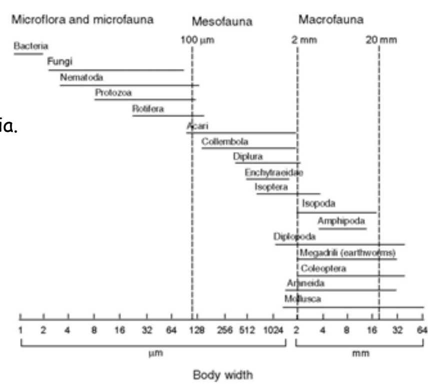
Collembolan

- **Mites** (**Acari**) are a more trophically diverse group of spider-like animals that consume decomposing litter or feed on bacteria and/or fungi

Mite

D. Soil animals: Macrofauna

>2 mm dia.



7.1

Soil animals: macrofauna

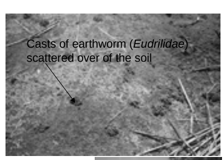
- Earthworms, termites, etc.
  - Fragment litter or ingest soil
- Earthworm digestive tract stimulates microbial activity, so soil microbes act as gut **mutualists**
- Earthworms are most abundant in the temperate zone, whereas termites are most abundant in tropical soils.
- Termites eat plant litter directly, digest the cellulose with the aid of mutualistic protozoans in their guts, and mix the organic matter into the soil

Earthworm : *Millsonia anomala*

Termites : *Macrotermes muelleri* on fungus comb

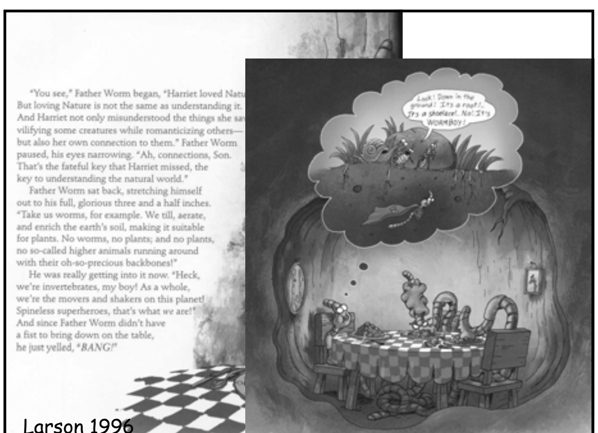
Soil Animals: Macrofauna

- Ecosystem engineers
  - Mix soil, carry organic matter to depth, new soil to surface
  - Reduce compaction
  - Create channels for water and roots
- In temperate pastures earthworms may process 4 kg m^{-2} y^{-1} of soil, moving 3 to 4 mm of new soil to the ground surface each year; this is a geomorphic force that is, on average, orders of magnitude larger than landslides or surface soil erosion



Casts of earthworm (*Eudrilidae*) scattered over of the soil

Termites nest (*Macrotermes bellicosus*)



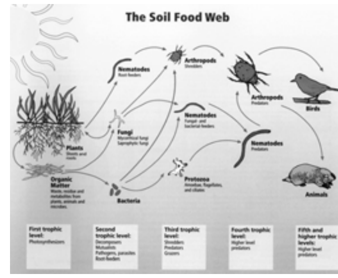
"You see," Father Worm began, "Harriet loved Natu
But loving Nature is not the same as understanding it.
And Harriet not only misunderstood the things she sa
vilifying some creatures while romanticizing others—
but also her own connection to them." Father Worm
paused, his eyes narrowing. "Ah, connections, Son.
That's the fateful key that Harriet missed, the
key to understanding the natural world."
Father Worm sat back, stretching himself
out to his full, glorious three and a half inches.
"Take us worms, for example. We till, aerate,
and enrich the earth's soil, making it suitable
for plants. No worms, no plants; and no plants,
no so-called higher animals running around
with their oh-so-precious backbones!"
He was really getting into it now. "Heck,
we're invertebrates, my boy! As a whole,
we're the movers and shakers on this planet!
Spineless superheroes, that's what *we* are!"
And since Father Worm didn't have
a fist to being down on the table,
he just yelled, "*BANG!*"

Larson 1996

Larson 1996

Soil Animals (Macrofauna)

- Soil food webs are complex, so many of the effects of soil animals on decomposition are indirect
- Loss or exclusion of soil invertebrates can reduce decomposition rate (and therefore nutrient cycling) substantially, indicating the important role of animals in the decomposition process



A GREATLY simplified soil food web.

Soil Animals

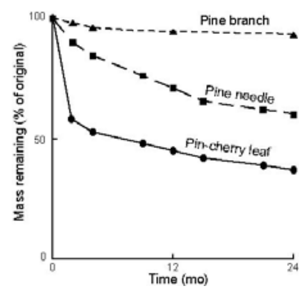
- The soil fauna is critical to the carbon and nutrient dynamics of soils. Microbes contain 70 to 80% of the labile C and N in soils, so variations in predation rates of microbes by fauna dramatically alter C and N turnover in soils
- Soil animals account for only about 5% of soil respiration, so their major effect on decomposition is their enhancement of microbial activity through fragmentation, rather than their own processing of energy derived from detritus

III. Temporal patterns of decomposition
A. Exponential decay

Litter mass declines almost exponentially with time (draw)

$L_t = L_0 e^{-kt}$

- k is the decomposition constant
- Proportion of litter lost per unit time
- $g_* g^{-1}{}_* t^{-1}$



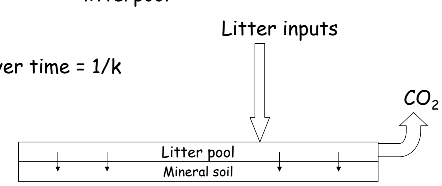
7.8

A. Exponential decay

Can also estimate k if you know rates of litter input and size of litter pool:

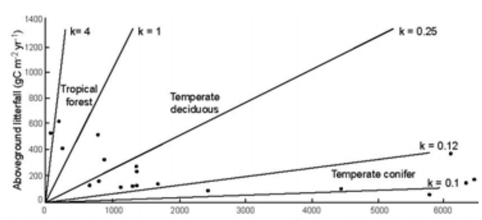
$$k = \frac{\text{litterfall}}{\text{litterpool}} = g*m^{-2}*yr^{-1} / g*m^{-2} = g*g^{-1}*yr^{-1}$$

Turnover time = 1/k



…Assuming steady state (i.e., no change in the size of the litter pool with time).

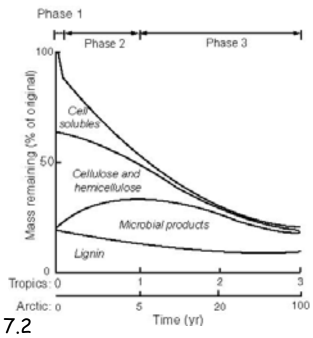
Relationship between forest floor mass (litter pool size) and aboveground litterfall (input) for different ecosystem types.



7.5

B. Phases of decomposition
- depends on substrates being decomposed

Phase 1: Leaching dominates
Phase 2: High value of k: labile substrates broken down
Phase 3: Low value of k: recalcitrant substrates predominate
Time scale depends on environment (tropics vs. arctic)

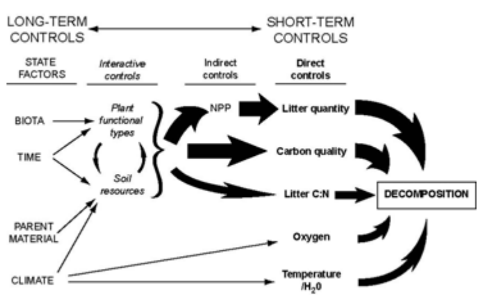


7.2

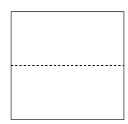
IV. Controls over decomposition

A. Physical environment
B. Substrate quantity and quality
C. Properties of microbial community
D. Humus formation

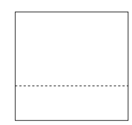
Controls over decomposition range from long-to-short term
Long-term: State factors
Intermediate: Interactive controls
Short-term: Indirect and direct physiological controls
Direct controls: Environment and substrate quality



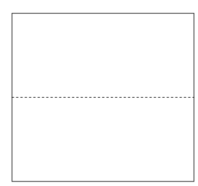
What's your decomp metric?
- % mass loss/t (k)
- total litter loss/t



100 g litter x 50% loss/yr = 50 g total loss

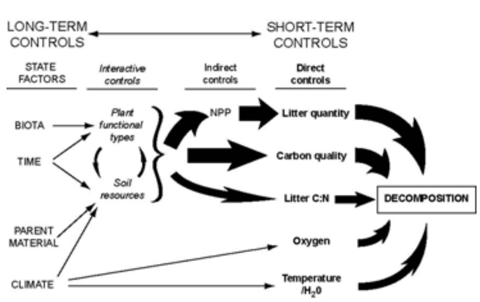


100 g litter x 70% loss/yr = 70 g total loss



200 g litter x 50% loss/yr = 100 g total loss

Size of the arrows in this figure reflects cross-ecosystem comparisons in TOTAL amount of decomp.



7.14

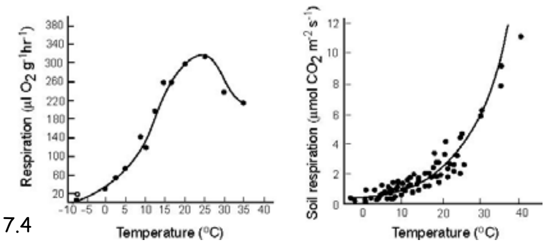
A. Physical Environment

1. Temperature
   a. Direct effects
      - Effects on microbial activity

   b. Indirect effects

A. Physical Environment, 1. Temperature

a.i. Direct temperature effect on microbial activity
Exponential increase in soil respiration
Temperature optimum is much higher than ambient temperature
Maintenance respiration is increasing proportion of total at high temperature
High temperature not necessarily optimal for microbes

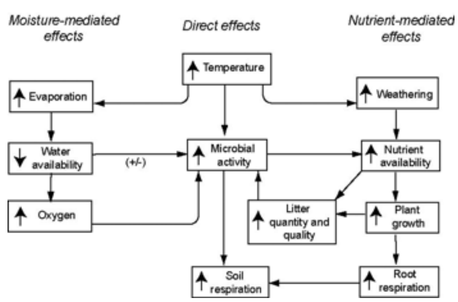


7.4

b. Indirect temperature effects

- Effects on evaporation and soil moisture
- Effects on permafrost
  - Changes in drainage
- Effects on quantity and quality of litter inputs

Some of most important temperature effects are indirect



7.6

2. Moisture effects

- Decomposition has similar shape of moisture response to that of NPP
  - Declines at extremely low and high moisture

Soil moisture-temperature interactive effects on microbial respiration

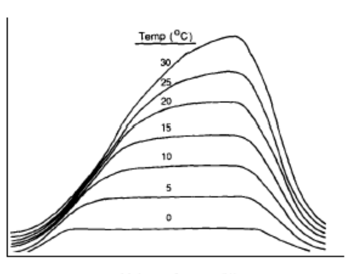
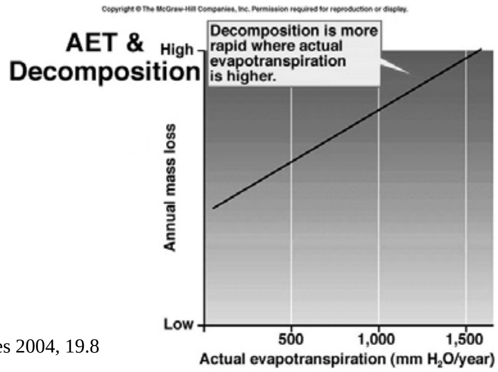


FIGURE 2.11 Semiperspective plot of computed respiration rate at different temperature and moisture levels. All curves actually begin at origin. (From Bunnell and Tait, 1974.)

Moisture

- Organic matter accumulation is greatest in wet soils.
- Decomp more sensitive to high moisture than is NPP (SOM accumulation in waterlogged soils)
- Oxygen diffusion is 10,000x slower through water than through air
- Decomp less sensitive to low moisture than is NPP (no litter accumulation in deserts)
- Generally, microbial activity optimal in moist soils

Temp x Moisture - AET



Molles 2004, 19.8

AET Effects on decomp

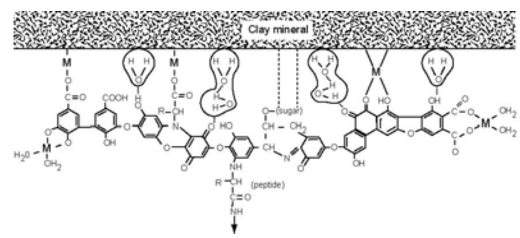
Schlesinger 1997

3. Other environmental effects

a. pH – circum neutral pH has highest decomp.
- bacteria predominate at high pH
- Low growth efficiency promotes breakdown

b. Soil texture
- Protection of SOM by clays
- Aggregate structure (anaerobic microsites)

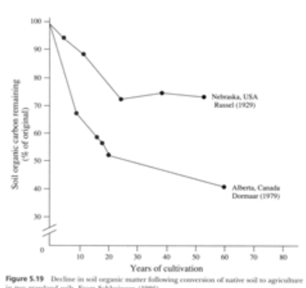
Some chemical groups unavailable to enzymes when organic matter binds to clay particles



7.7

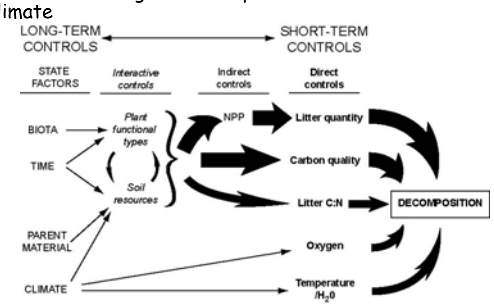
3. Other environmental effects

c. Soil disturbance
- Reduces SOM protection by clays
- Breaks up soil aggregates



Schlesinger 1997

B. Substrate quantity and quality
- major controls over decomposition looking at total amount of decomp across ecosystems
- five- to ten-fold range in decomposition rate of litter in a given climate



7.14

Substrate Quality

Substrate quality: susceptibility of a substrate to decomposition measured under standardized conditions

- (1) labile, metabolic compounds, such as sugars and amino acids
- (2) moderately labile structural compounds such as cellulose and hemicellulose
- (3) recalcitrant structural material such as lignin and defensive compounds such as condensed polyphenols

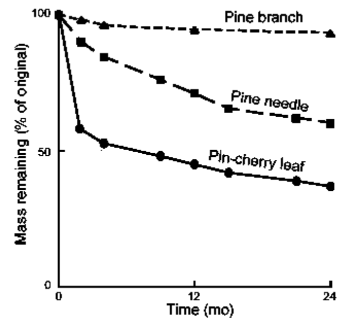


Fig. 7.8 – Comparison of decomposition dynamics of substrates of varying qualities.

Substrate quality depends on:

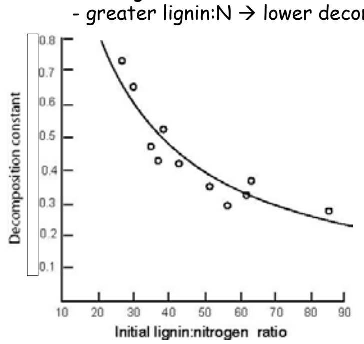
- 1. Size of molecule
- 2. Types of chemical bonds
- 3. Regularity of structure
- 4. Toxicity
- 5. Nutrient concentrations

Substrate Quality Predictors

- C:N ratio (or [N]) – Why does it work?
  - Litter C:N = 100:1, microbe 10:1
  - If respire 50% of C, C:N 50:1; still too much C
  - Need to import N, slows decomposition (but direct additions of N only speed decomp when not limited by available C).
- Lignin:N ratio
  - Integrated measure of N concentration and substrate size/complexity

Effects of Lignin on k

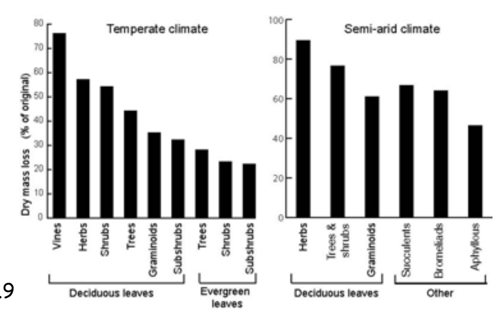
- greater lignin:N → lower decomp rate



7.10

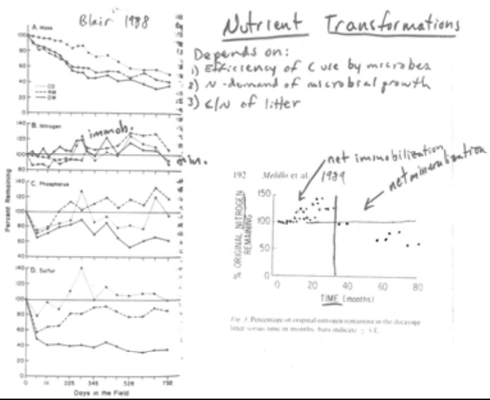
Plant species differ predictably in litter quality

High-resource-adapted leaves decompose quickly due to higher concentrations of labile C



7.9

Litter quality affects nutrient immobilization



Climate interacts with Litter Quality

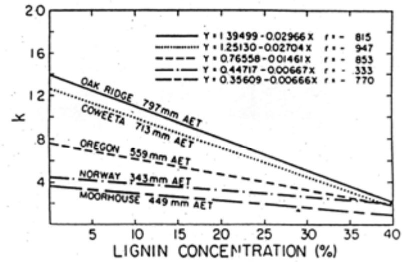


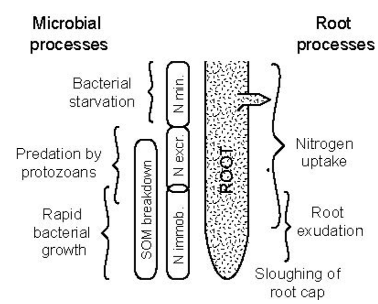
FIG. 1. Simple correlation-regression between initial lignin concentration (%) and annual decomposition rate (k) for 5 locations ranging in climate from subpolar to warm temperate. AET = actual evapotranspiration.

Meentemeyer 1978

Substrate quality of SOM

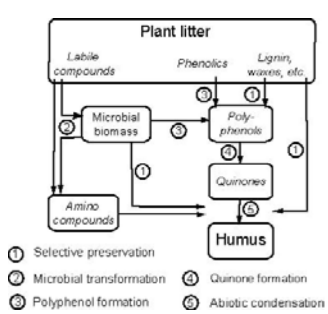
- Much of SOM is old and recalcitrant
- Consists of "leftovers" and microbial products
- Binds to clay minerals
- Bulk soil is a "nutritional desert"

Rhizosphere is major zone of decomposition in mineral soil
High inputs of labile C "prime" decomposition
Microbes break down SOM for nitrogen



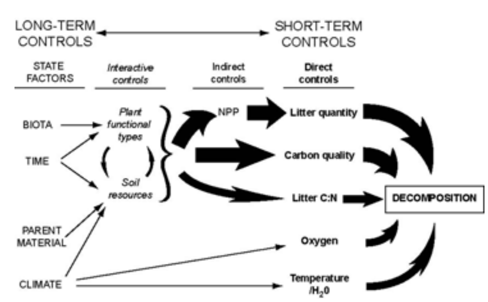
7.11

D. Long-term storage of SOM
Humus formation
Formation of SOM that doesn't decompose easily
Critical determinant of soil properties



7.12

V. Decomposition at the ecosystem scale
Controls over stand-level decomposition are similar to controls of GPP and NPP

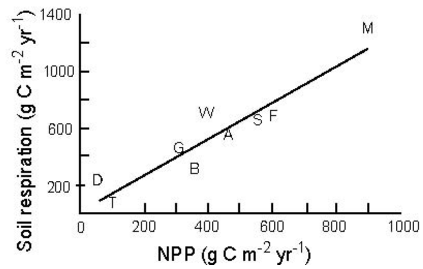


7.14

Major controls over decomposition

- Quantity of litter input
- Quality of litter input
- Environmental conditions that favor biological activity

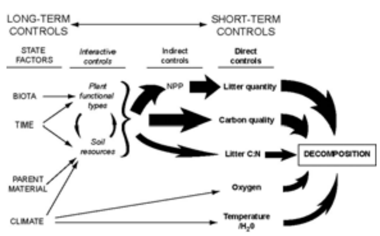
Soil respiration correlates closely with NPP because
Some (75%) is decomposition, which depends on litter quantity and quality
Some (25%) is root respiration which correlates with NPP



7.15

Summary

- Decomposition is the major avenue of carbon loss from ecosystems
- Determined primarily by factors regulating NPP
- Sensitive to global change
- Has potentially large feedbacks to climate



7.14