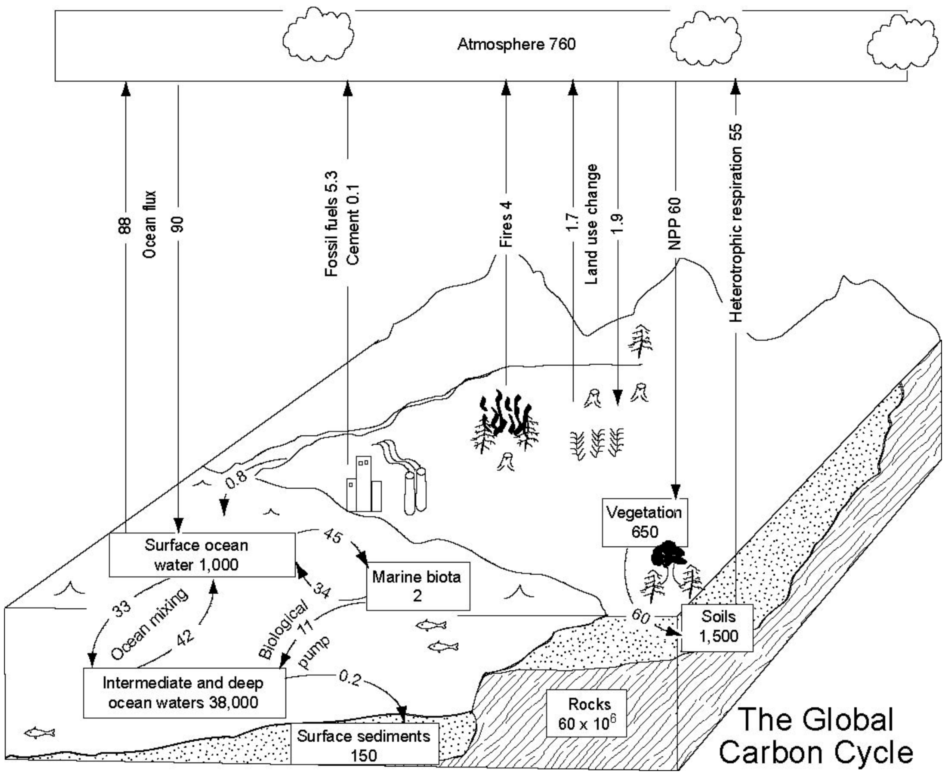
Terrestrial Decomposition

- Objectives
  - Controls over decomposition
    - Litter breakdown
    - Soil organic matter formation and dynamics
  - Carbon balance of ecosystems
    - Soil carbon storage

Overview

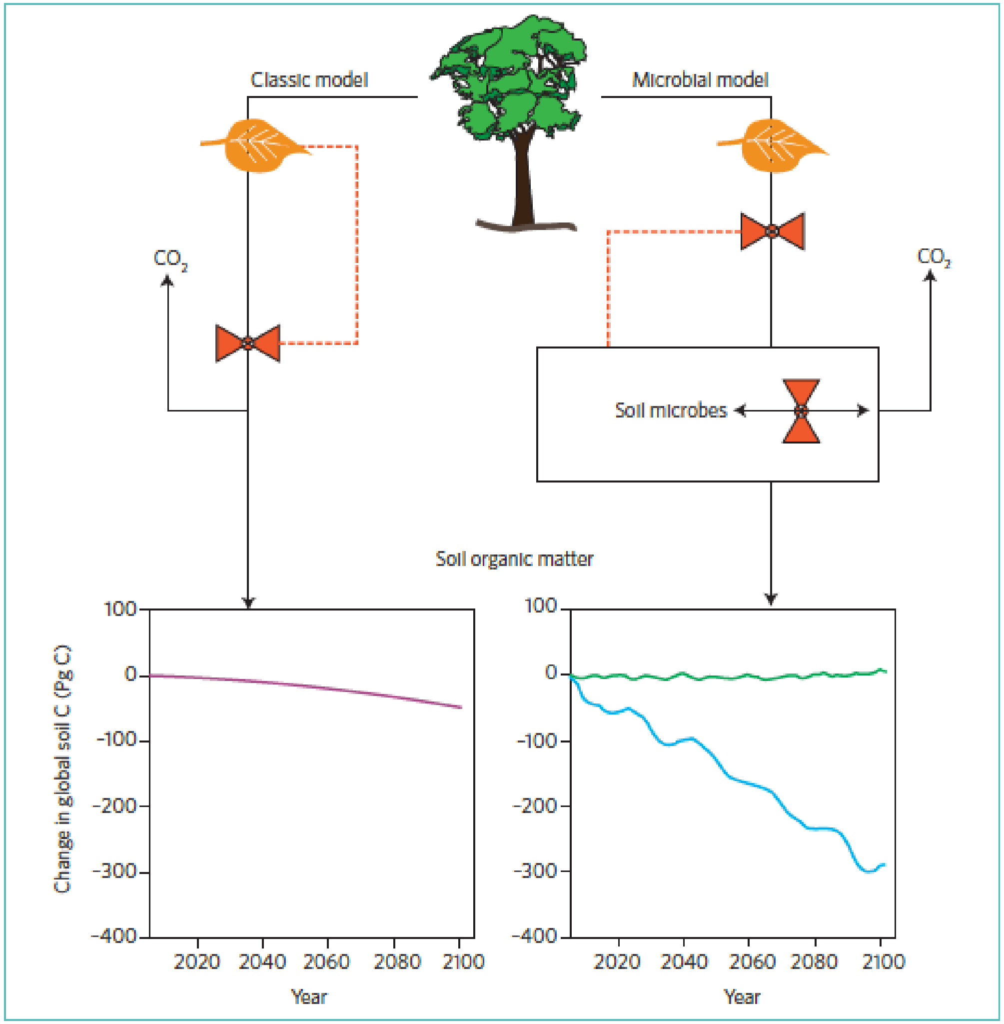
- In terrestrial ecosystems, soils (organic horizon + mineral soil) > C than in vegetation and atmosphere combined



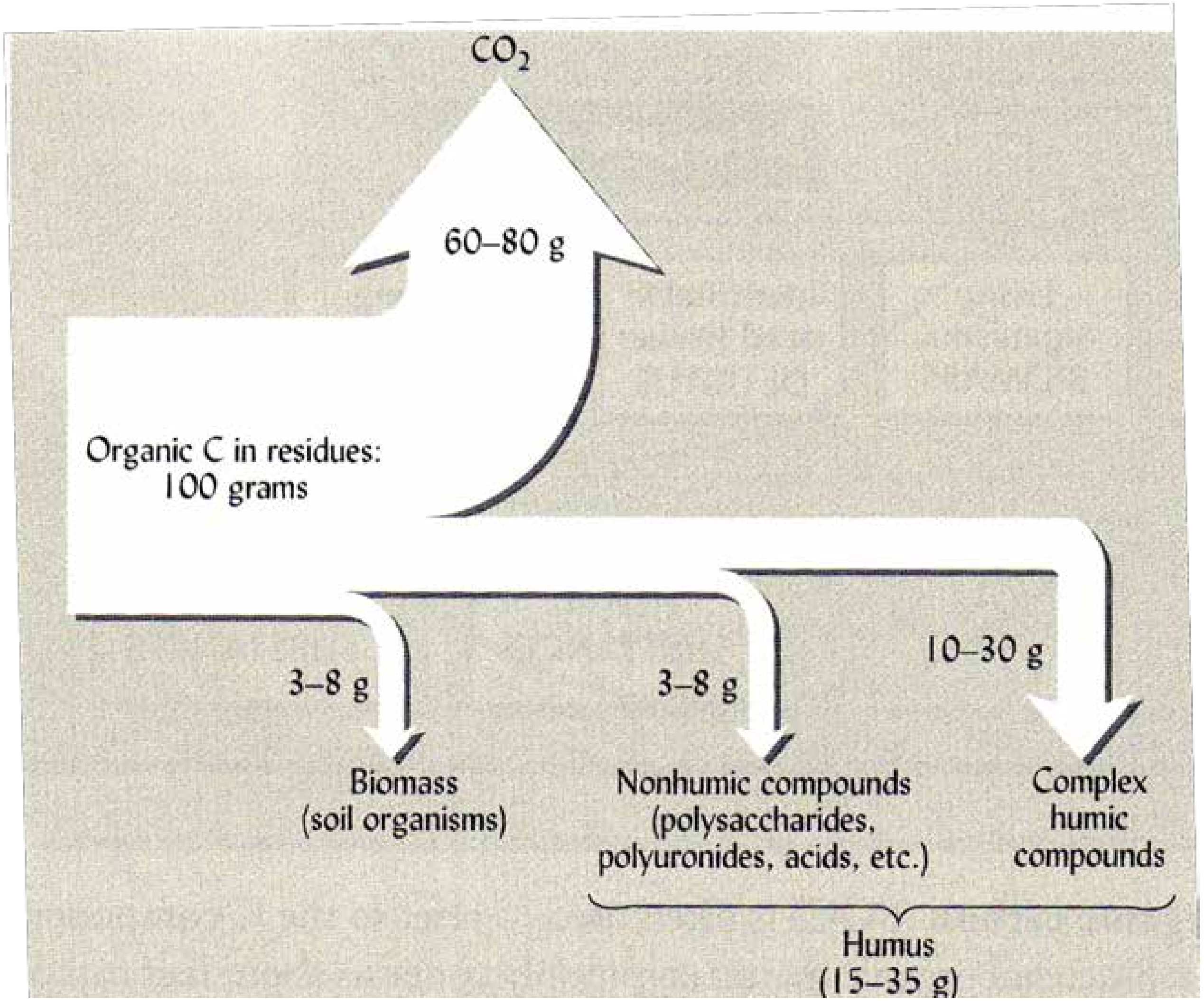
Overview

- Decomposition is:

1. Major pathway for C loss from ecosystems
2. Central to ecosystem C loss and storage



Overview



Incorporation → 1 year later

Overview

- Predominant controls on litter decomposition are fairly well constrained
    1. Temperature and moisture
    2. Litter quality
        - N availability
        - Lignin concentration
        - Lignin:N
- Mechanisms for soil organic matter stabilization:
    1. Recalcitrance (refers to chemistry)
    2. Physical protection
        - Within soil aggregates
        - Organo-mineral associations
    3. Substrate supply regulation (energetic limitation)

Overview

- Disturbance can override millenia in a matter of days or years:
    1. Land use change
    2. Invasive species
    3. Climate change

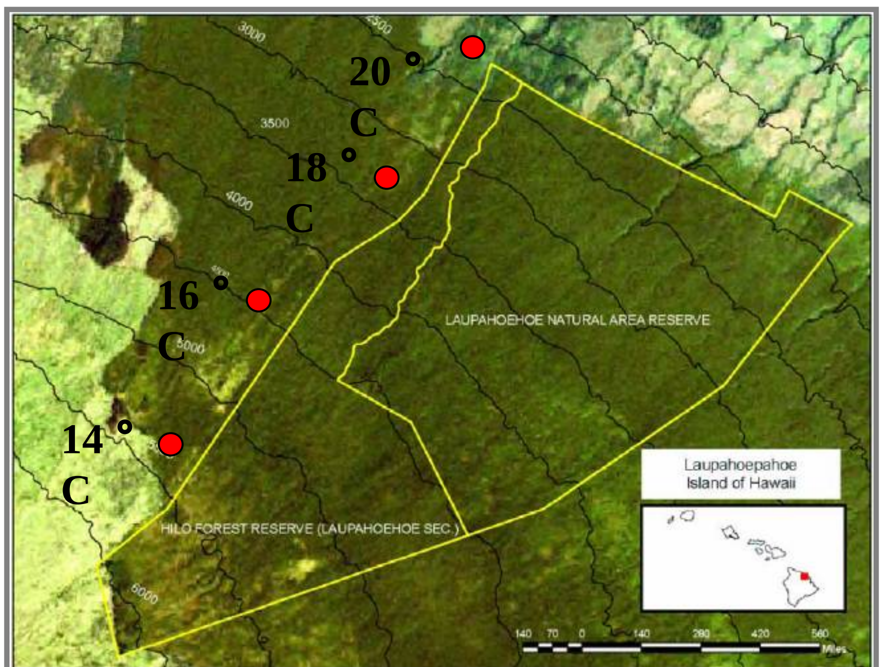
- Understanding the mechanistic drivers of decomposition, soil organic matter formation, and carbon stabilization help us make management decisions, take mitigation steps, and protect resources.

Overview

Native Ōhi‘a - Koa forest

Conversion to grass-dominated pasture (80 yr)

Reforestation in *Eucalyptus* plantation (10 yr)



Conventional sugar cane harvest.

Sustainable ratoon harvest.

Decomposition

- Decomposition is the biological, physical and chemical breakdown of organic material
  - Provides energy for microbial growth (heterotrophs)
  - Releases nutrients for uptake by plants & microbes
    - inorganic and organic
  - Influences ecosystem C storage

Decomposition

- Decomposition consists of abiotic and biotic processes that transform litter into CO_2, DOC, and/or SOM.

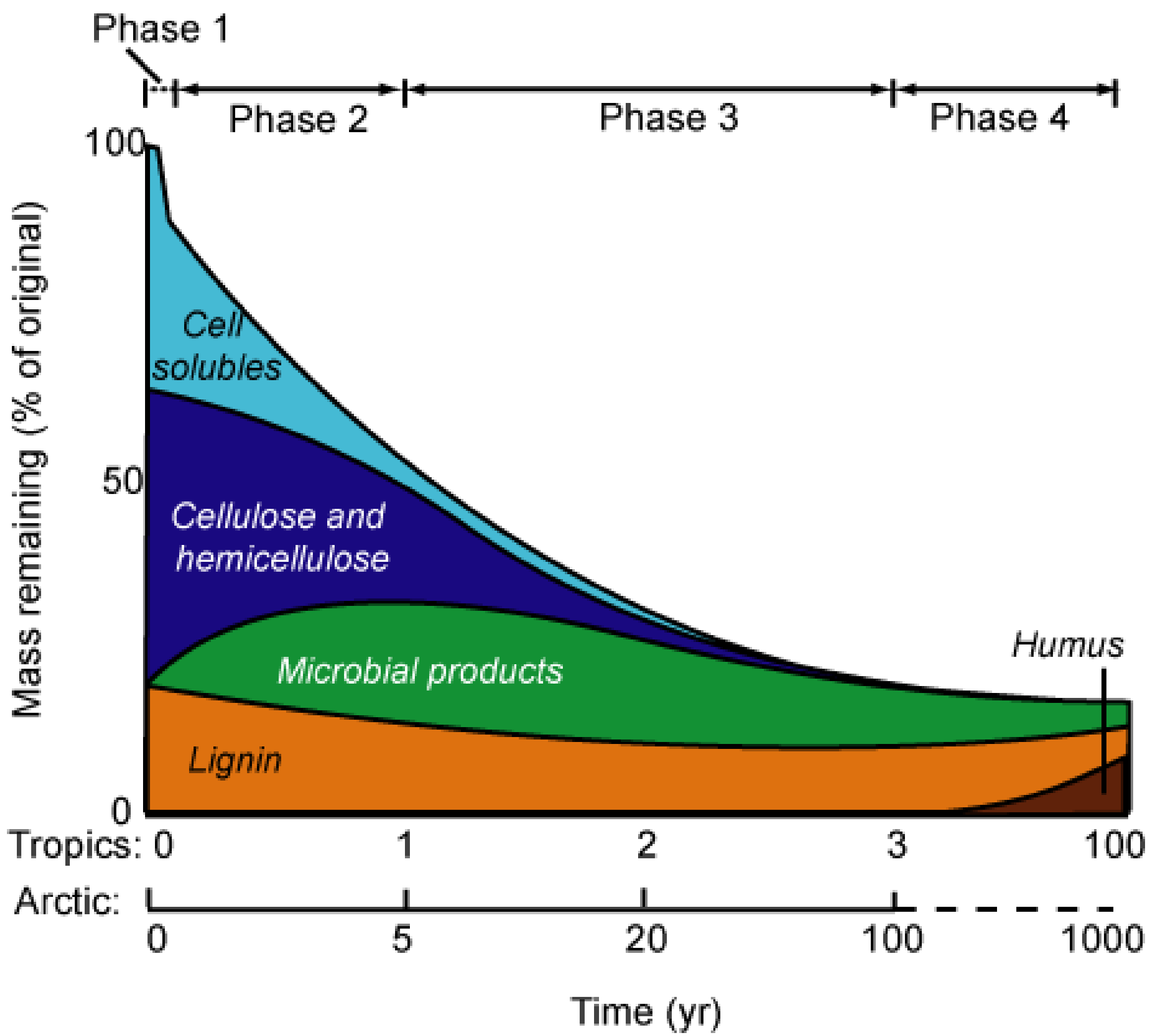
  1. Leaching (water)
  2. Fragmentation (soil macro- and mesofauna, freeze-thaw)
  3. Chemical alteration (UV degradation or microbially mediated)

Decomposition

Phase 1 ≈ Leaching

Phase 2 ≈ Fragmentation

Phase 3 ≈ Chemical Alteration

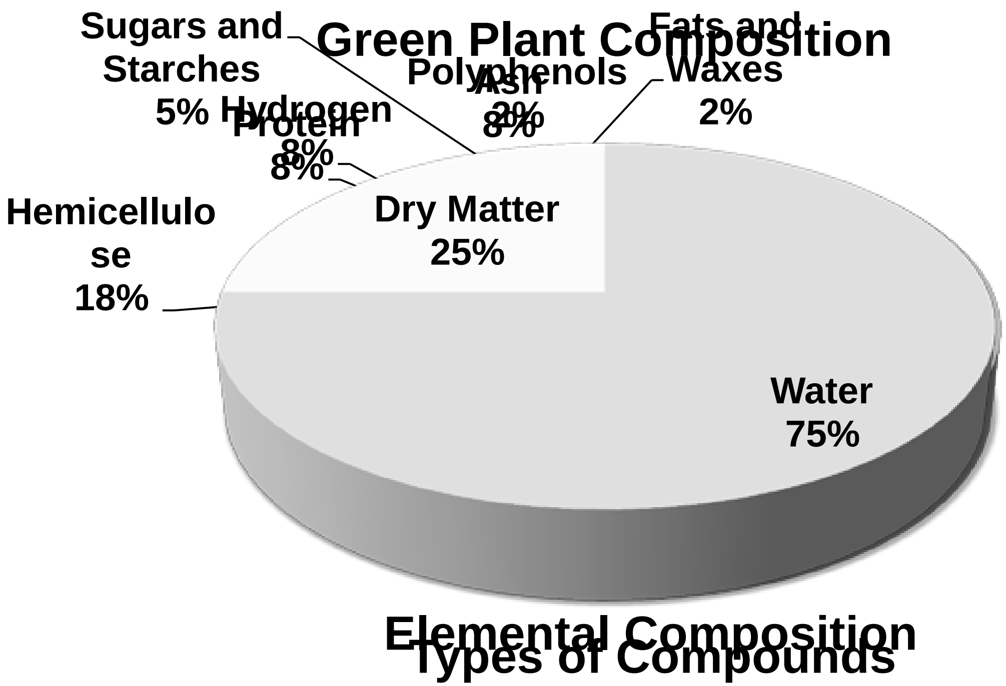


Decomposition

- Leaching
  - Moves water-soluble compounds (sugars, amino acids, mineral ions) away from decomposing material & down through soil profile
  - Begins while leaves are still on plant
    - Stemflow, throughfall
    - Enhanced during/after senescence by resorption of leaf compounds
  - Most important for labile compounds early in decomposition
    - More important for areas of higher MAP

Composition of plant material

- Plant litter is an important source of soil organic matter.



Plants = 75% Water,
25% Dry Matter

Elemental analysis of dry matter?

Structural components of dry matter?

- Carbohydrates
- Lignins and polyphenols
- Proteins

Controls on litter decomposition

1. Sugars, starches, simple proteins
2. Crude proteins
3. Hemicellulose
4. Cellulose
5. Fats and waxes
6. Lignins and phenolic compounds

Rapid Decomposition

↕

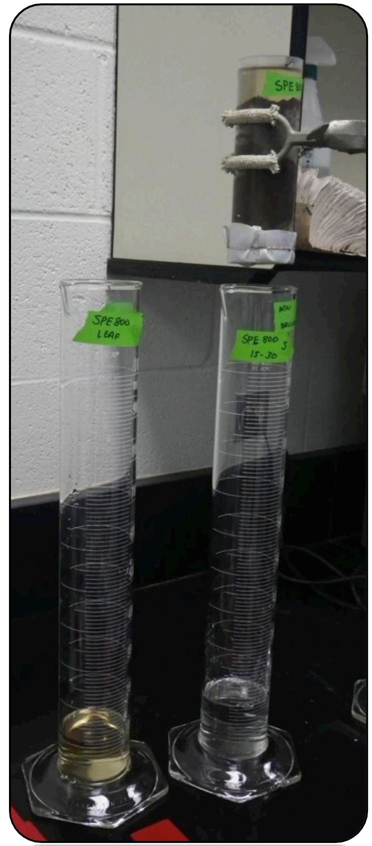
Very slow decomposition

Fate of Forest Floor Leachates

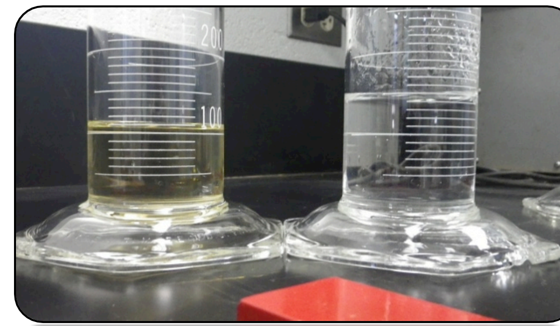
Leaf litter

Organic Horizon

Constructed forest floor



Mineral soil core sorption



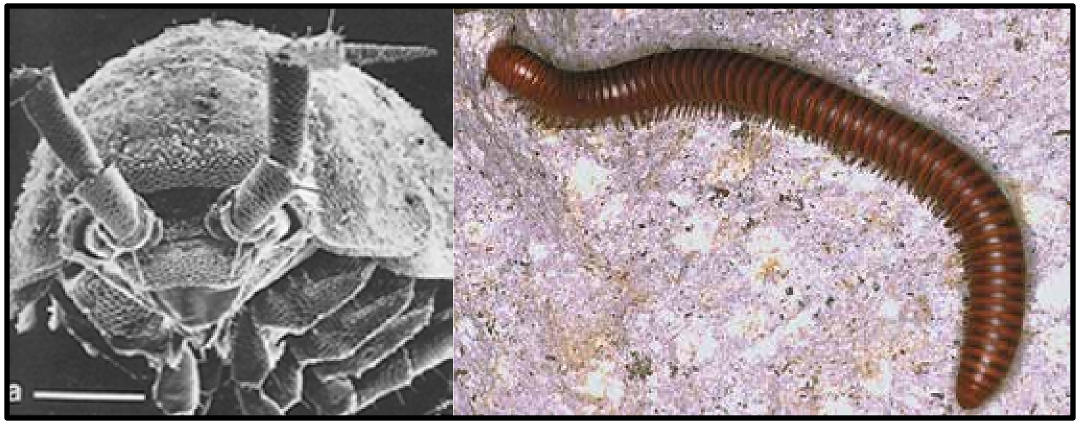
Leachates removed from soil solution and retained

Michelle Lazaro

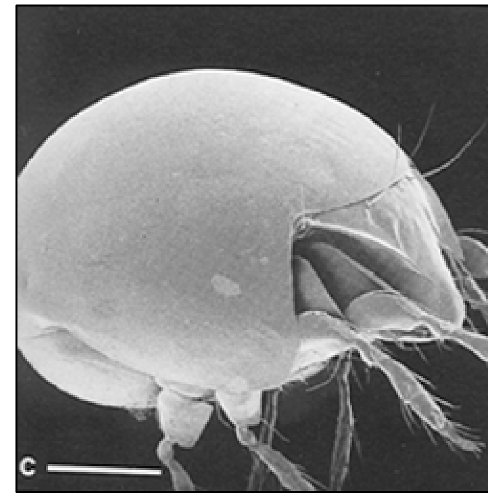
Decomposition

- Fragmentation
  - – Fresh litter is ~protected from microbial attack
    - Bark, cuticle, or skin on exterior
    - Plant cells protected by lignin in cell walls
  - – Fragmentation breaks down protective barriers
  - – Also increases surface area:volume for microbial activity and mixes OM throughout soils
    - Biological mixing (soil animals)
    - Physical mixing (freeze-thaw, wet-dry)

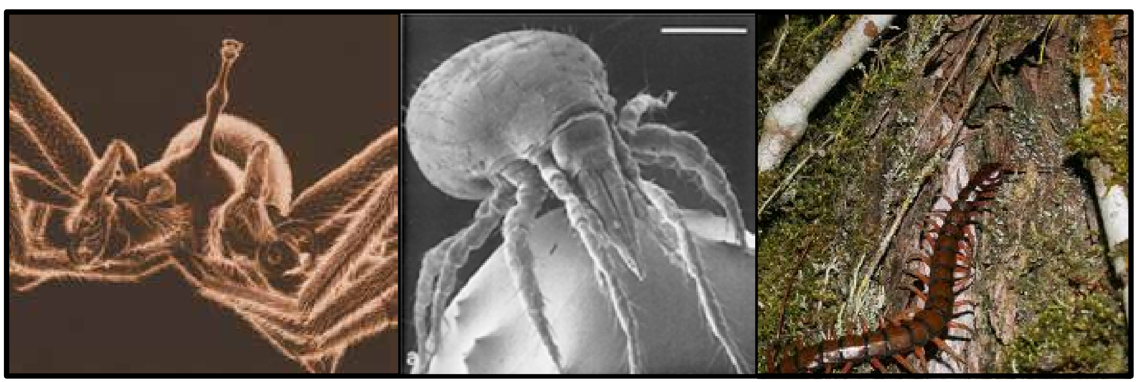
Soil Mesofauna and Macrofauna



Shredders



Fungal feeder – orabatid mite



Predators

Herbivore

Images from NRCS: http://soils.usda.gov/sqi/concepts/soil_biology/biology.html

Functional Ecology

- Soil animals: mesofauna (0.1 – 2 mm)
  - Animals with greatest effect on decomposition
    - Fragment litter
    - Ingest litter particles and digest the “microbial jam”
    - Fecal matter has increased surface area & water-holding capacity
  - Collembolans
    - Important in Northern soils (feed on fungi)
  - Mites (many trophic roles)
    - Consume litter, feed on bacteria & fungi

Functional Ecology

- Soil animals: macrofauna (>2 mm)
  - Earthworms, termites, etc.
    - Fragment litter or ingest soil
  - Ecosystem engineers
    - Mix soil, carry organic matter to depth
    - Reduce compaction
    - Create channels for water and roots
    - Overall, alters resource availability
    - In many places, invasive earthworms are transforming soils

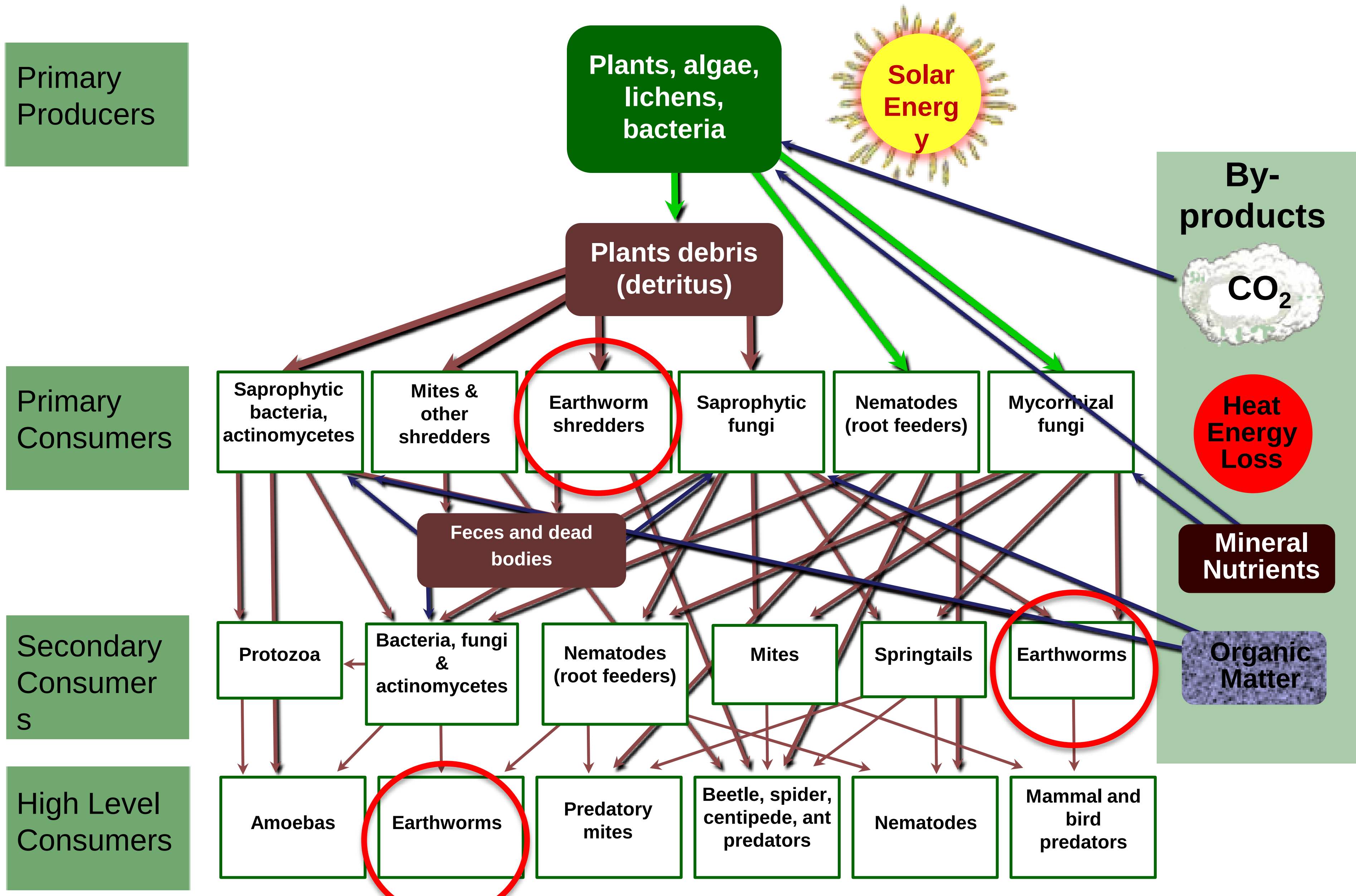
Ecosystem Engineers

Organisms that make major alterations to the physical environment, influencing habitats for many other organisms within the ecosystem

- Humans
- Biotic crusts in deserts
- Burrowing macrofauna, such as earthworms, ant, termites



Soil Food Web



What Do Earthworms Do?

Stimulate microbial activity

- Earthworms derive nutrition from microbes
- Organic matter is fragmented and inoculated in gut
- Greater microbial biomass in feces and casts than in surrounding soil – microbial hotspot

http://soils.usda.gov/sqi/concepts/soil_biology/earthworms.html

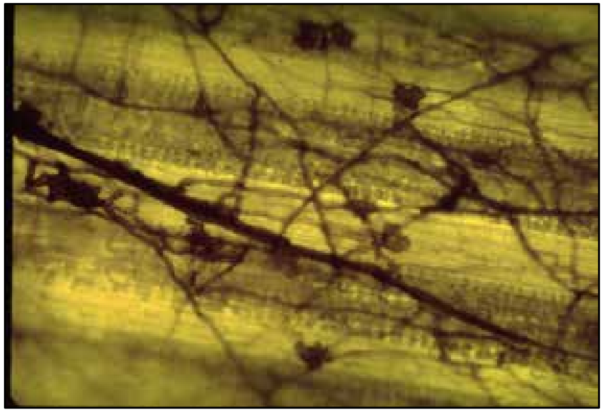
Decomposition

- Chemical alteration
  - **Mineralization** breaks down *organic* matter to *inorganic* CO_2 and nutrients
  - **Immobilization** in microbial biomass temporarily makes C and nutrients unavailable to other organisms (e.g., plants)
  - Microbial biomass and byproducts become incorporated into SOM along with the organic residue (forming humus), and often are stabilized

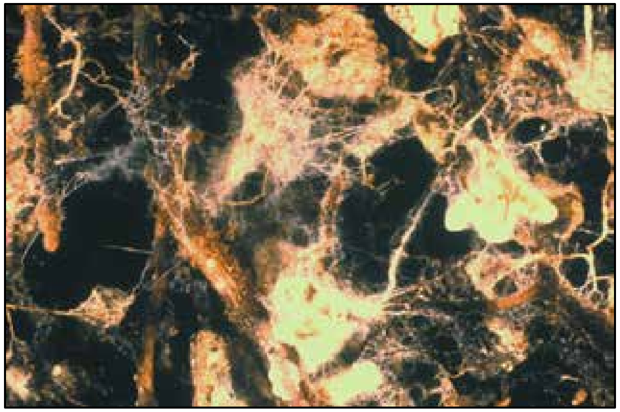
Soil Microorganisms

Soil bacteria

Bacteria on fungi

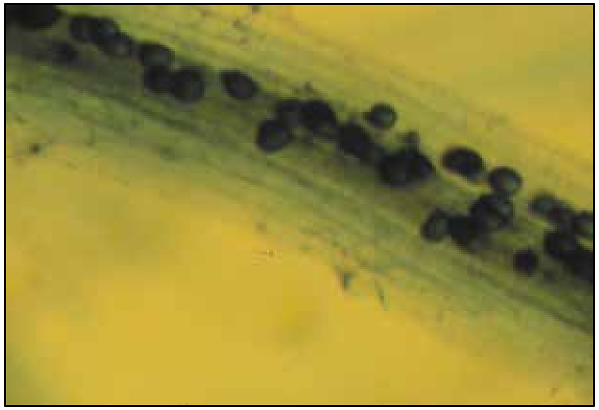


Fungi decomposing leaf tissue



Mycorrhizal bodies and hyphae

Ectomycorrhizae



Vesicles

Images from NRCS: http://soils.usda.gov/sqi/concepts/soil_biology/biology.html

Terrestrial Decomposers

- Fungi
  - Main initial decomposers of dead plant material
  - Account for most litter decomposition in aerobic environments
    - 60-90% of microbial biomass in forests
    - About 1/2 of microbial biomass in grasslands

WHY?

  - Broad enzymatic capability; secrete **exoenzymes**
    - Cell walls (lignin, cellulose, hemicellulose)
      - Fungi are main lignin degraders
    - Cell contents (proteins, sugars, lipids)
      - Fungi and bacteria

Terrestrial Decomposers

- Brown-Rot Fungi – breakdown cellulose and hemicellulose, lignin remains

- White-Rot Fungi – breakdown lignin, leaving cellulose and hemicellulose

(*from* the Australian Fungi Website)

http://www.anbg.gov.au/fungi/images-captions/brown%2Bwhite-rot-wood-0123.html

Terrestrial Decomposers

- Fungi (con't)
  - Composed of long networks of hyphae
  - Can transport metabolites and nutrients through hyphal network
    - Surface litter & wood degraders
      - import nitrogen from soil to decompose material with low nutrient content
    - Mycorrhizae (trade carbohydrates for nutrients)
      - Fungal hyphae greatly expand soil volume explored → increase nutrient pool available to plants

Terrestrial Decomposers

- Bacteria
  - Grow and reproduce rapidly when resources are readily available (live fast, die young)
  - Specialize on labile substrates
    - Rhizosphere, dead animals, microbes
  - Completely dependent on substrates that diffuse to them (unlike fungi)
    - **Exoenzymes** and diffusion
    - Water movement thru soils
    - Root and hyphal growth

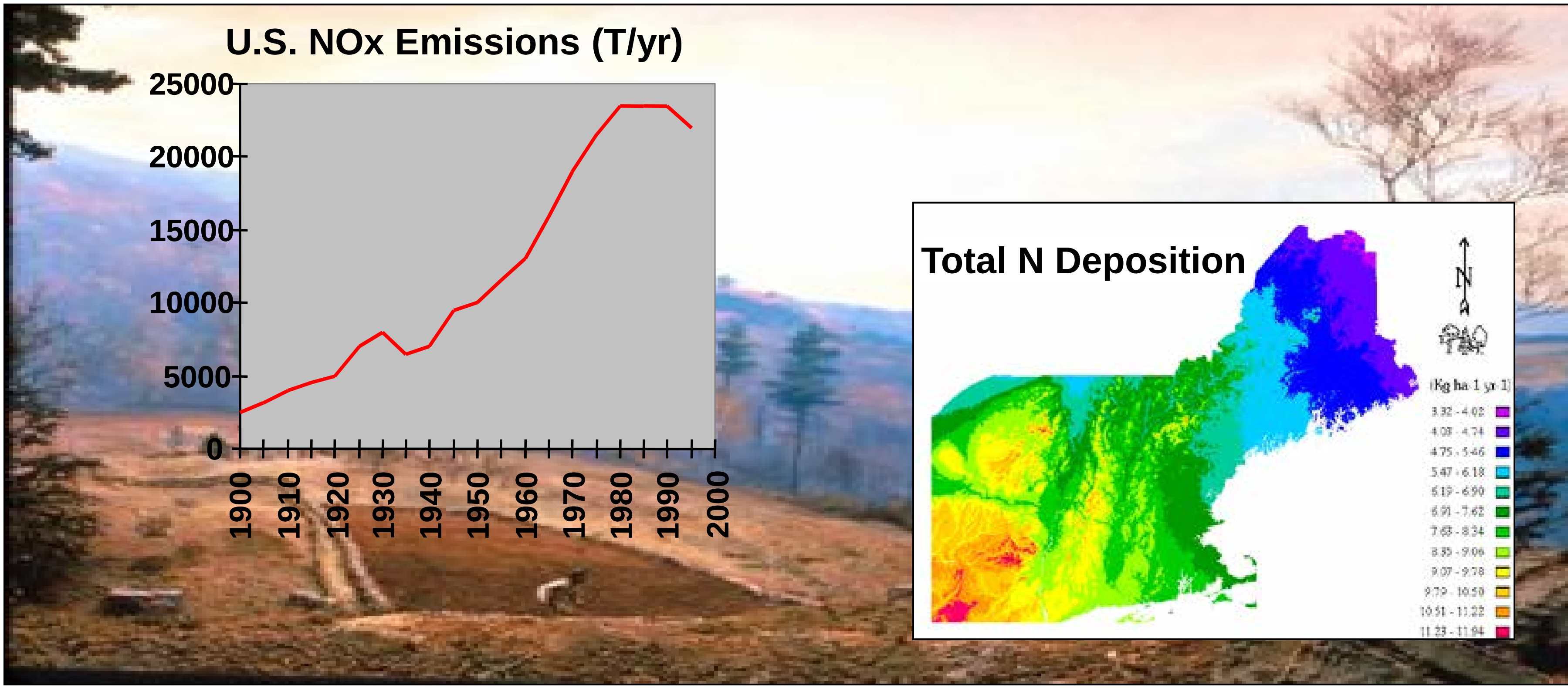
Terrestrial Decomposers

- Bacteria (con’t)
  - Spatial specialists
    - Rhizosphere, macropores, interior of aggregates
    - Form biofilms on particle surfaces
  - Chemical specialists
    - Different bacteria produce different enzymes
      - consortium
    - Aerobic and anaerobic environments

Terrestrial Decomposers

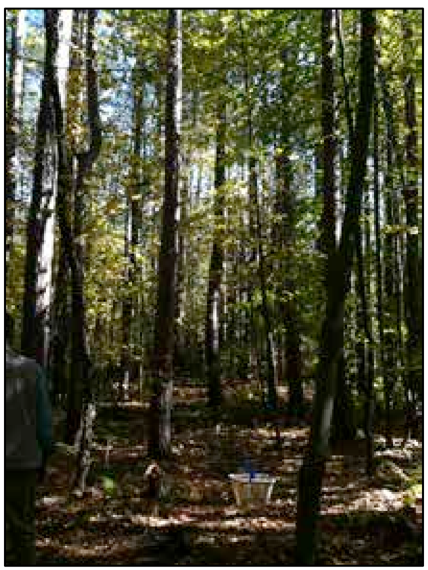
- Bacteria (con’t)
  - Most bacteria are immobile
  - Become inactive when labile substrate is exhausted
    - 50 to 80% of soil bacteria inactive at any given time, and can remain so for years
  - Activated by presence of substrate
    - e.g., when root grows past; after a precipitation event

The Chronic Nitrogen Addition Experiment at Harvard Forest—A 20-year Synthesis



Experiment initiated in 1988 to better understand the process of forest N saturation due to anthropogenic N deposition.

20-years: Ecosystem Response



<u>Stand Type</u>

Pine and Hardwood

<u>N Deposition Rate</u>

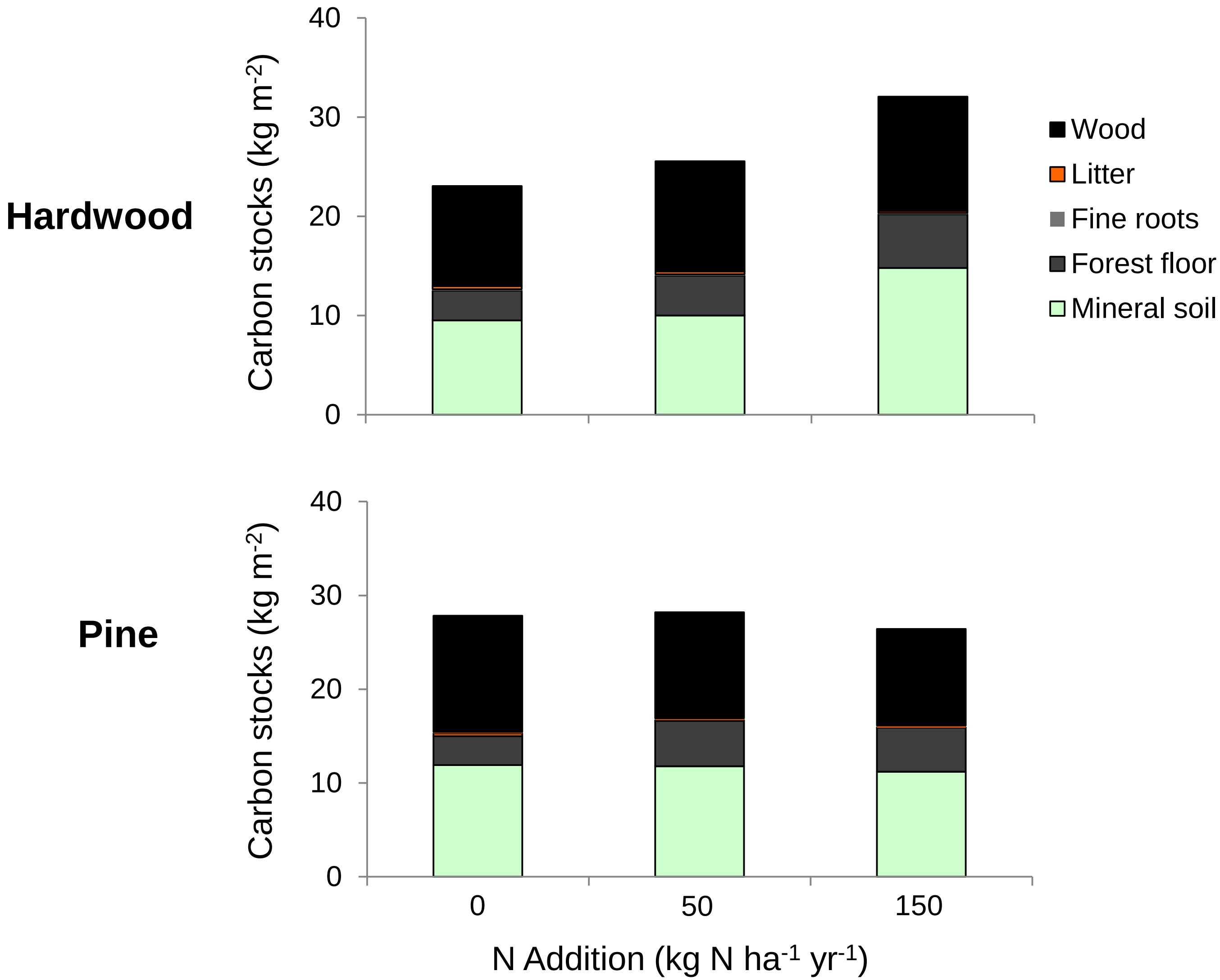
0, 50, 150

kg N ha^{-1} yr^{-1}

Nitrogen deposition is known to increase carbon storage in tree biomass, but soils are an important component of global carbon storage and the effects of nitrogen addition on soil carbon sequestration is less known.

Enhanced carbon inputs to soil via litterfall and root production would drive increases in soil carbon.

20-years: Ecosystem C Stocks

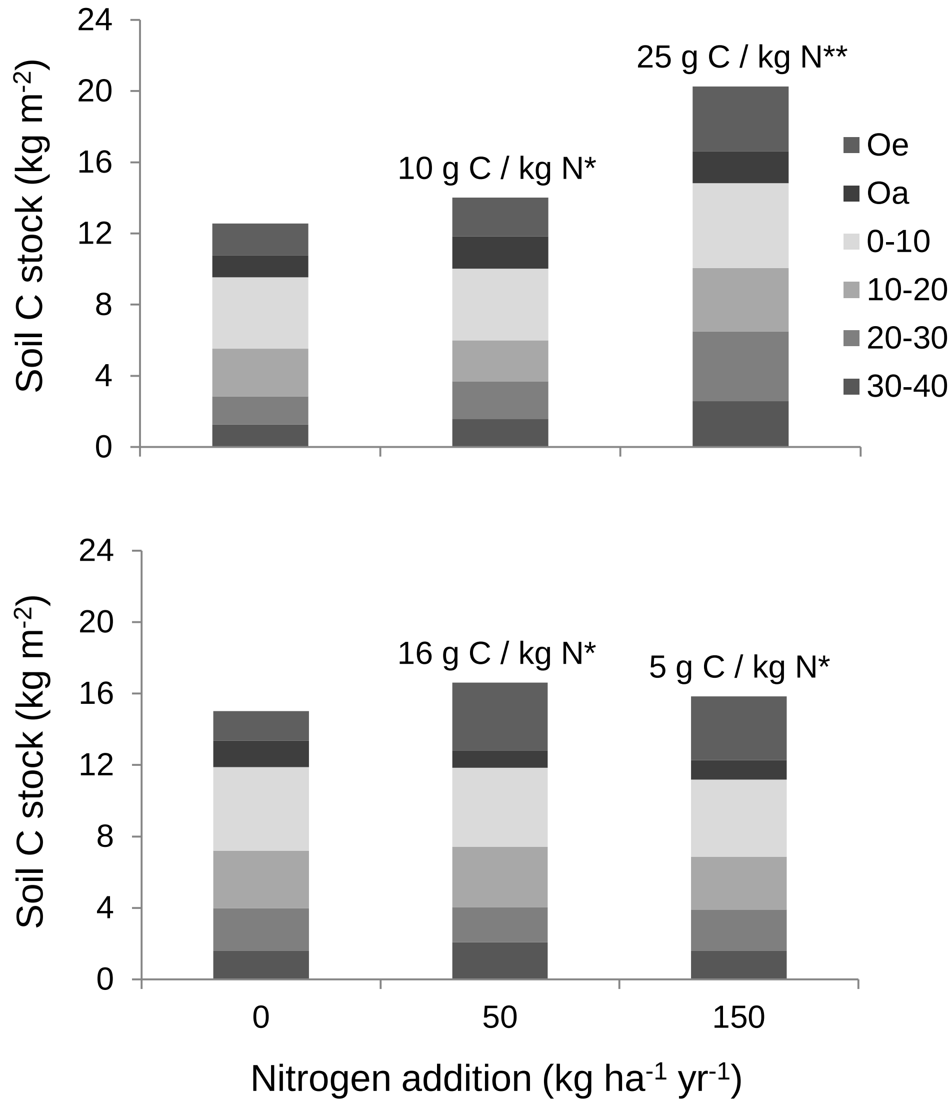


Frey et al. *in review* Biogeochemistry

20-years: Soil C stocks

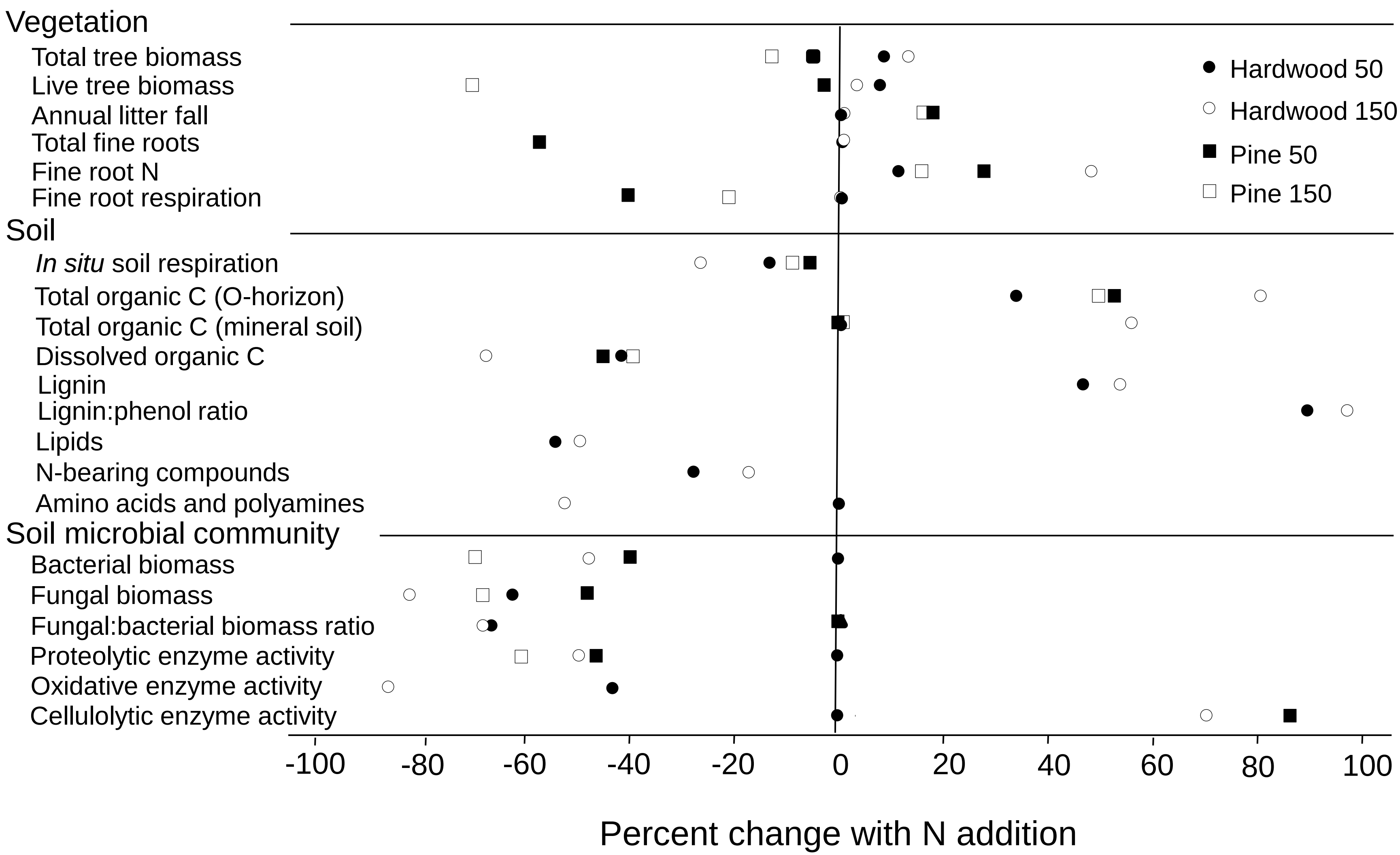
Hardwood

Pine



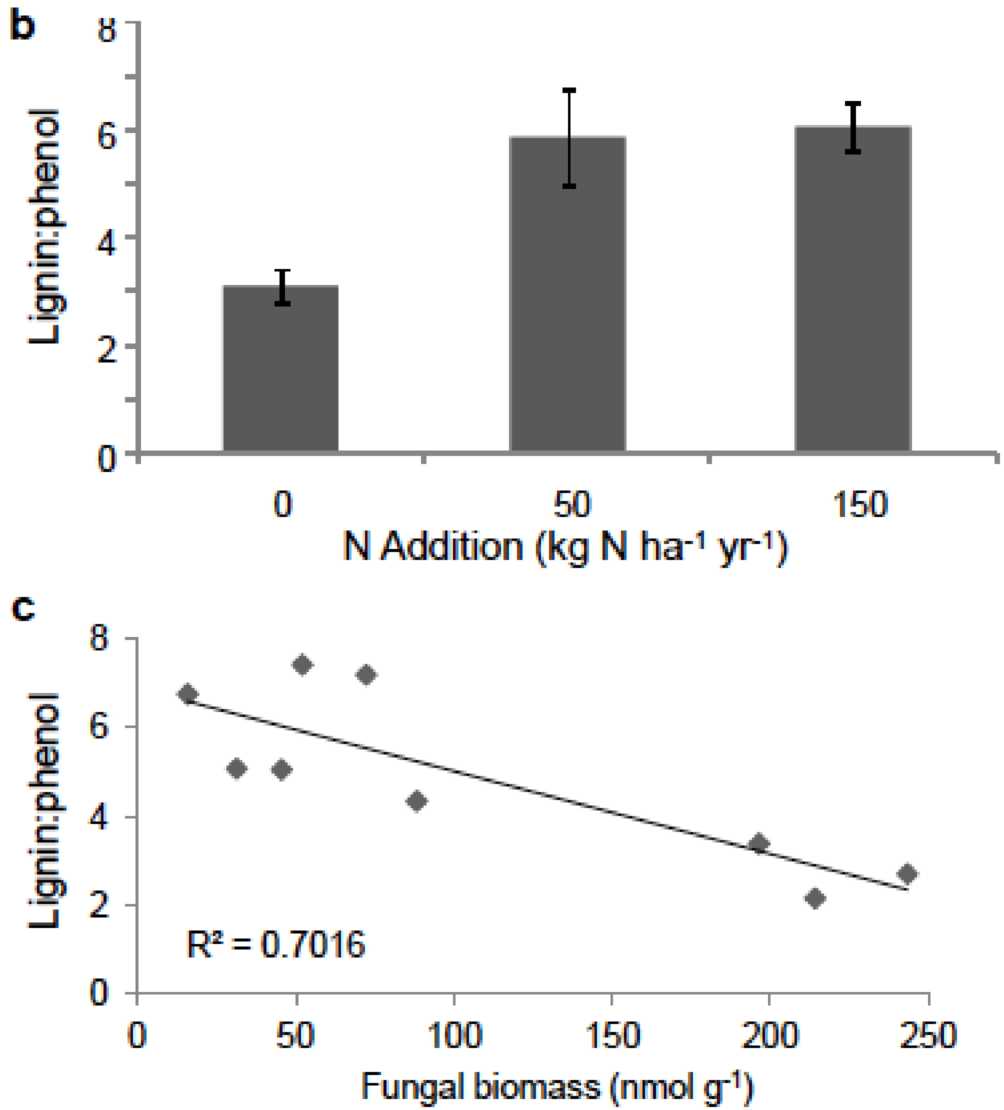
Frey et al. *in review* Biogeochemistry

20-years: Relative Change in Ecosystem Components



Frey et al. *in review* Biogeochemistry

20-years: Inhibition of Fungal Enzymes



Frey et al. *in review* Biogeochemistry

20-years: Conclusion

- Nitrogen-induced soil carbon accumulation is of equal or greater magnitude to carbon stored in trees.
- Nitrogen enrichment resulted in reduced fungal biomass and activity as well as higher rates of lignin accumulation
- Soil carbon accumulation in response to nitrogen amendment was due to a suppression of organic matter decomposition rather than enhanced carbon inputs.

Terrestrial Decomposition

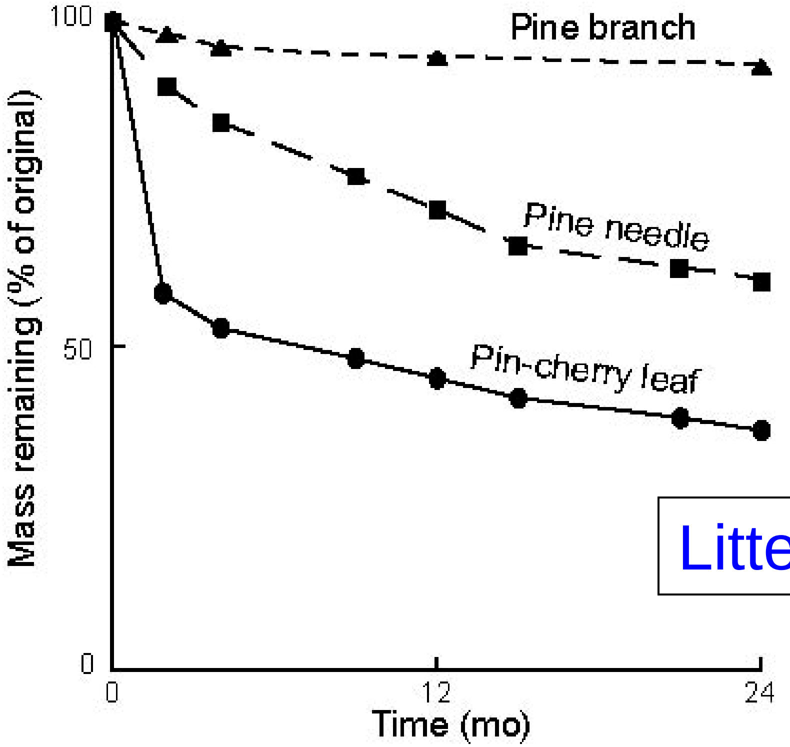
- Controls over decomposition:

1. Properties of microbial community
2. Physical environment
   Temperature, moisture, soil properties
3. Substrate quantity and quality

Litter Decomposition

Respiration

- Decomposition is ~exponential with time
  - Fast initially, and then very slow
  - K is a rough approx. of decomp. over time
  - Rate differs among substrates



Litter bags

Litter Decomposition

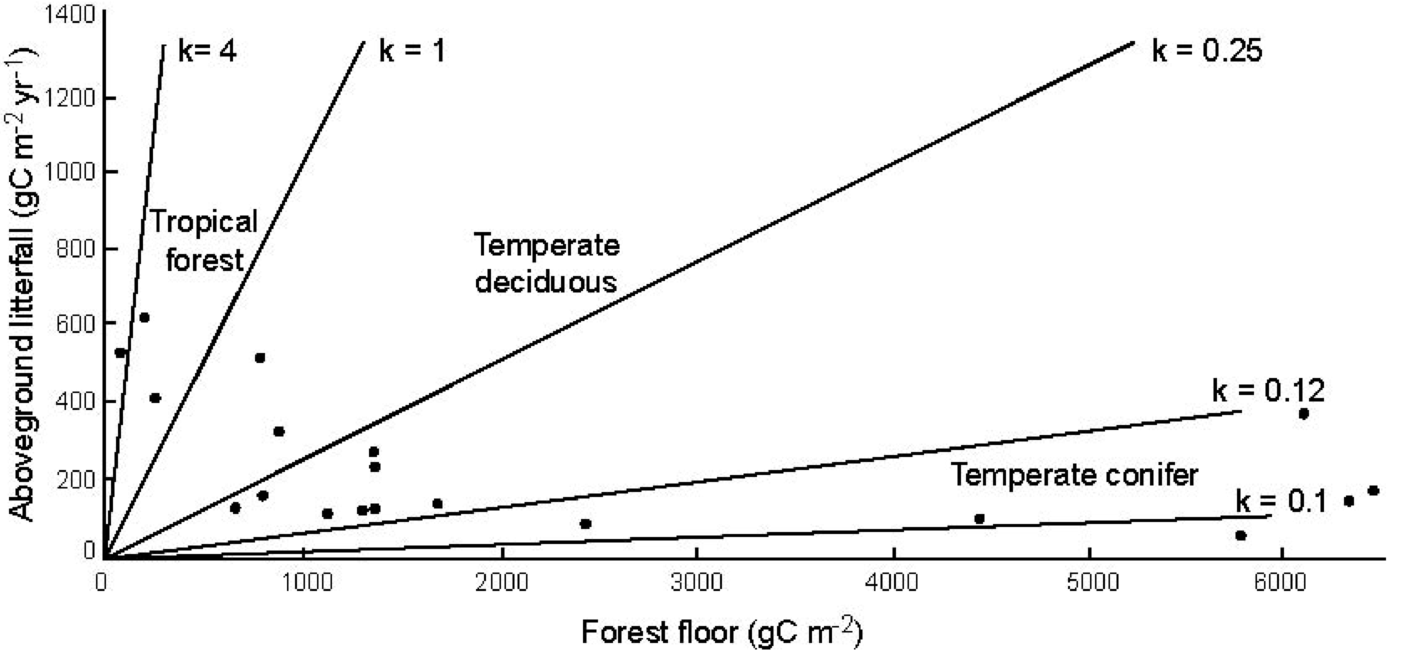
- Litter mass declines ~exponentially with time
  - ~Constant proportion of litter decomposed every year

$$\mathbf{L_t = L_0\, e^{-kt} \quad or \quad lnL_t/L_0 = -kt}$$

L_0 = mass at time zero
L_t = mass at time t
k = the decomposition constant

k = litterfall / litterpool (mass balance at steady state)
1/k = mean residence time (MRT)

Litter Decomposition

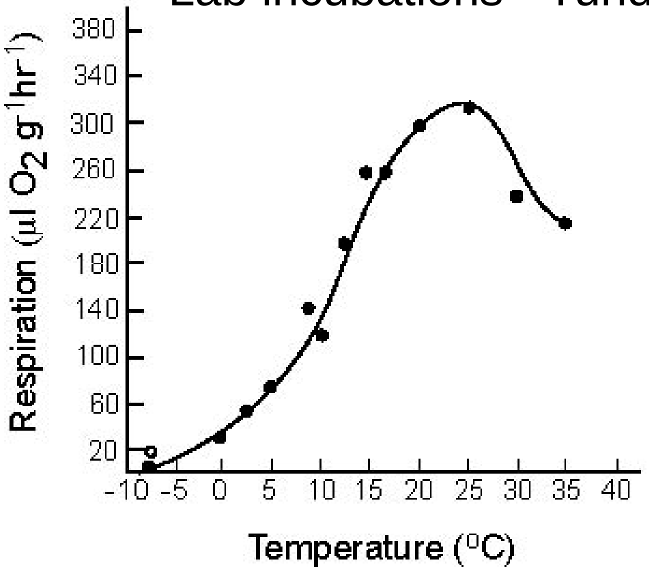


Decomposition rates are highest where it’s warm and moist, lowest where it’s cool and/or dry (or really wet)

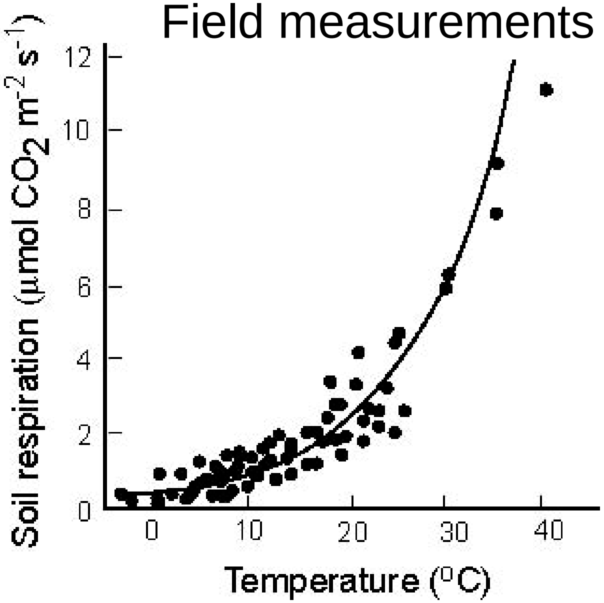
Terrestrial Decomposition

- Direct temperature effect on microbial activity
  - Temperature optimum is usually higher than ambient temperature
  - High temperature not always optimal for microbes, especially those adapted to colder environments

Lab incubations - Tundra



Field measurements – 15 studies



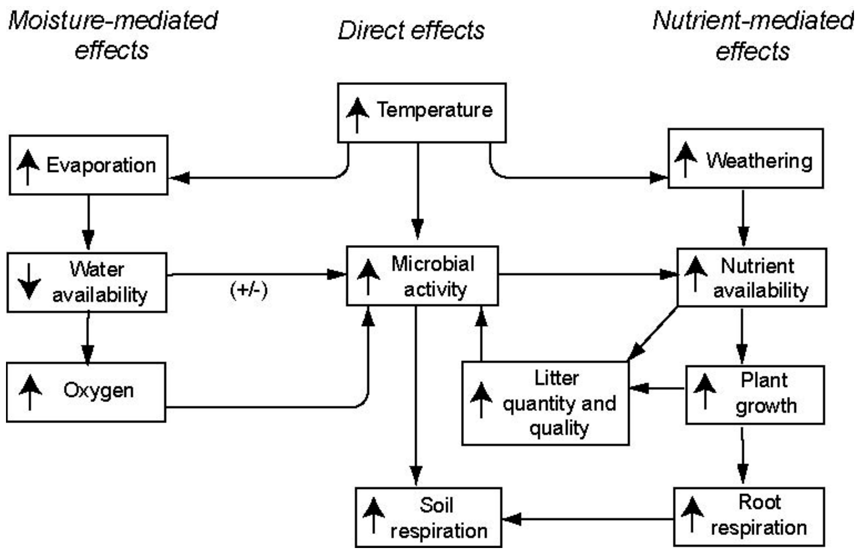
**Soil respiration is a good index of decomposition rates

Terrestrial Decomposition

- Direct temperature effects
  - Effects on microbial activity
    - R_{growth} dominates at optimal temp's, but R_{maint} increases with temperature
  - Effect of temperature fluctuations
    - Freeze-thaw lyses microbes & increases substrate supply seasonally

Terrestrial Decomposition

- Indirect temperature effects
  - High temperature ↑ ET and ↓ soil moisture
  - High temperature ↑ quantity & quality of litter inputs
  - High temperature ↑ chemical weathering and ↑ nutrient supply



Terrestrial Decomposition

- Moisture effects
  - Response of decomposition to moisture is similar to that of NPP
    - Declines at extremely low and high moisture
    - Enhanced by moisture "pulses"
  - Less sensitive to low moisture than is NPP (little litter accumulation in deserts - photodegradation)
  - More sensitive to high moisture than is NPP (SOM accumulation in waterlogged soils)
    - O_2 diffuses 10,000 more slowly in H_2O than air
    - Plants can transport O_2 from leaves to roots, but not microbes

Terrestrial Decomposition

- Other environmental effects
  - pH
    - Bacteria predominate at high and fungi at low pH
    - Higher rates at neutral pH, lower rates at low pH
  - Soil texture
    - Increased water-holding capacity
    - Binding of SOM by clays (- and + charge sites)
    - Adsorption and deactivation of enzymes by clay
    - *Aggregate structure (anaerobic microsites)

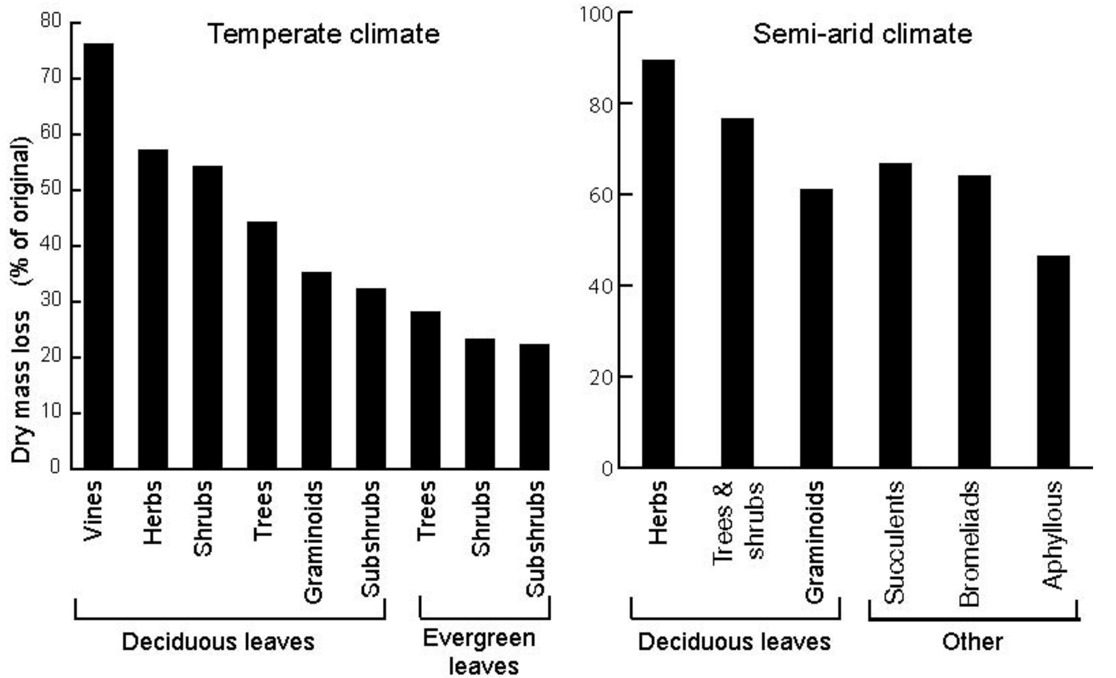
Terrestrial Decomposition

- Substrate quality depends on:

1. Size of molecule (e.g., large molecules must be broken down with enzymes)
2. Types of chemical bonds (e.g., ester linkages versus double bonds)
3. Regularity of structures (e.g., irregular lignin more complex to breakdown)
4. Toxicity (e.g., byproducts may be toxic)
5. Nutrient concentration (e.g., high C:N ratio associated with slow decay)

Litter Decomposition

- Plant species differ predictably in litter quality
  - High-resource-adapted leaves decompose quickly due to higher concentrations of labile C and N
  - Belowground resources are the dominant control over litter quality

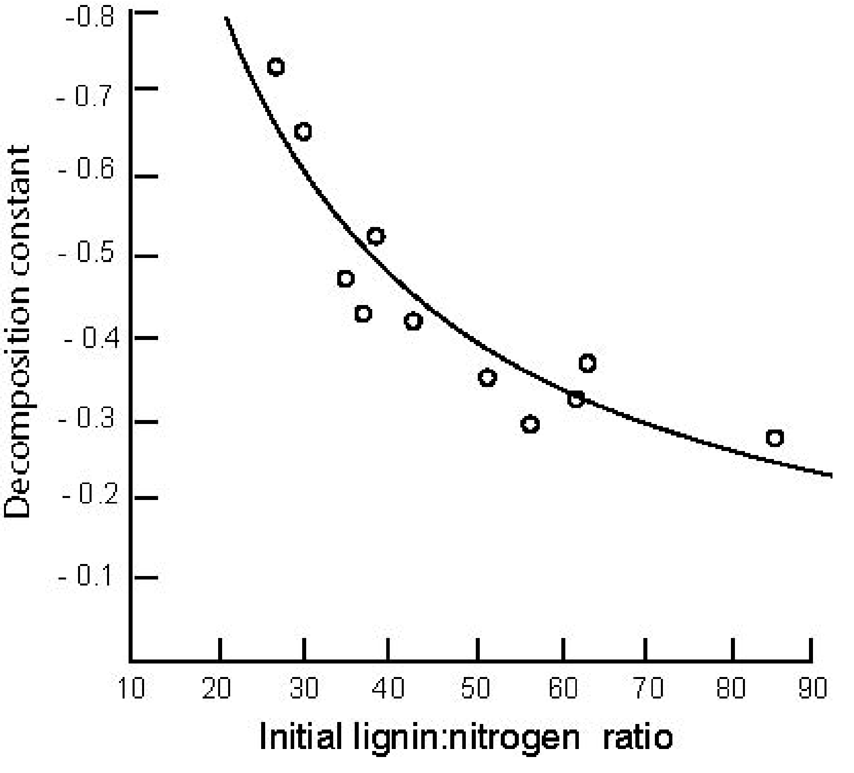


Litter Decomposition

- Predictors of decomposition
  - C:N ratio
    - Widely used in the past, not as much now
    - Directly affects decomposition mainly in presence of readily available labile C
      - e.g., Rhizosphere
  - Lignin:N ratio
    - Integrated measure of N concentration and substrate size/complexity
    - Better index in recalcitrant litter

Litter Decomposition

- As lignin:N in leaf litter increases, decomposition rate decreases



Terrestrial Decomposition

- Substrate quality
  - Susceptibility to decomposition
  - Perhaps THE predominant control over litter decomposition in many ecosystems
    - Climate exerts large effect on substrate quality through effects on vegetation
    - 5 to 10-fold difference in decomposition of different materials in a given climate

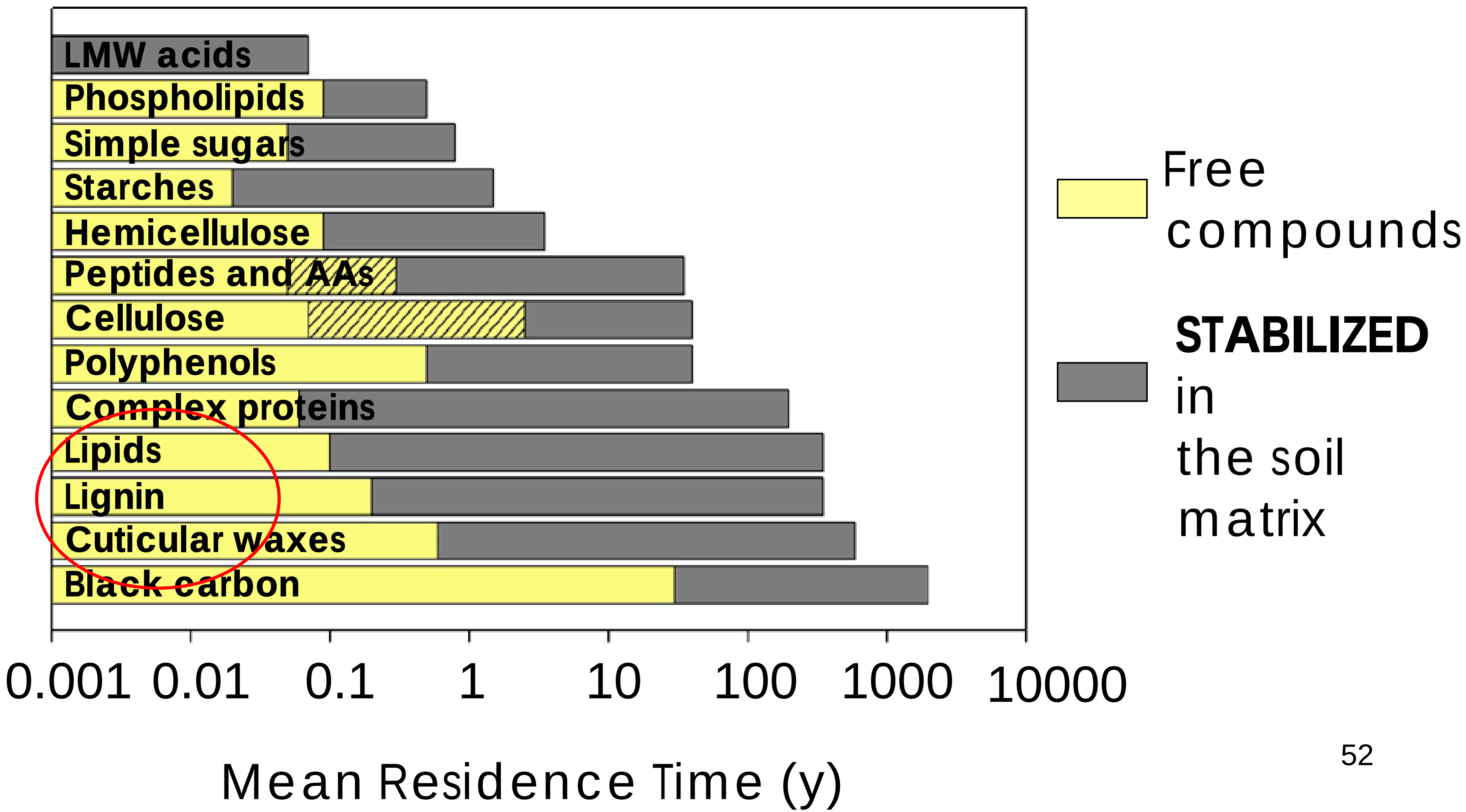
Soil Organic Matter

- Mechanisms for soil organic matter stabilization:

1. Recalcitrance (refers to chemistry)
2. Physical protection
    - Within soil aggregates
    - Organo-mineral associations
3. Substrate supply regulation (energetic limitation)

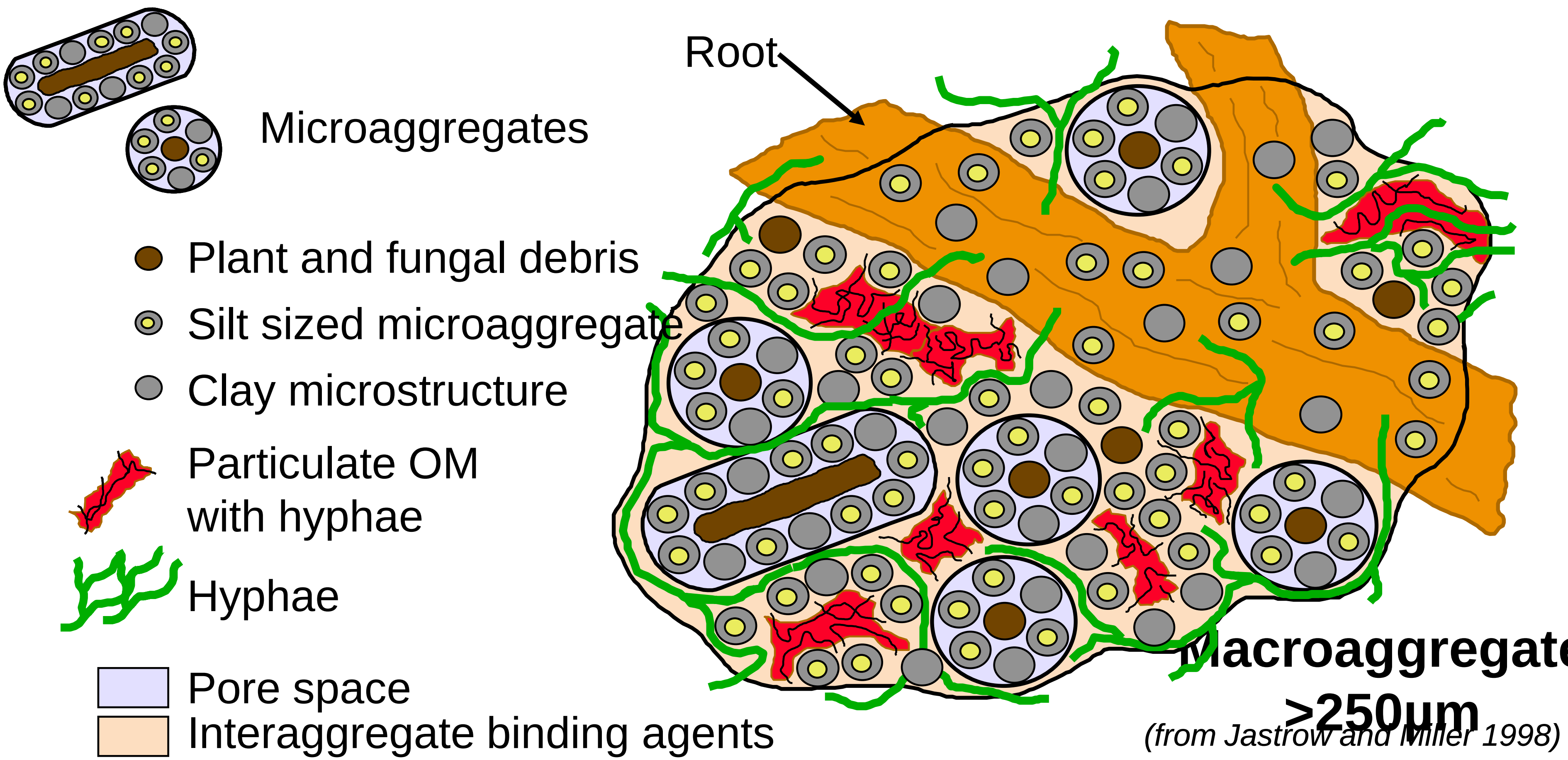
Primary mechanisms for SOM stabilization

1. Recalcitrance



Primary mechanisms for SOM stabilization

2a. Physical protection within aggregates

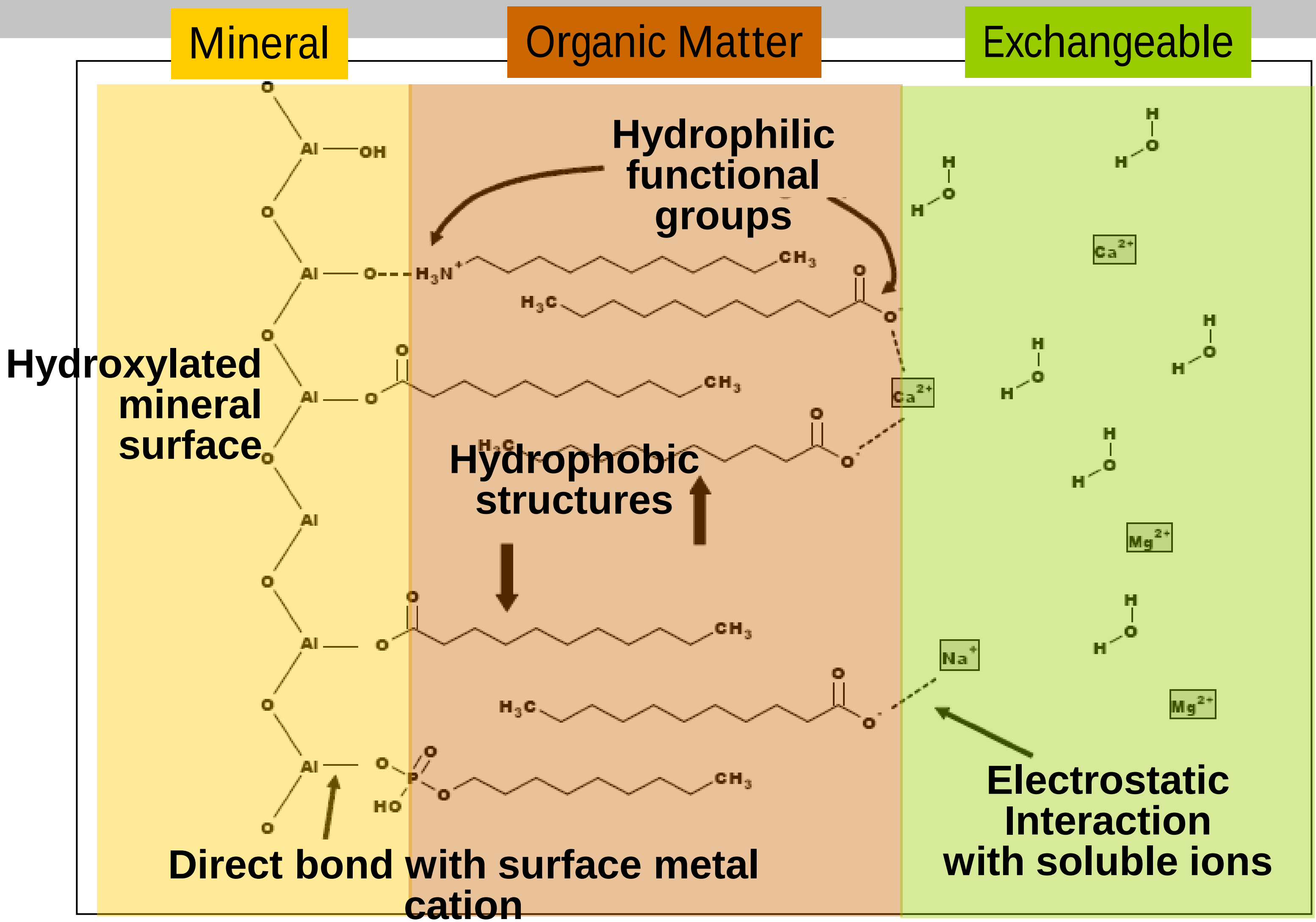


(from Jastrow and Miller 1998)

Soil Processes and the Carbon Cycle, CRC Press.

Primary mechanisms for SOM stabilization

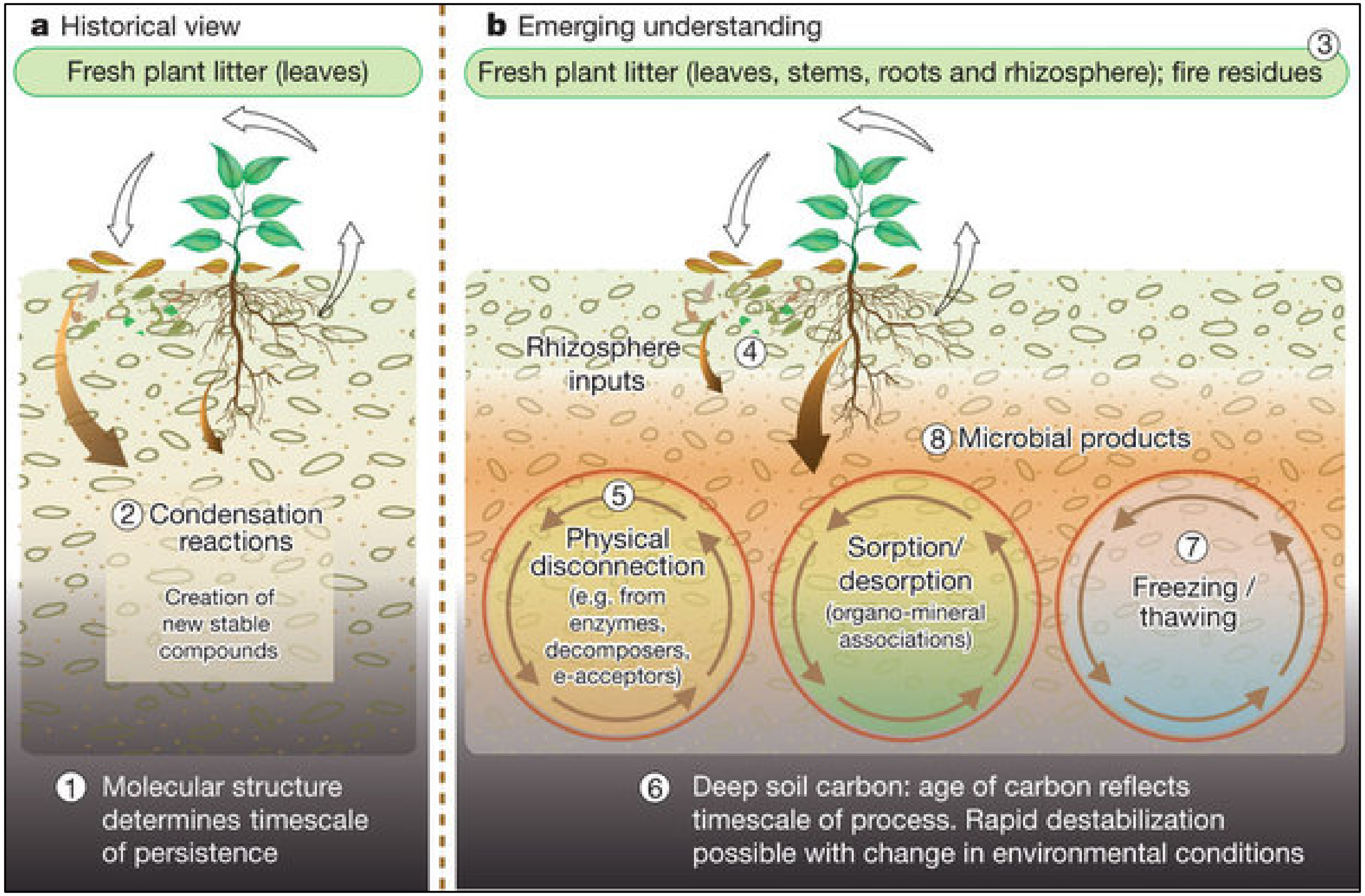
2b. Binding to mineral surfaces



(Kleber et al. 2007, Biogeochemistry)

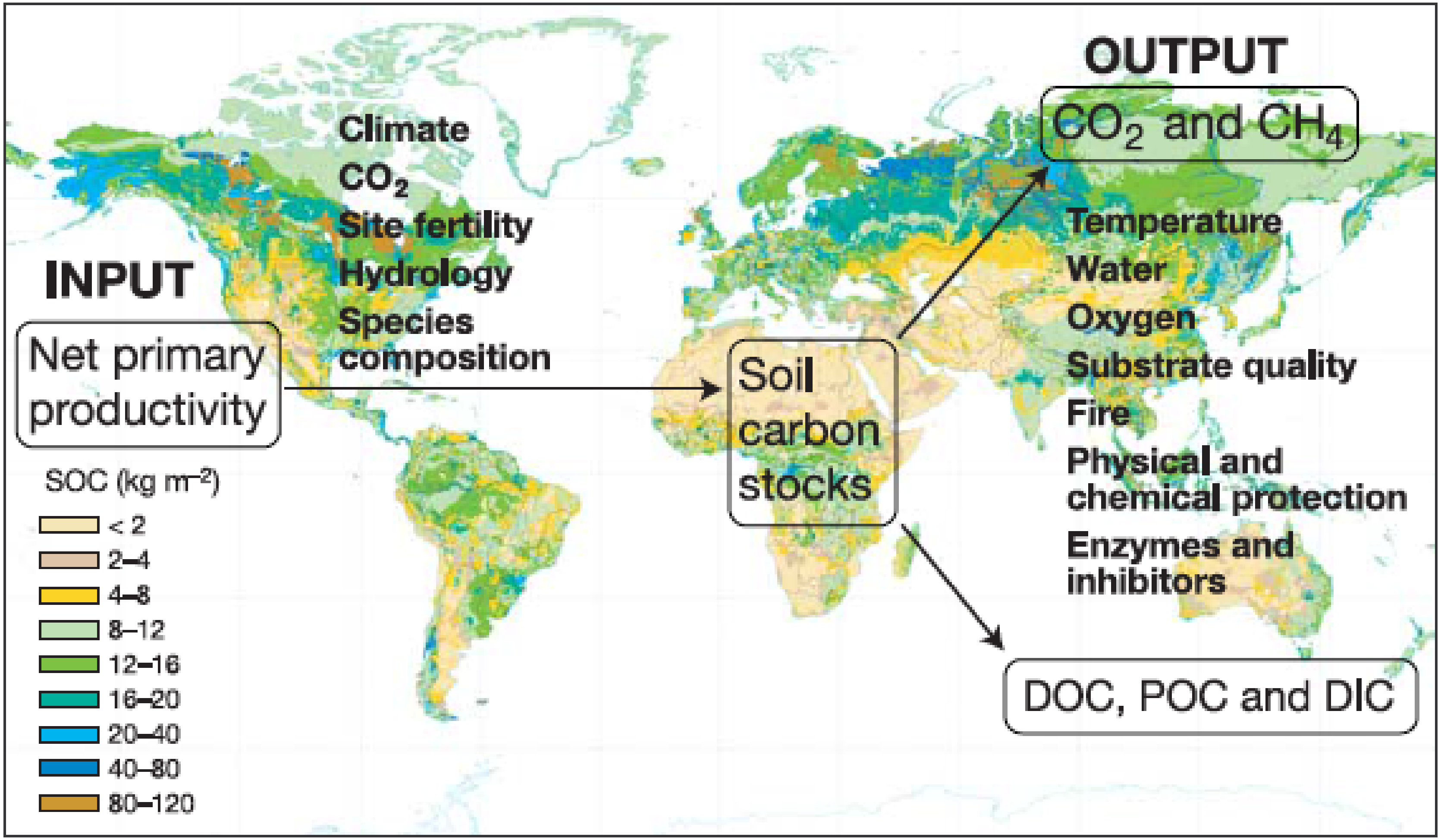
Changing paradigms

* Key is that these factors limit microbial accessibility to otherwise decomposable organic matter*



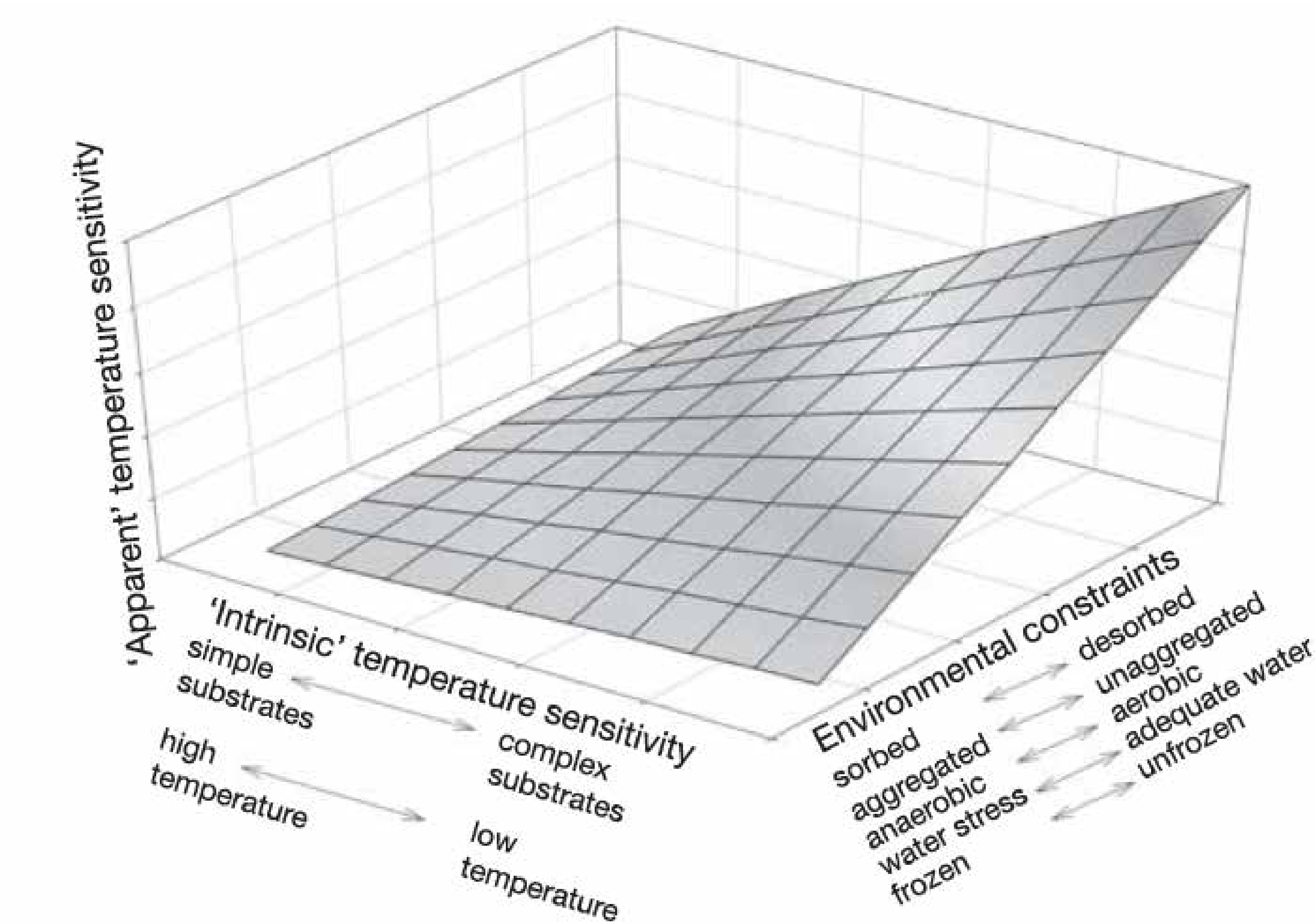
Schmidt et al. 2011, Nature

Soil C Stock and Climate Change



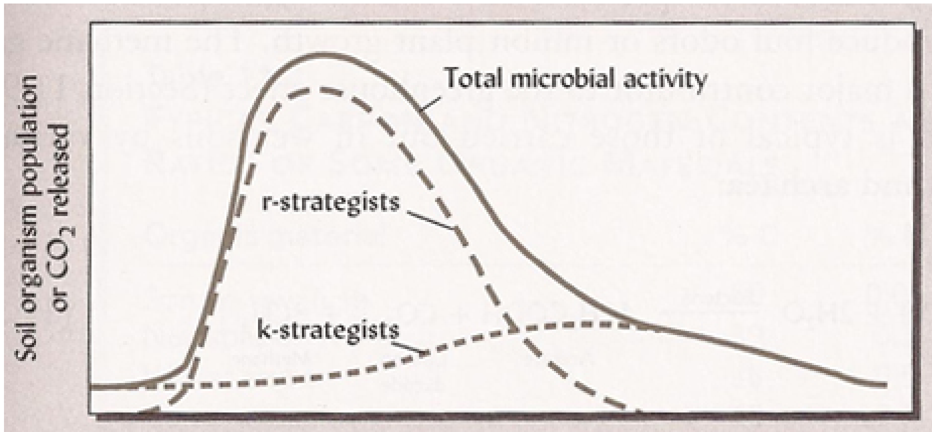
Because of large stable pools within soil C stock, small changes in the decomposition rate of those stable pools may impact decadal scale changes in global soil C reservoir (from Davidson and Janssens 2006)

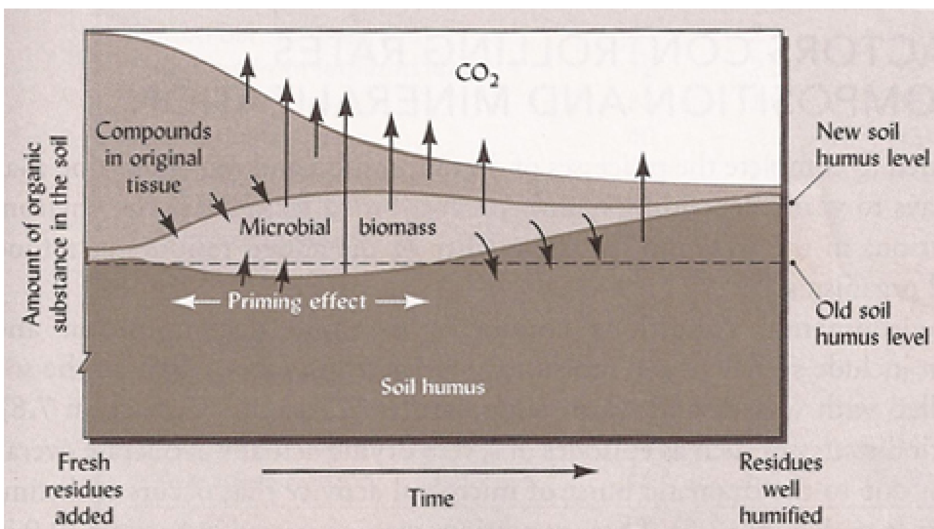
Temperature Sensitivity



Environmental constraints drive differences between intrinsic and apparent temperature sensitivity; and those constraints may themselves be temperature dependent (from Davidson and Janssens 2006).

Microbial Response to Litter Input

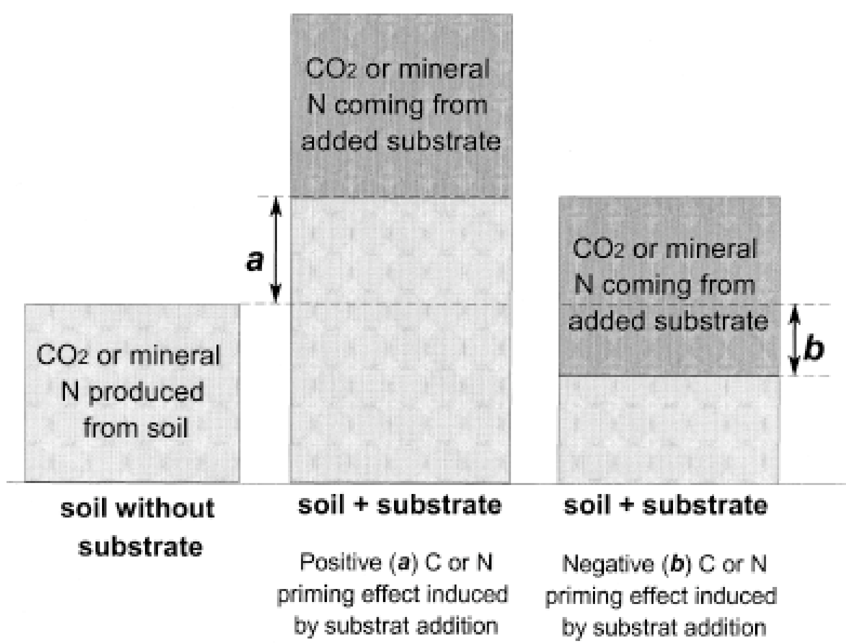




- Activity of r-strategist (opportunistic) community increases and overtakes k-strategists (slow and steady decomposers)
- During r-strategists reign: respiration high, microbial biomass high
- r-strategists go dormant or die when preferred substrate is gone, k-strategists consume biomass and remaining litter
- Some carbon from decomposition process is converted to soil humus

Soil Priming

"Priming Effect"

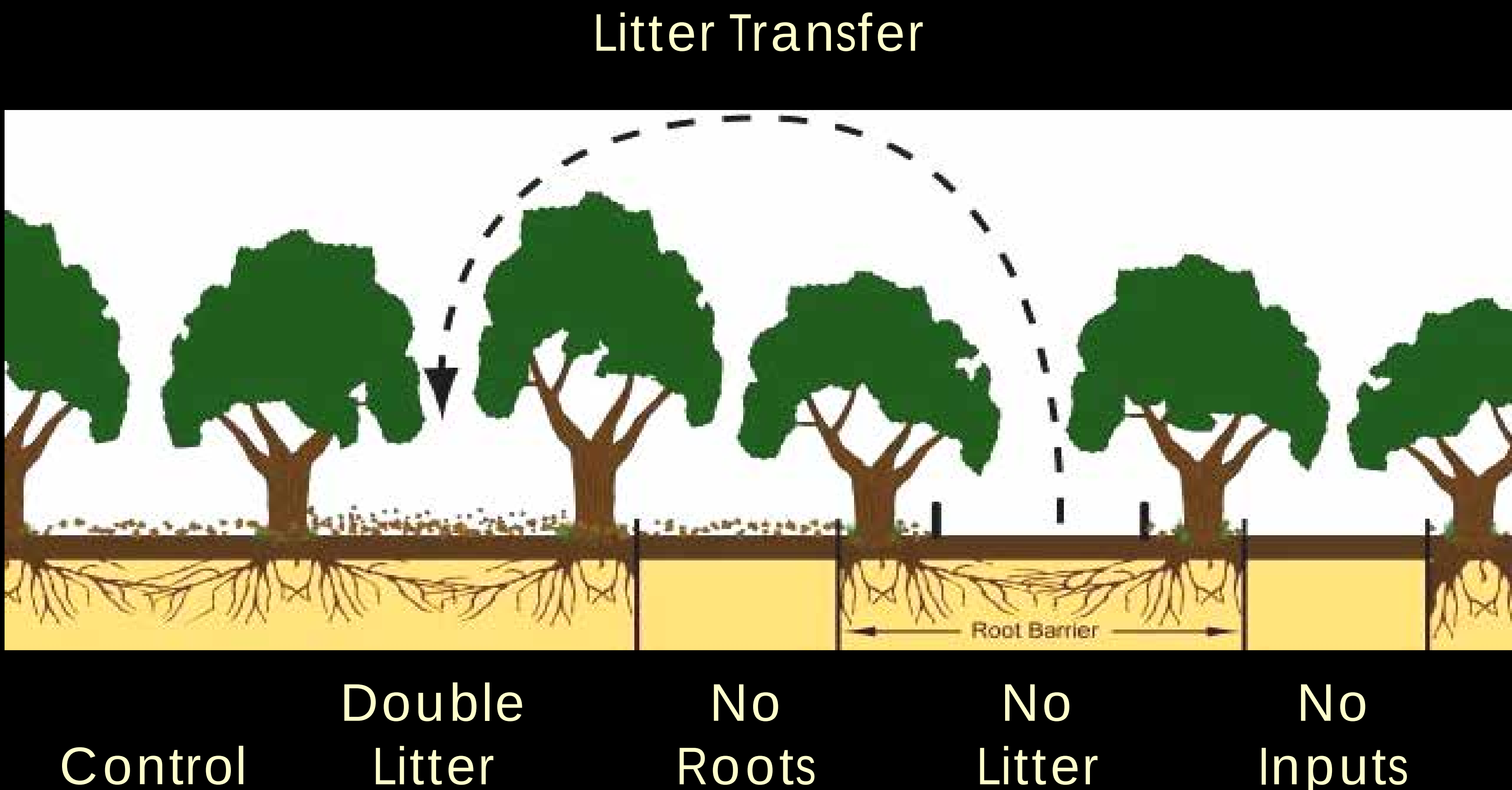


(*from* Kuzyakov *et al*. 2000)

•Non-additive interaction between the decomposition of the added substrate and of SOM.

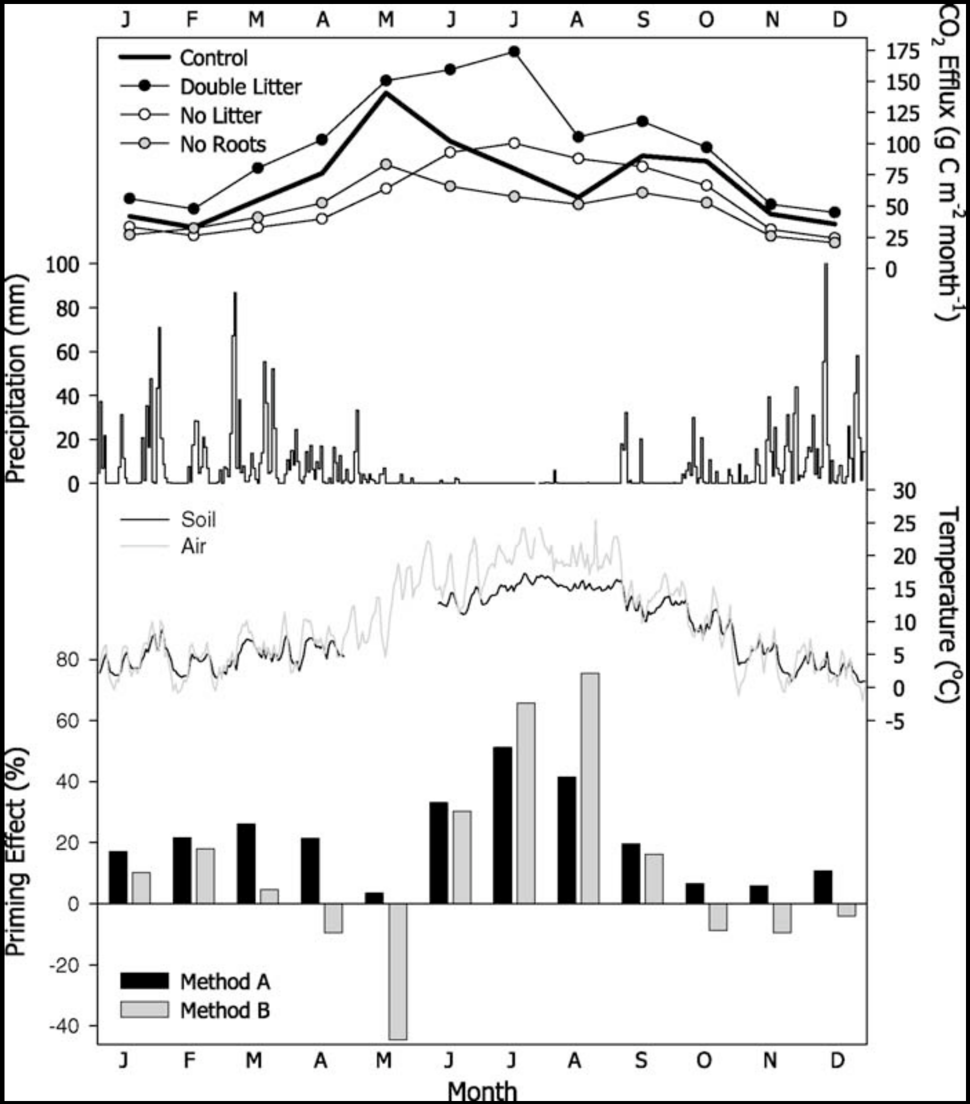
•One possible mechanism is rapid response of bacteria to fresh inputs (Fontaine *et al.* 2003).

Soil Priming: DIRT Treatments



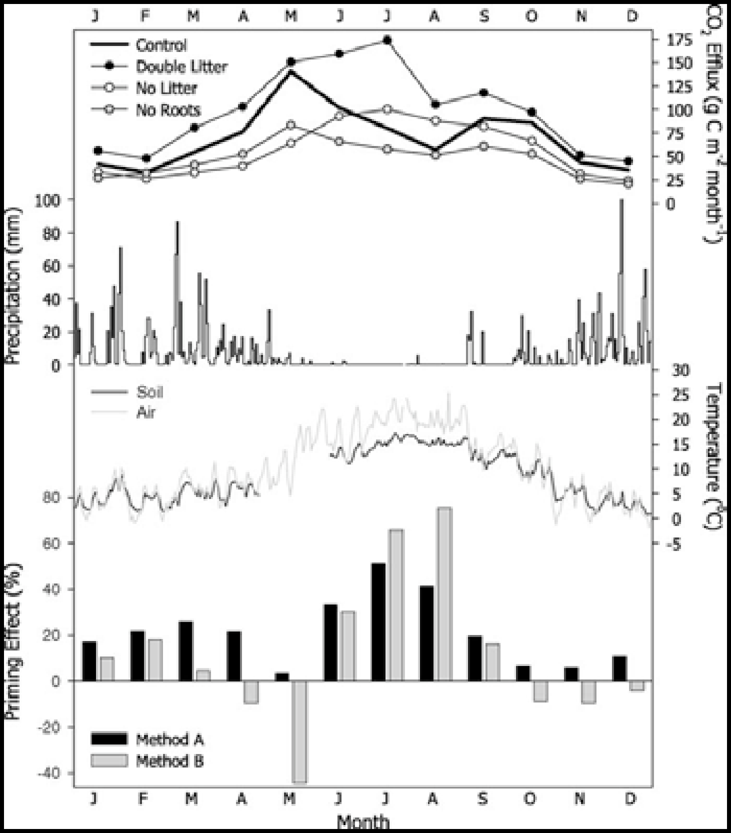
From Nadelhoffer et al. 2004

Soil Priming: Measurements



(*from* Crow *et al.* 2009)

Soil Priming: Net Effect



-Dec. in %C
-Inc. in degradation index
-Inc. in stability of residual SOM

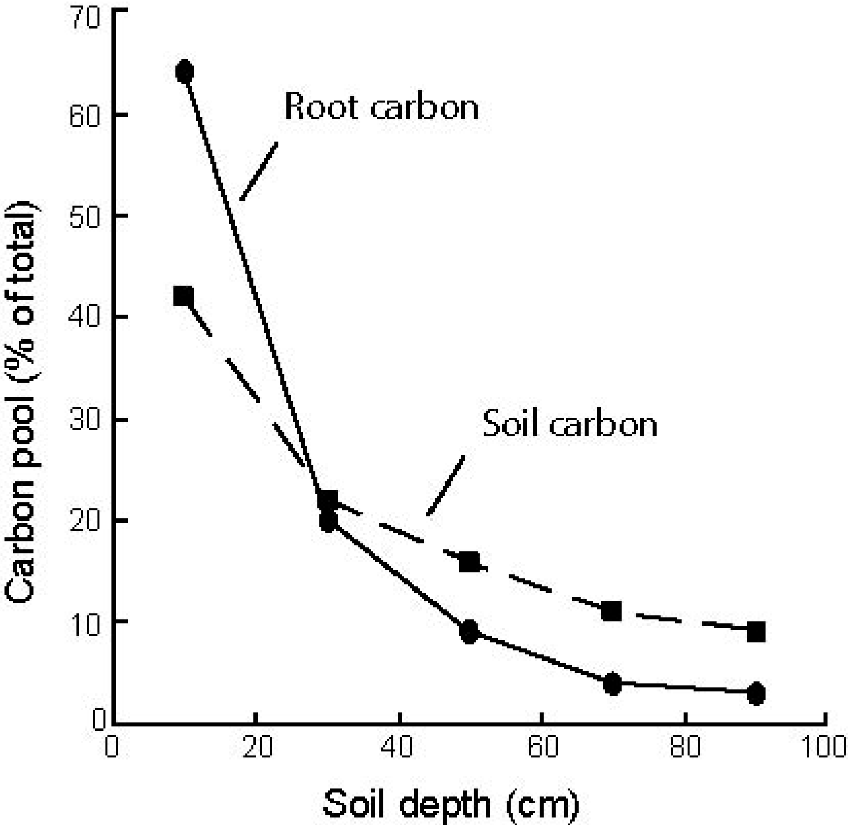
-No change in the functional microbial community

(*from* Crow *et al.* 2009)

Soil Organic Matter

- Soil (and decomposition) is spatially heterogeneous

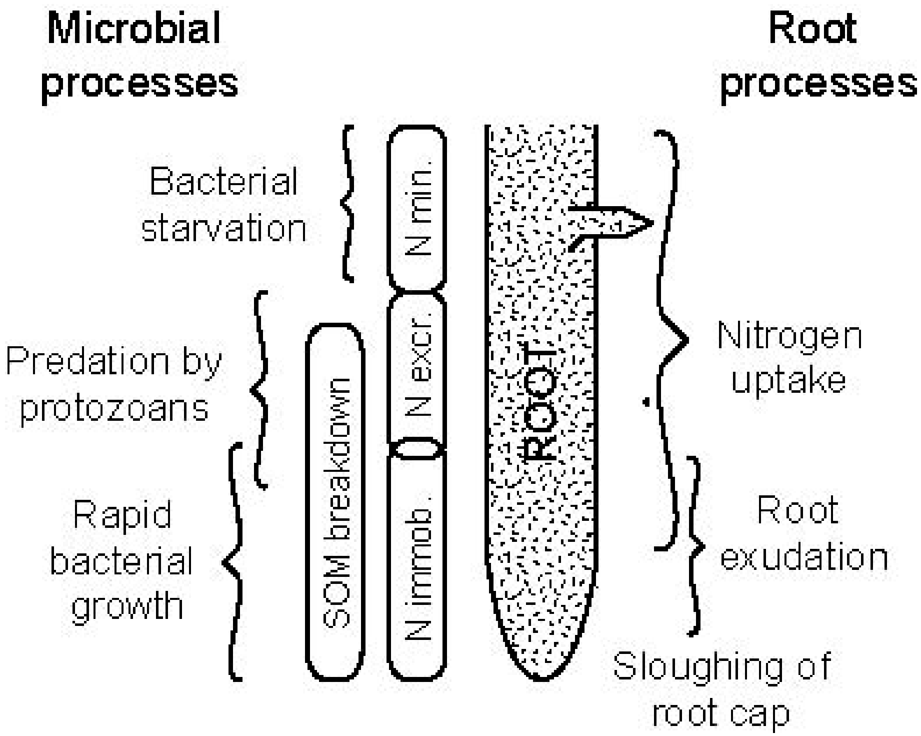
1. Aboveground litter layer, soil organic matter, and mineral soil
   - Most decomposition in litter
   - Roots and nutrients concentrated near soil surface
2. Surface roots/SOM vs. deep roots/SOM
3. Soil aggregates and macropores
4. Rhizosphere vs. bulk soil



SOM Decomposition

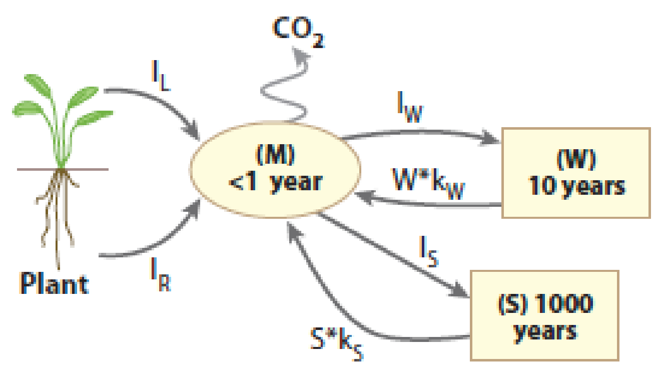
- Rhizosphere is the major zone of SOM decomposition

1. High inputs of labile C "prime" decomposition
2. Microbes break down SOM for nitrogen
   - Grazing vs. starvation



SOM Decomposition

- Soil is chemically heterogeneous
  - Fresh litter vs. old soil organic matter
  - Different plant parts (leaves vs. wood vs. roots)
  - Cell walls (structural) vs. cell contents (metabolic)
  - Conceptual pools
    - Labile vs. recalcitrant
    - Active vs. slow vs. passive



(*From* Trumbore 2009)

SOM Decomposition

- Other environmental effects
  - Soil disturbance (e.g., tilling in ag. fields)
    - Reduces SOM protection by clays
    - Breaks up soil aggregates
    - Increases aeration
    - Compaction

SOM Decomposition

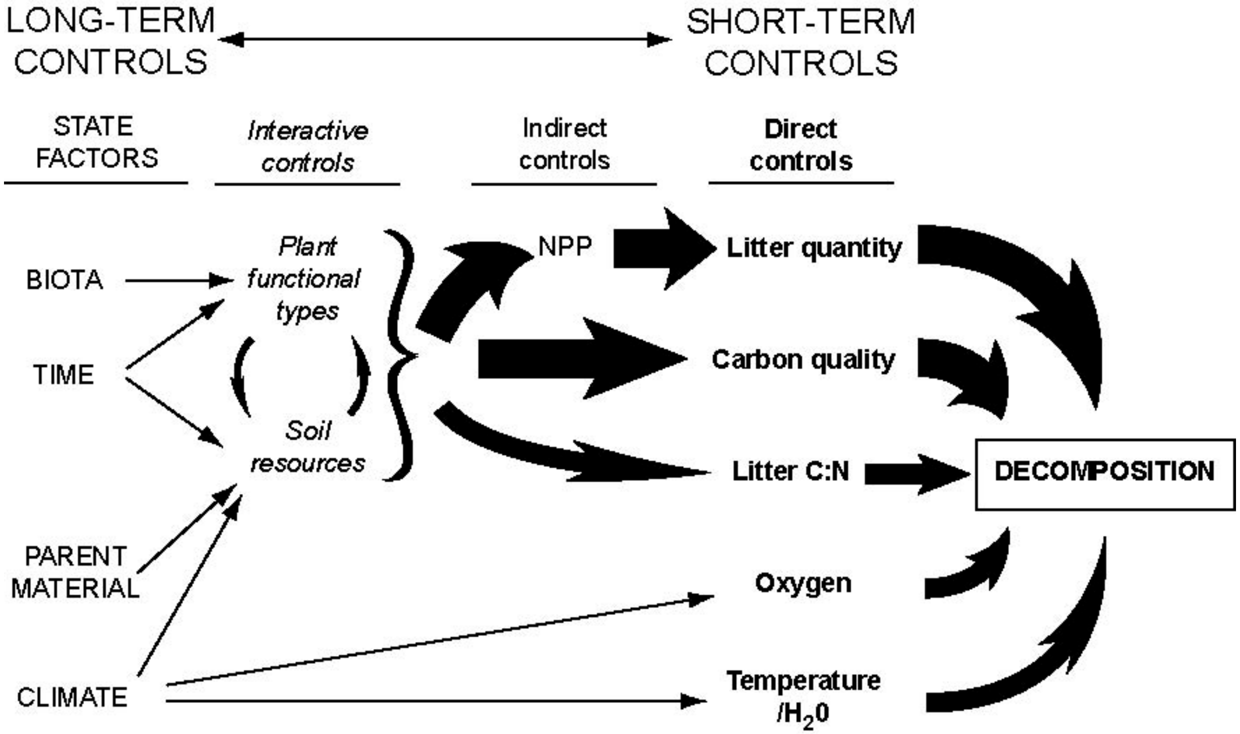
- Influenced by age of SOM and initial quality of litter
- Much of SOM is old and recalcitrant
  - But not all of it.
- Low C:N
  - but not more N available!
- Average residence time of SOM of 20-50 years
  - Ranges from days to 1000s of yrs both across and within sites
- SOM decomposition faster in rhizosphere than bulk soil

Terrestrial Decomposition

- Soil-surface CO_2 efflux ('soil respiration')
  - –Major pathway for return of CO_2 to the atmosphere
  - –Production of CO_2 in soils is a biological process
    - R_{autotr} and $R_{heterotr}$
  - –Flux of CO_2 from soils is a physical process
    - Diffusion (and mass flow)
  - –Soil respiration consists of both autotrophic and heterotrophic components
    - Lots of effort to separate these components
    - To date, ~½ vs. ~½

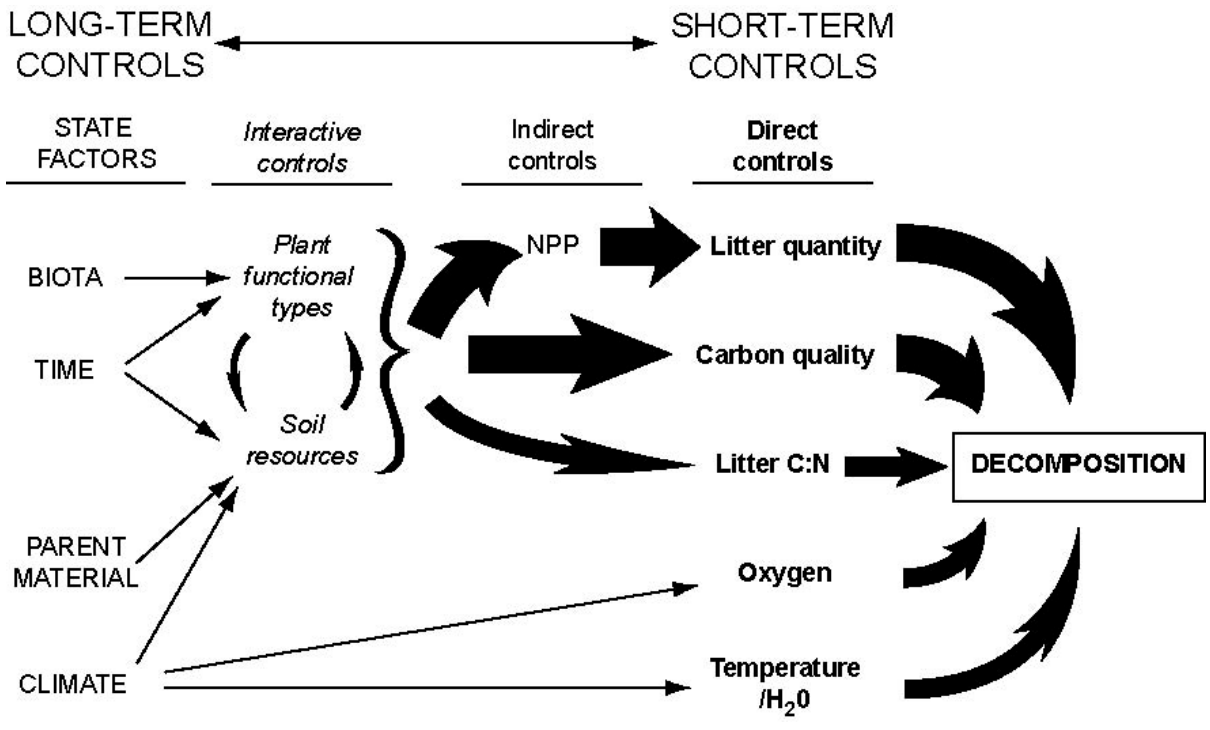
Terrestrial Decomposition

- Substrate quantity and quality are the major short-term controls over decomposition



Terrestrial Decomposition

- Short-term controls over ecosystem-level decomposition are largely controlled by the same variables that control GPP (and NPP)
    - ***Availability of soil resources



Terrestrial Decomposition

- Soil-surface CO_2 efflux ('soil respiration')
  - –Very, very important flux in the C cycle
    - 2nd in magnitude only to GPP
    - Primary component of ecosystem respiration (60-90% in forest ecosystems)
    - Largely determines source/sink dynamics of ecosystems
  - –Lots of emphasis on determining what controls soil respiration
    - Temperature (when moisture is not limiting)
    - Moisture (when temperature is not limiting)
    - Canopy processes
      - – Increasing recognition that recent photosynthetic products largely drive soil respiration

Terrestrial Decomposition: Summary

- Major controls over decomposition
  - Quantity of litter input
  - Quality of litter input
  - Environmental conditions that control biological activity
  - Interactions with soil minerals and aggregates
  - Microbial activity is more important than microbial biomass

Predicting Ecosystem Response to Change

nature climate change

LETTERS

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Global soil carbon projections are improved by modelling microbial processes

William R. Wieder[1]*, Gordon B. Bonan[1] and Steven D. Allison[2]

Society relies on Earth system models (ESMs) to project future climate and carbon (C) cycle feedbacks. However, the soil C response to climate change is highly uncertain in these models[1,2] and they omit key biogeochemical mechanisms[3-5]. Specifically, the traditional approach in ESMs lacks direct microbial control over soil C dynamics[6-8]. Thus, we tested a new model that explicitly represents microbial mechanisms of soil C cycling on the global scale. Compared with traditional models, the microbial model simulates soil C pools that more closely match contemporary observations. It also projects a much wider range of soil C responses to climate change over the twenty-first century. Global soils accumulate C if microbial growth efficiency declines with warming in the microbial model. If growth efficiency adapts to warming, the microbial model projects large soil C losses. By comparison, traditional models project modest soil C losses with global warming. Microbes also change the soil response to increased C inputs, as might occur with CO_2 or nutrient fertilization. In the microbial model, microbes consume these additional inputs; whereas in traditional models, additional inputs lead to C storage. Our results indicate that ESMs should simulate microbial physiology to more accurately project climate change feedbacks.