CHAPTER

5

The Biosphere
The Carbon Cycle of Terrestrial Ecosystems

OUTLINE

Oxidized → Reduced (columns); Oxidized ↑ Reduced (rows)

	H_2O/O_2	C	N	S
H_2O/O_2	X	Photosynthesis $CO_2 \longrightarrow C$ $H_2O \longrightarrow O_2$		
C	Respiration $C \longrightarrow CO_2$ $O_2 \longrightarrow H_2O$	X	Denitrification $C \longrightarrow CO_2$ $NO_3 \longrightarrow N_2$	Sulfate-Reduction $C \longrightarrow CO_2$ $SO_4 \longrightarrow H_2S$
N	Heterotrophic Nitrification $NH_4 \longrightarrow NO_3$ $O_2 \longrightarrow H_2O$	Chemoautotrophy (Nitrification) $NH_4 \longrightarrow NO_3$ $CO_2 \longrightarrow C$	Anammox $NH_4 + NO_2 \rightarrow N_2 + 2H_2O$	?
S	Sulfur Oxidation $S \longrightarrow SO_4$ $O_2 \longrightarrow H_2O$	Chemoautotrophy (Sulfur-based Photosynthesis) $S \longrightarrow SO_4$ $CO_2 \longrightarrow C$	Autotrophic Denitrification $S \longrightarrow SO_4$ $NO_3 \longrightarrow N_2/NH_4$	X

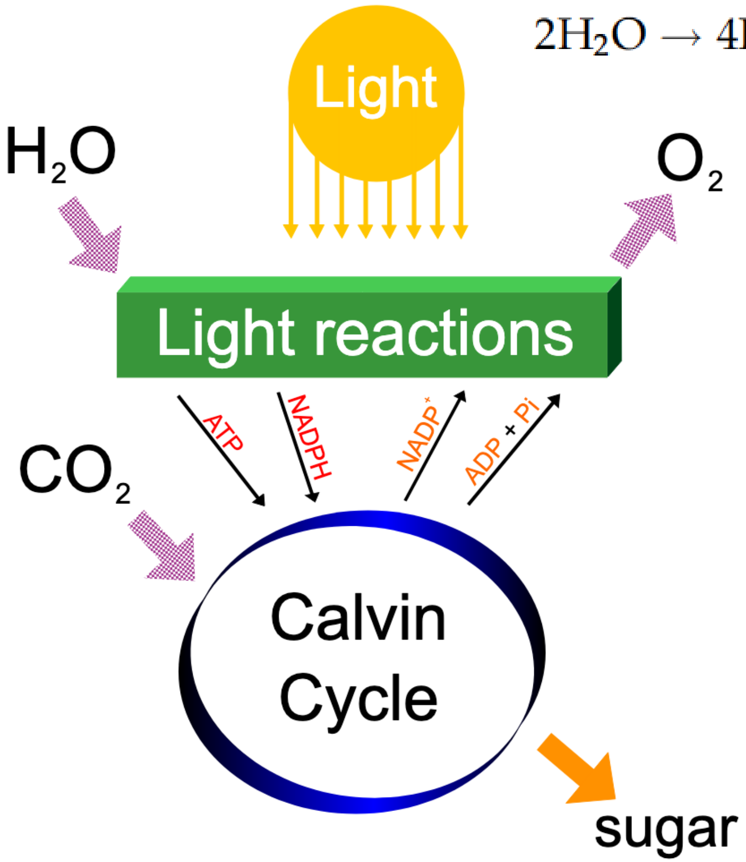
FIGURE 1.4 A matrix showing how cellular metabolisms couple oxidation and reduction reactions. The cells in the matrix are occupied by organisms or a consortium of organisms that reduce the element at the top of the column, while oxidizing an element at the beginning of the row. *Source: From Schlesinger et al. (2011).*

TABLE 4.1 Approximate Mean Composition of Earth's Continental Crust

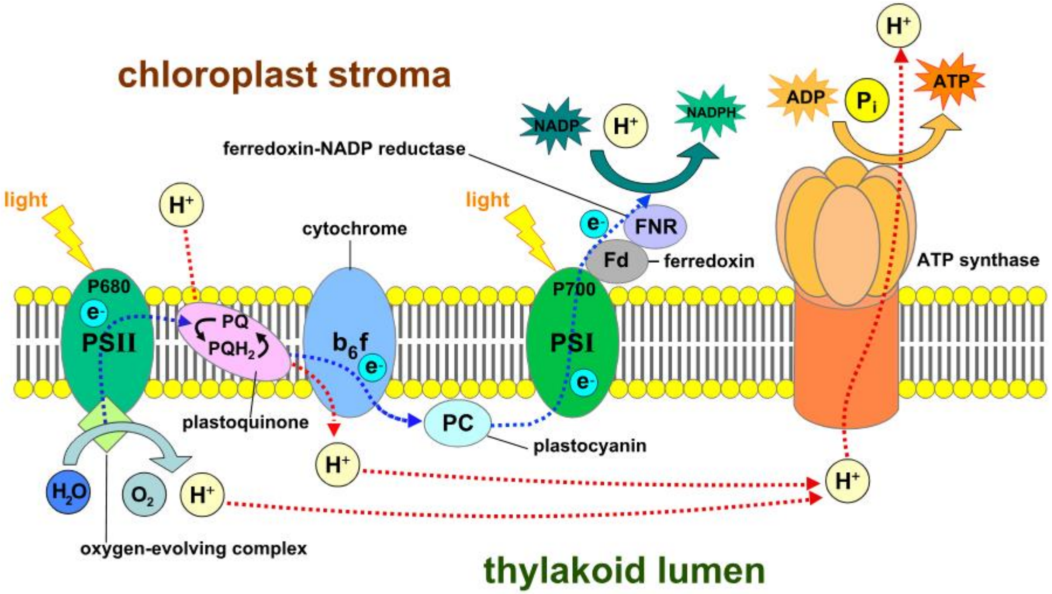
Constituent	Percentage composition
Si	28.8
Al	7.96
Fe	4.32
Ca	3.85
Na	2.36
Mg	2.20
K	2.14
Ti	0.40
P	0.076
Mn	0.072
S	0.070

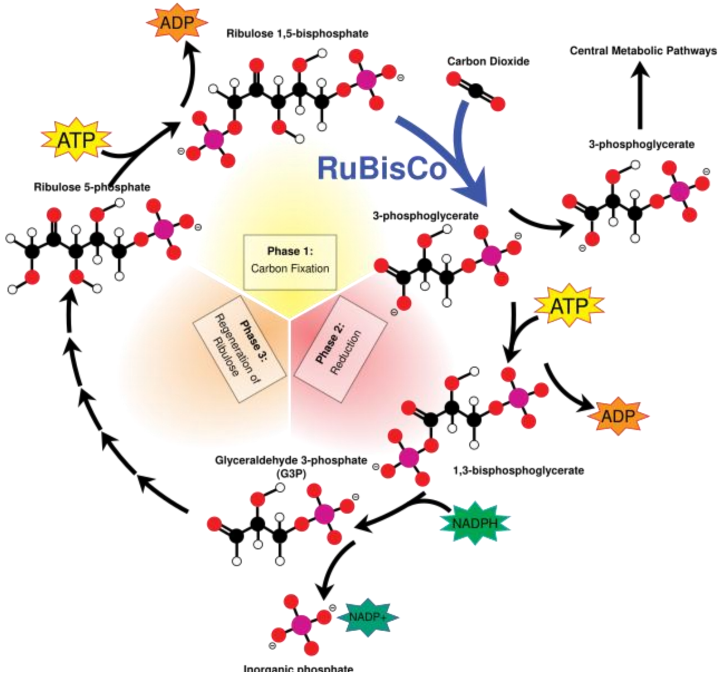
Source: Data from Wedepohl (1995).

$$2H_2O \rightarrow 4H^+ + 4e^- + O_2 \uparrow$$

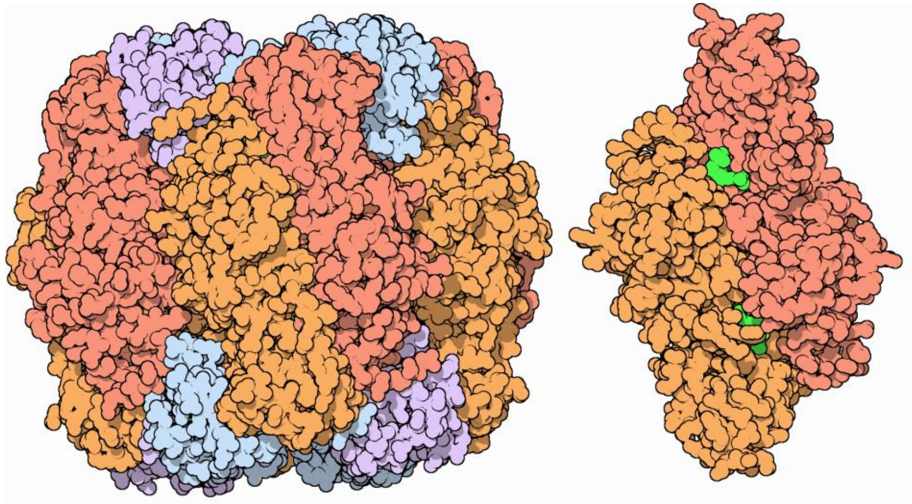


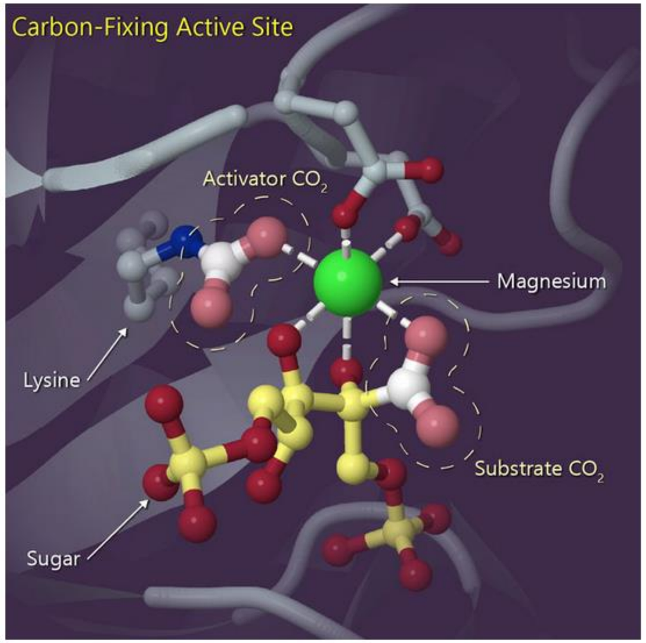
$$CO_2 + H_2O \rightarrow CH_2O + O_2,$$



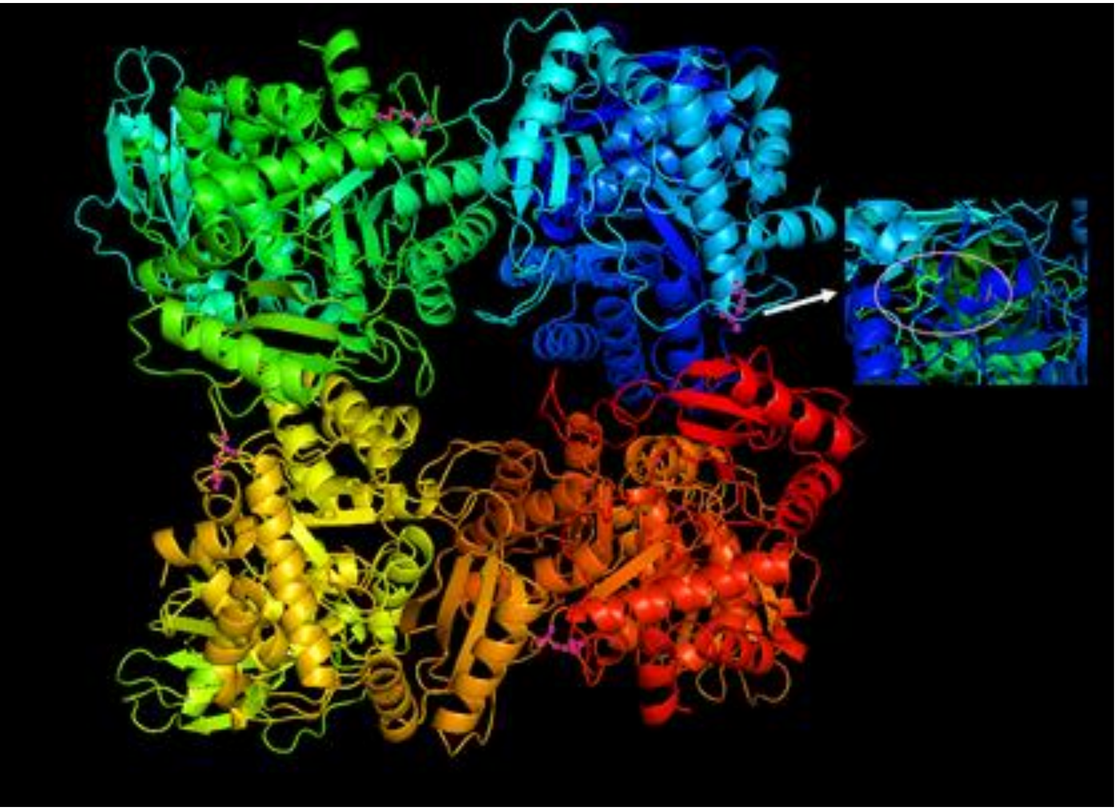


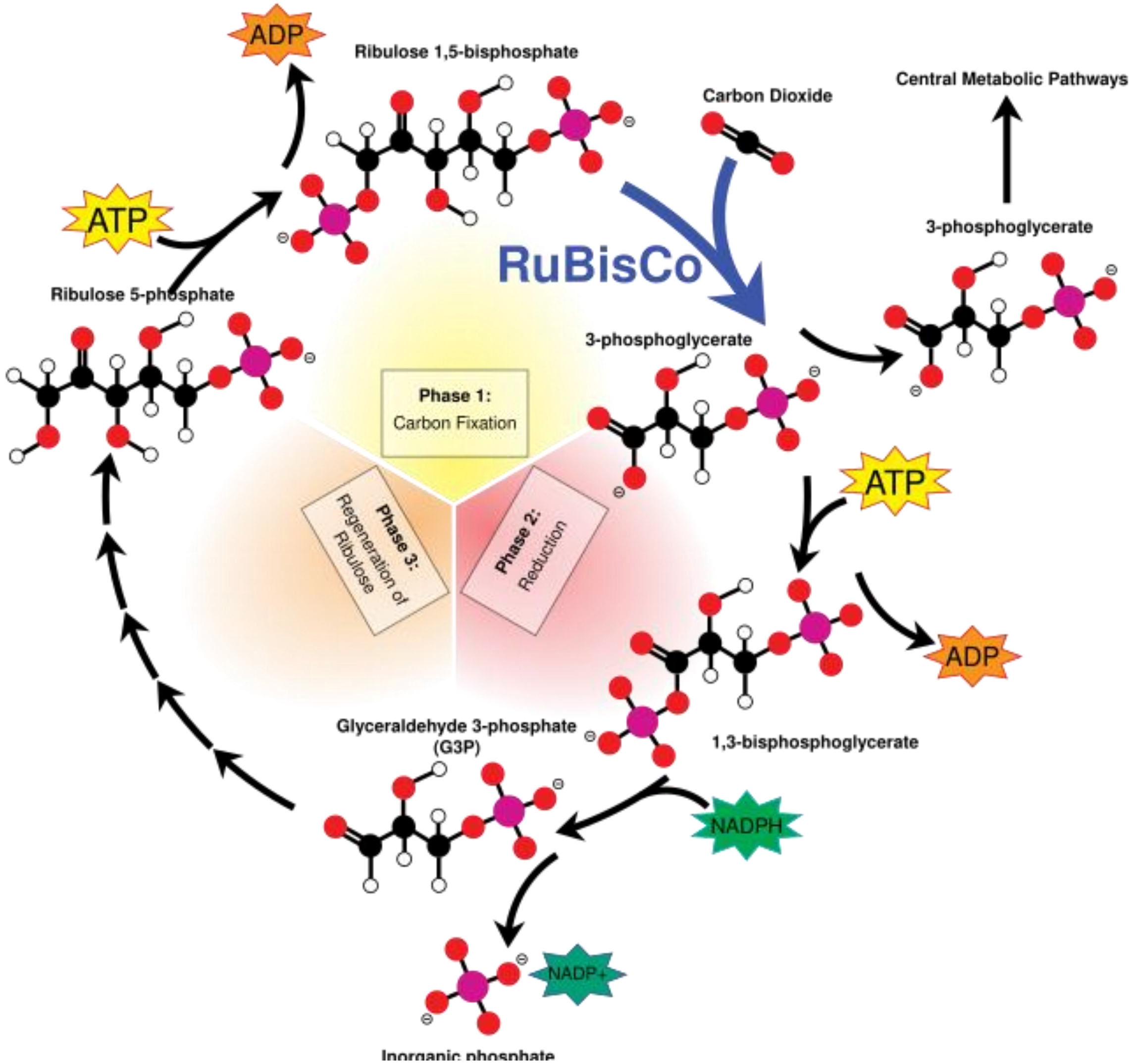
Ribulose-1,5-bisphosphate carboxylase/oxygenase





The active site of rubisco is centered on a magnesium ion (green). It is held tightly by three amino acids: an asparagine, glutamic acid, and a modified form of lysine. The carbon dioxide molecule (left, dotted outline) attached to this lysine serves as an activator in the carbon fixing reaction. This activator carbon dioxide is different from the carbon dioxide molecule that is fixed to the sugar. During the day, the activator carbon dioxide is attached to rubisco, and removed at night to turn the enzyme "off." When rubisco is active, the exposed side of the magnesium ion is free to bind to the sugar molecule and catalyze the reaction with a substrate carbon dioxide. In this structure (PDB ID 8ruc), the carbon dioxide is already attached to the sugar (right, dotted outline), giving a snapshot of rubisco in action.





ADP
Ribulose 1,5-bisphosphate
Carbon Dioxide
Central Metabolic Pathways
ATP
RuBisCo
3-phosphoglycerate
Ribulose 5-phosphate
3-phosphoglycerate
Phase 1:
Carbon Fixation
Phase 3:
Regeneration of
Ribulose
Phase 2:
Reduction
ATP
ADP
Glyceraldehyde 3-phosphate
(G3P)
1,3-bisphosphoglycerate
NADPH
NADP+
Inorganic phosphate

Water-Use Efficiency

Transpiration – Loss of water through plant stomates.

$$\text{WUE} = \text{mmoles of } CO_2 \text{ fixed/moles of } H_2O \text{ lost.}$$

Nutrient –Use Efficiency

Rate of photosynthesis per unit of leaf nitrogen

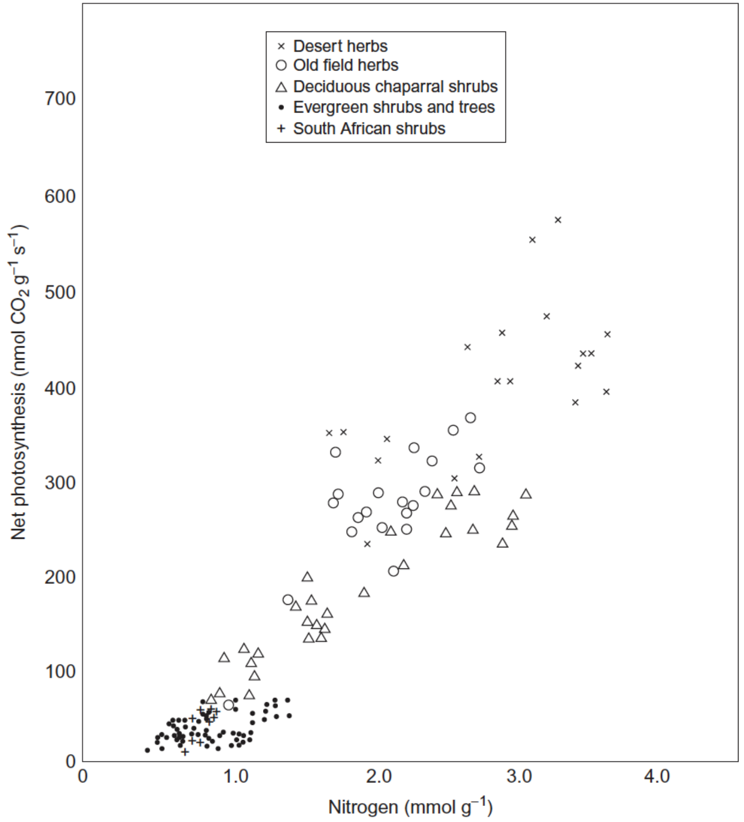


FIGURE 5.3 Relationship between net photosynthesis and leaf nitrogen content among 21 species from different environments. *Source: From Field and Mooney (1986). Used with permission of Cambridge University Press.*

Respiration

Photorespiration

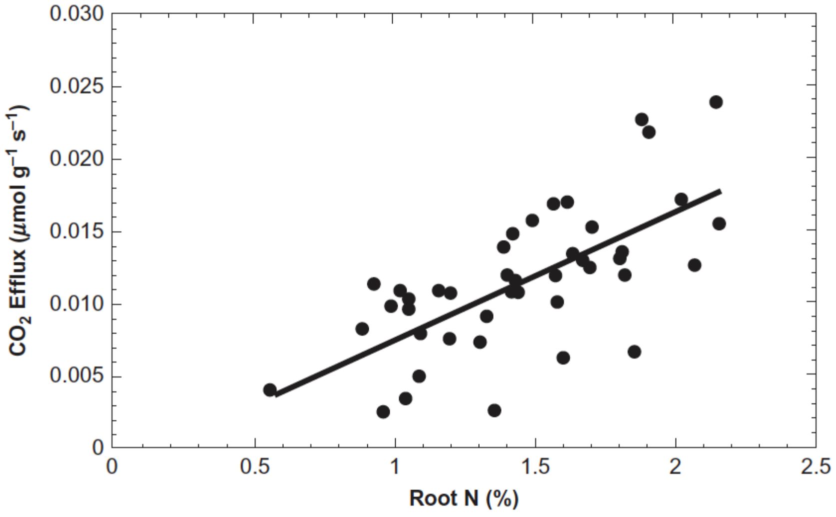
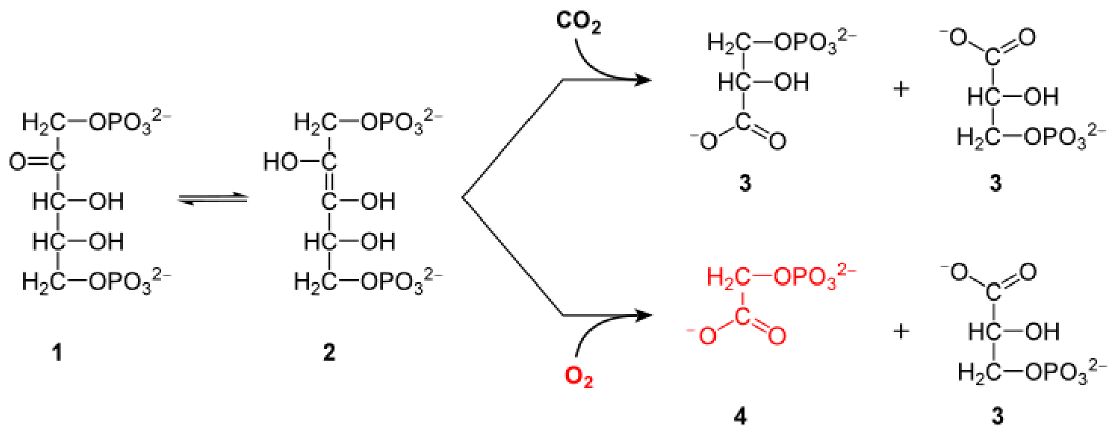
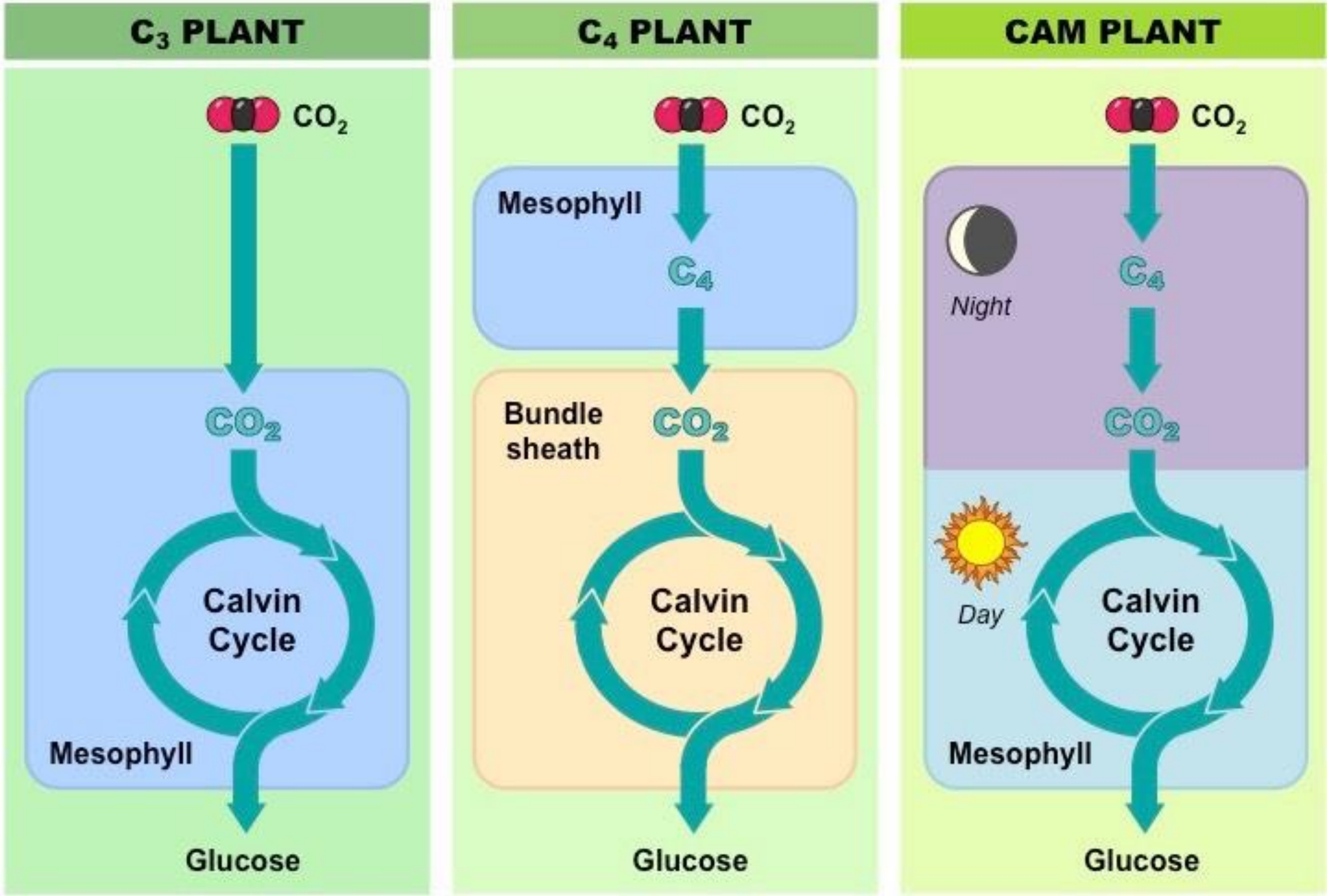


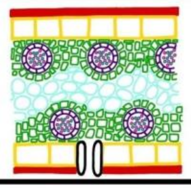
FIGURE 5.4 Root respiration as a function of nitrogen content (%) in roots of loblolly and ponderosa pine. *Source: From Griffin et al. (1997). Used with permission of Springer.*



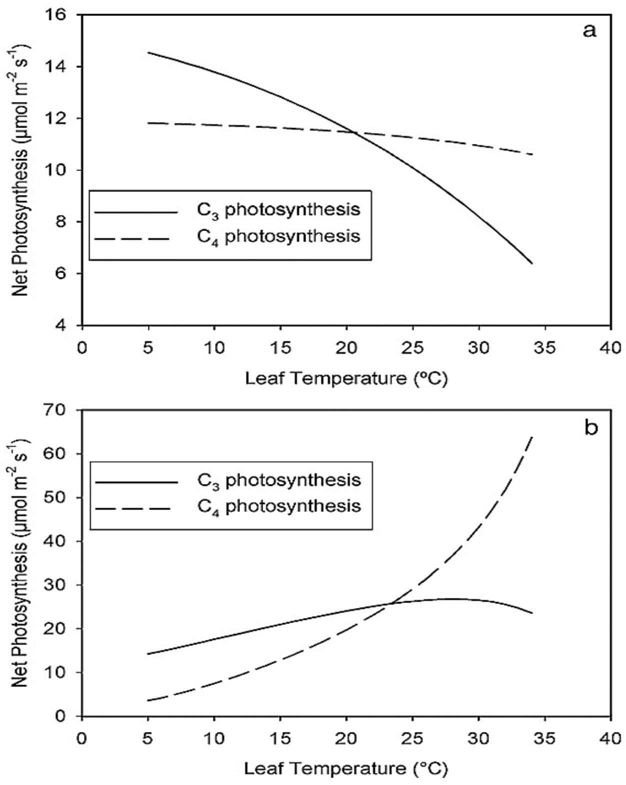


C3 PLANT
C4 PLANT
CAM PLANT
CO2
CO2
Calvin
Cycle
Mesophyll
Glucose
CO2
Mesophyll
C4
Bundle
sheath
CO2
Calvin
Cycle
Glucose
CO2
Night
C4
CO2
Day
Calvin
Cycle
Mesophyll
Glucose

C3 C4 AND CAM PLANTS SUMMARIZED!

	C3 PLANT	C4 PLANT	CAM PLANT
SUMMARY	TEMPERATE PLANTS NO SPECIAL MODS	HOT WEATHER PLANTS SEPARATE FIXATION & CALVIN CYCLE	DESERT PLANTS NIGHT: GAS EXCHANGE DAY: PHOTOSYNTHESIS
STRUCTURE			
EXAMPLES	MOST PLANTS ARE C3 RICE, CANNABIS	CORN, SUGARCANE	CACTI, PINEAPPLES
KEY CELLS	PALISADE MESOPHYLL	PALISADE MESOPHYLL BUNDLE SHEATH	PALISADE MESOPHYLL
IDEAL TEMPERATURE	20-30°C (65-85 °F)	30-40°C (85-105 °F)	NIGHT: 10-15 °C (50-60 °F) DAY: 30-40 °C (85-105 °F)

Global distribution of C3 and C4 vegetation: Carbon cycle implications



Light Limited Conditions

Light Saturated Conditions

Global Biogeochemical Cycles, Volume: 17, Issue: 1, Pages: 6-1-6-14, First published: 10 January 2003, DOI: (10.1029/2001GB001807)

Net Primary Production

Gross primary production – plant respiration = net primary production

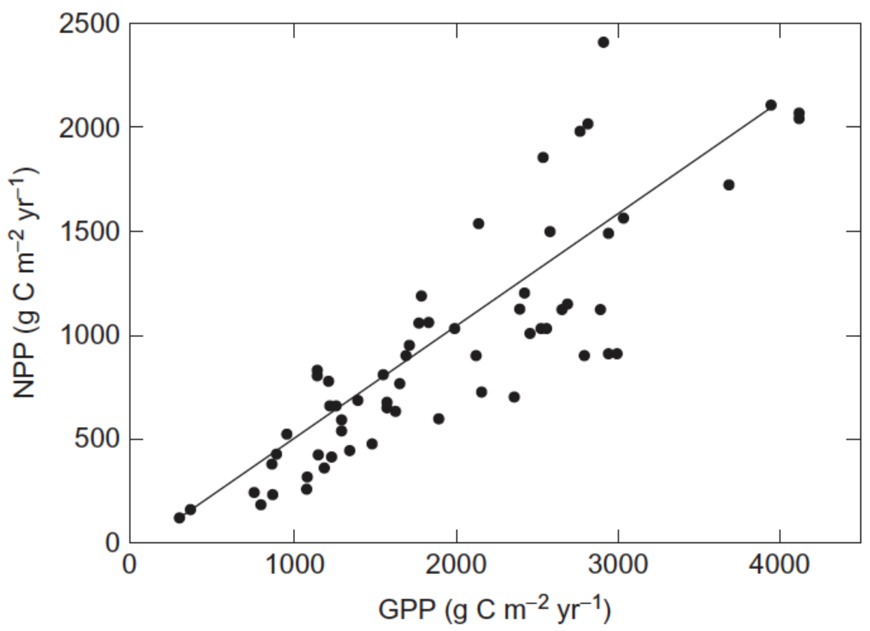


FIGURE 5.5 Relationship between net primary production (NPP) and gross primary production (GPP) in different forest types. *Source: From DeLucia et al. (2007).*

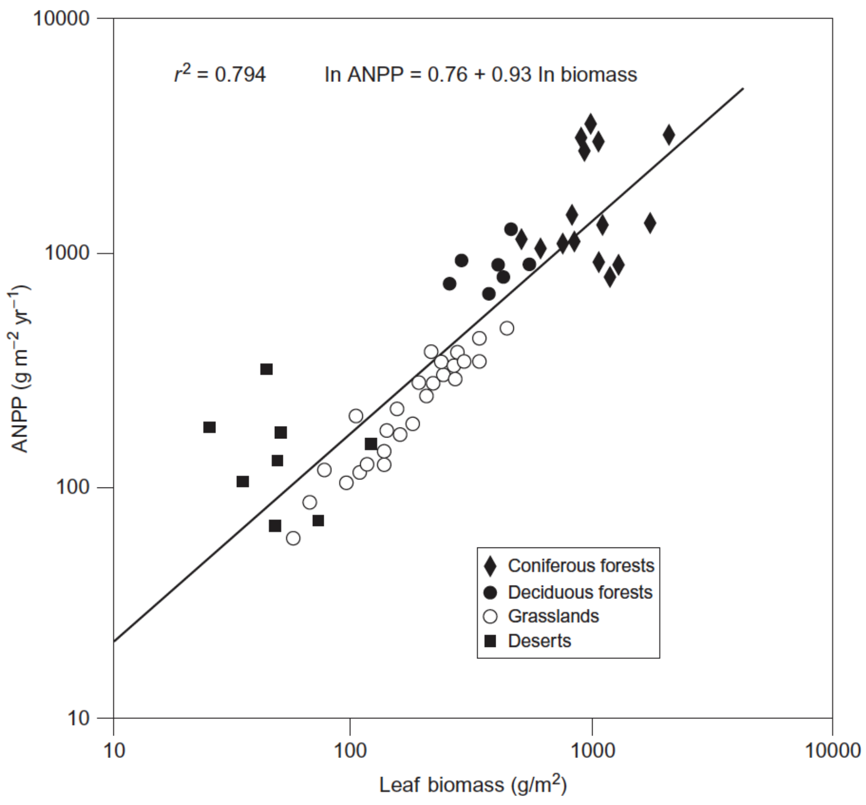


TABLE 5.1 Net Primary Production in 23- and 180-yr-old *Abies amabilis* Forests in the Cascade Mountains in Washington

	23-yr-old		180-yr-old	
Aboveground	$g\,m^{-2}yr^{-1}$	% of total	$g\,m^{-2}yr^{-1}$	% of total
Biomass increment				
Tree total	426		232	
Shrub stems	6		<1	
Total	432	18.37	232	9.33
Detritus production				
Litterfall	151		218	
Mortality	30			
Herb layer turnover	32		5	
Total	213	9.06	223	8.97
Total aboveground	**645**	**27.42**	**455**	**18.30**
Belowground				
Roots				
Fine (≤2 mm)	650	27.64	1290	51.87
Fibrous-textured	571		1196	
Mycorrhizal	79		94	
Coarse (>2 mm)	358		324	
Angiosperm fine root turnover	373		44	
Total root turnover	1381	58.72	1658	66.67
Mycorrhizal fungal component	326	13.86	374	15.04
Total below ground	1707	72.58	2032	81.70
Ecosystem total	**2352**	**2352**	**2487**	

Source: Form Vogt et al. (1982). Used with permission of Ecological Society of America.

Assignments I-IV lead to the development of an NSF GRFP proposal. Each assignment successively builds and adds to each other.
In Assignment I you accomplished the following:

1) Familiarized yourself with the GRFP program and requirements
2) Developed a reverse outline and summaries of the NSF GRFP RFP.
3) Developed a CV.
4) Started a formal reference section (literature cited)

Assignment II builds on the work you started with Assignment I by developing drafts of the required materials to be entered into the GRFP Application Module and an outline of the literature review for your Research/Program Plan.

Assignment II has three parts.
I. Develop drafts of the materials required to be entered into the GRFP Application Module.
The sections that are required include:
•Personal Information
•Education
•Work and Other Experience
•Transcript PDFs
•Proposed Field(s) of Study
•Proposed Graduate Study and Graduate School Information
•Names and Addresses of at least 3 reference letter writers
•Personal, Relevant Background and Future Goals Statement PDF
•Graduate Research/Program Plan Statement PDF
Draw information from your draft CV and update your CV as needed.

II. Develop draft paragraphs for your Personal, Relevant Background and Future Goals Statement.
Draw from what you posted for Reflection 1 where you summarized your career goals and choice of major, and from your draft CV from Assignment 1.

III. Develop a draft Research/Program Plan Statement that includes the start of a literature review/background section. The literature review will include publications that inspired your choice of research or program plan and will serve as background materials that you are basing your Research/Program Plan on.
a. Identify 1-2 papers to start your literature review.
b. Develop reverse outlines and summaries of the papers.
c. Identify key aspects of the papers for your literature review.
d. Update your reference section from Assignment I to include the papers in your literature review.

Net Ecosystem Production

$$\mathrm{NEP} = \mathrm{NPP} - (\mathrm{R_h} + \mathrm{R_d})$$

$$\mathrm{NEP} = \mathrm{GPP} - (\mathrm{R_p} + \mathrm{R_h} + \mathrm{R_d})$$

Net Ecosystem Production

$$\text{NEP} = \text{NPP} - (R_h + R_d)$$

$$\text{NEP} = \text{GPP} - (R_p + R_h + R_d)$$

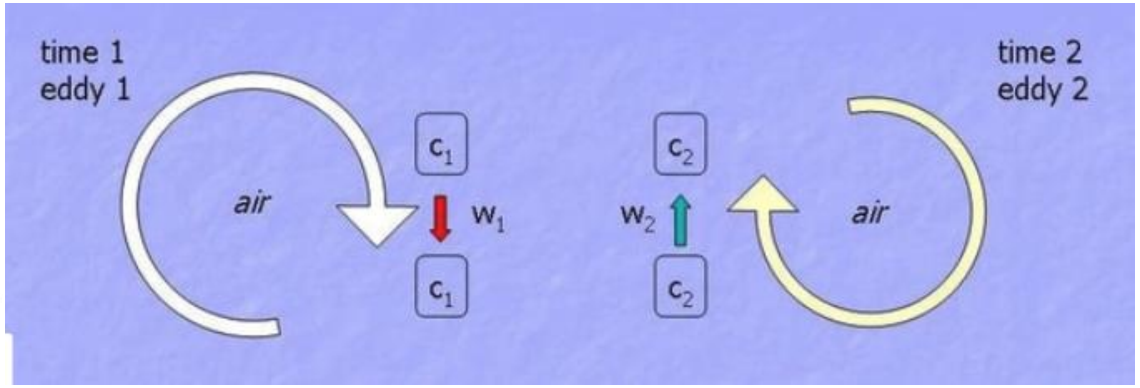
R_P = Respiration of Plants

R_h = Respiration of Herbivores

R_d = Respiration of Decomposers

Eddy Co-Variance Flux

FIGURE 5.7 An eddy-covariance (flux) tower in a deciduous forest in North Carolina. *Photo courtesy of G. Katul, Duke University.*



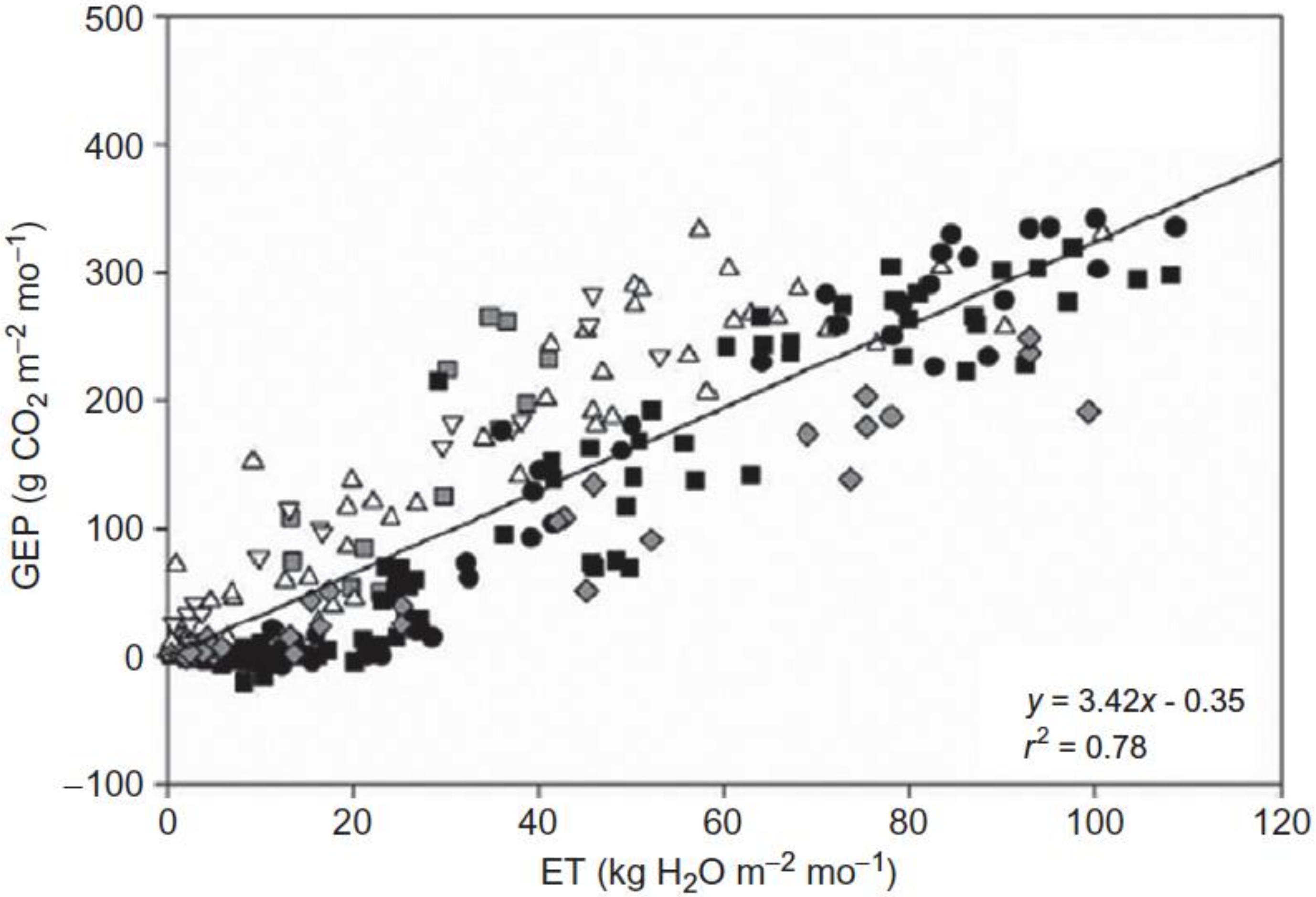


FIGURE 5.8 Monthly gross primary production and evaporation in various temperate deciduous forests, measured by eddy-covariance techniques. The slope of the line is an estimate of water-use efficiency, here equivalent to 1.4 mmol/mol (see Eq. 5.3). *Source: From Law et al. (2002).*

TABLE 5.2 GPP, NPP, and NEP for Some Young Temperate and Boreal Forest Ecosystems Measured by Harvest (H) and Eddy Covariance (CV) Methods

Ecosystem type	Age	Method	GPP	NPP	NEP	References
Pinus sylvestris (Finland)	40	CV H	1005		185 228	Kolari et al. 2004
Picea rubens (Maine)	90	CV	1339		174	Hollinger et al. 2004
Pinus taeda (North Carolina)	16	CV H	2238	 986	433 428	Juang et al. 2006 Hamilton et al. 2002 McCarthy et al. 2010
Pinus elliottii (Florida)	24	CV H	2606		675 745	Clark et al. 2004
Pinus ponderosa (Oregon)	56–89	CV H	1208	 400	324 118	Law et al. 2000 Law et al. 2003
Mixed deciduous (Massachusetts)	60	CV H	1300		200 160	Barford et al. 2001
Mixed deciduous (Michigan)	85	CV H	 654		151 153	Gough et al. 2008

Note: All data in g C m^{-2} yr^{-1}

Remote Sensing

The normalized difference vegetation index (NDVI) is calculated as:

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{VIS})/(\mathrm{NIR} + \mathrm{VIS}),$$

where NIR is reflectance in the near-infrared and VIS is reflectance in the visible red wavebands, respectively. This index minimizes the effects of variations in background reflectance and emphasizes variations in the data that occur because of the density of green vegetation. NDVI allows global mapping of a greenness index for the Earth's land surface, and satellite measurements of greenness can provide estimates of NPP, assuming that greenness is directly related to leaf area[7] and that LAI is a good predictor of NPP (Gholz 1982; Figures 5.6 and 5.10).

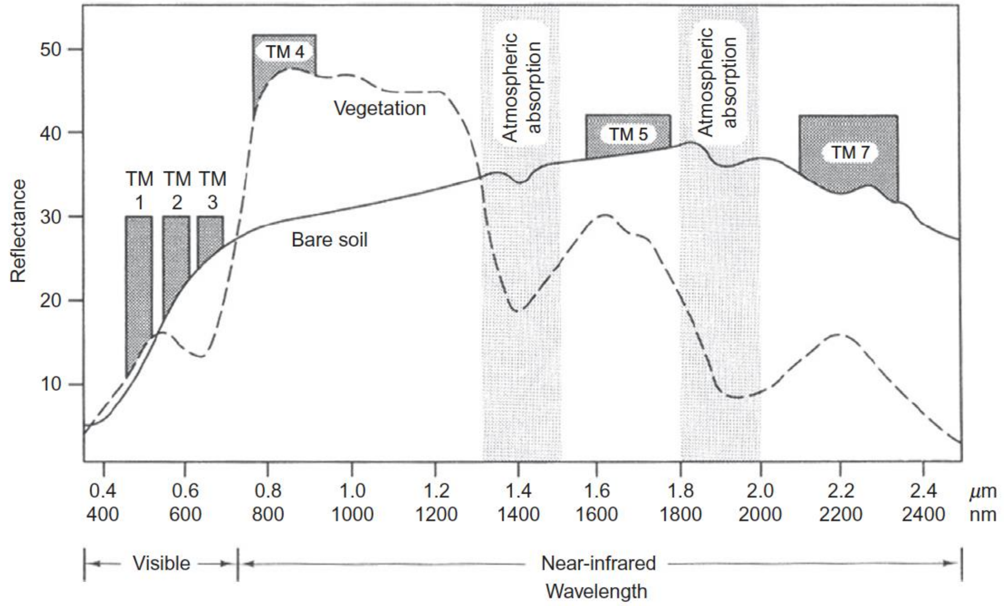


FIGURE 5.9 A portion of the solar spectrum showing the typical reflectance from soil (–) and leaf (– – –) surfaces and the portions of the spectrum that are measured by the LANDSAT satellite.

$$\mathrm{GPP} = \varepsilon \times \mathrm{NDVI} \times \mathrm{PAR},$$

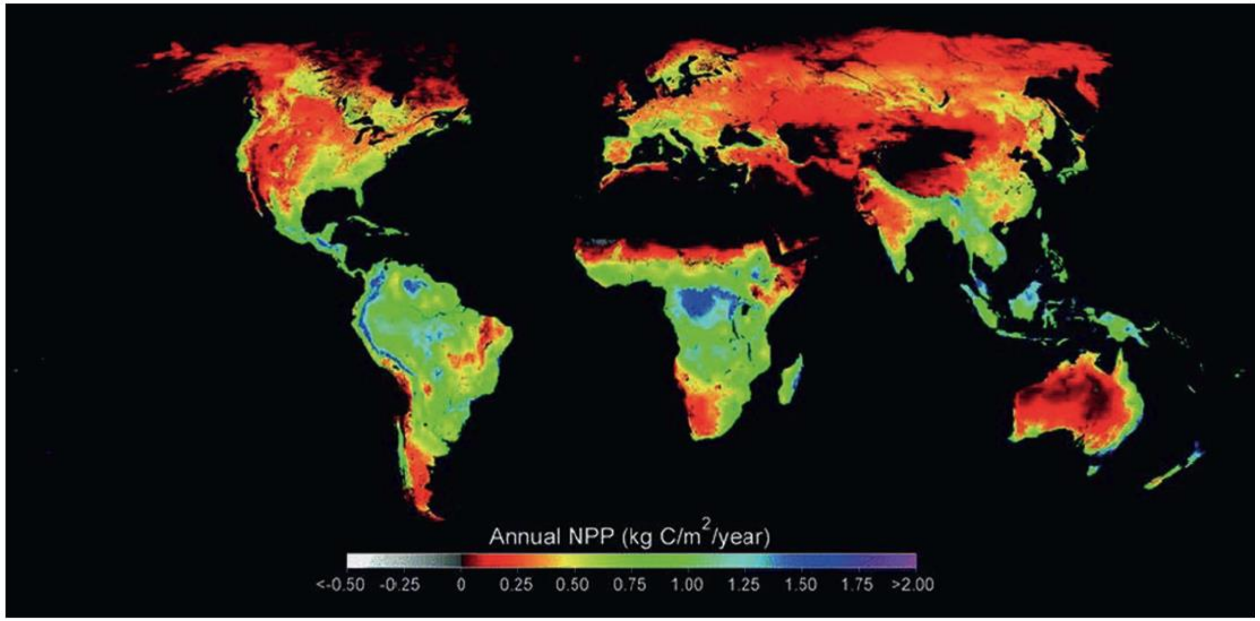


FIGURE 5.12 Distribution of global NPP on land for 2002, computed from MODIS data. *Source: From Running et al. 2004, Figure 5 in BioScience, June 2004; used with permission.*

TABLE 5.3 Biomass and Net Primary Production in Terrestrial Ecosystems

Biome	Area (10^6 km^2)	NPP (g C m^{-2} yr^{-1})	Total NPP (10^{15}g C yr^{-1})	Biomass (g C m^{-2})	Total plant C pool (10^{15}g C)
Tropical forests	17.5	1250	20.6	19,400	320
Temperate forests	10.4	775	7.6	13,350	130
Boreal forests	13.7	190	2.4	4150	54
Mediterranean shrublands	2.8	500	1.3	6000	16
Tropical savannas/grasslands	27.6	540	14.0	2850	74
Temperate grasslands	15.0	375	5.3	375	6
Deserts	27.7	125	3.3	350	9
Arctic tundra	5.6	90	0.5	325	2
Crops	13.5	305	3.9	305	4
Ice	15.5				
Total	**149.3**		**58.9**		**615**

From data compiled by Saugier et al. 2001, assuming a 50% carbon content in plant tissues.

TABLE 5.3 Biomass and Net Primary Production in Terrestrial Ecosystems

FIGURE 5.15 The Free-Air CO_2 Enrichment experiment in Duke Forest in central North Carolina. Each plot is 30 m in diameter and surrounded by 16 towers, which emit CO_2 so as to maintain a specified concentration in the cylindrical volume of the plot to the height of the forest canopy. All other factors, including soil fertility, are allowed to vary naturally in the control and experimental plots.

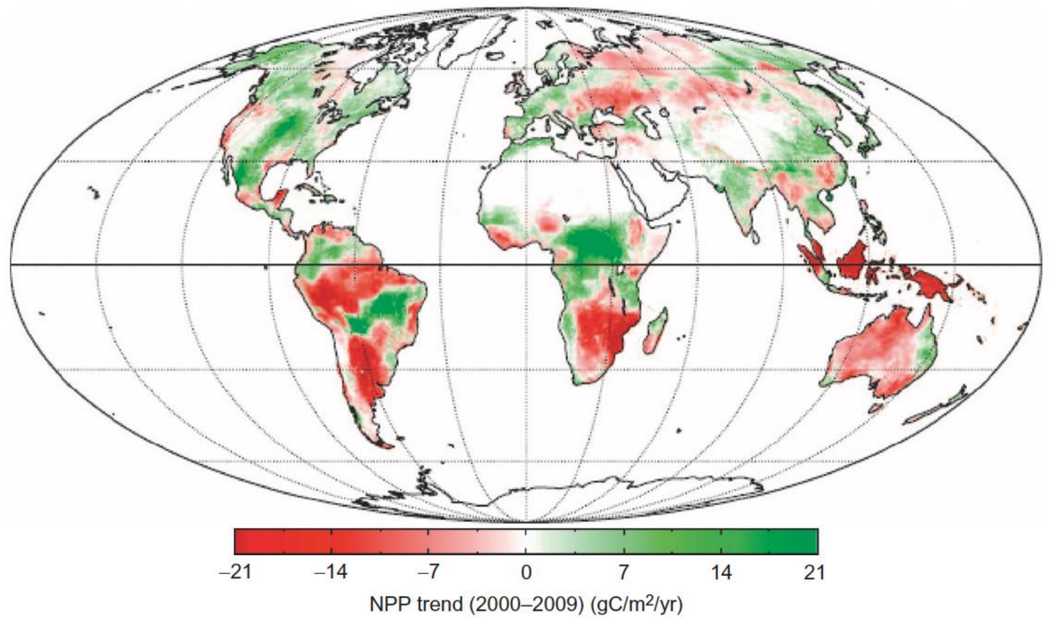
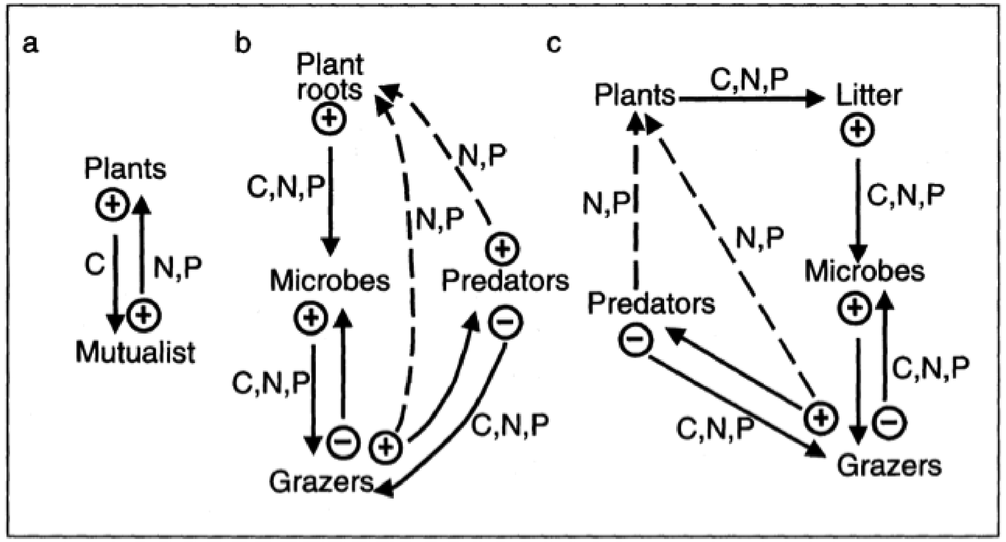


FIGURE 5.16 Change in terrestrial NPP from 2000 to 2009 from MODIS. *Source: From Zhao and Running 2010. Used with permission of the American Association for the Advancement of Science.*

Soil Fauna

Function

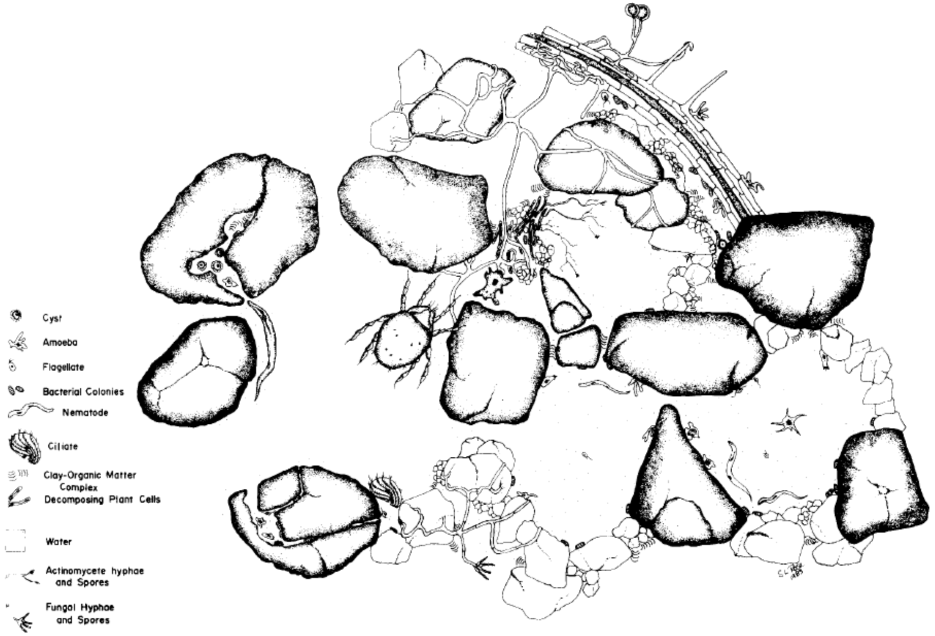
- Comminution
- Dissemination
- Trophic Interactions



A. Rhizosphere Mutualisms

B. Rhizosphere Trophic Interactions

C. Litter Layer



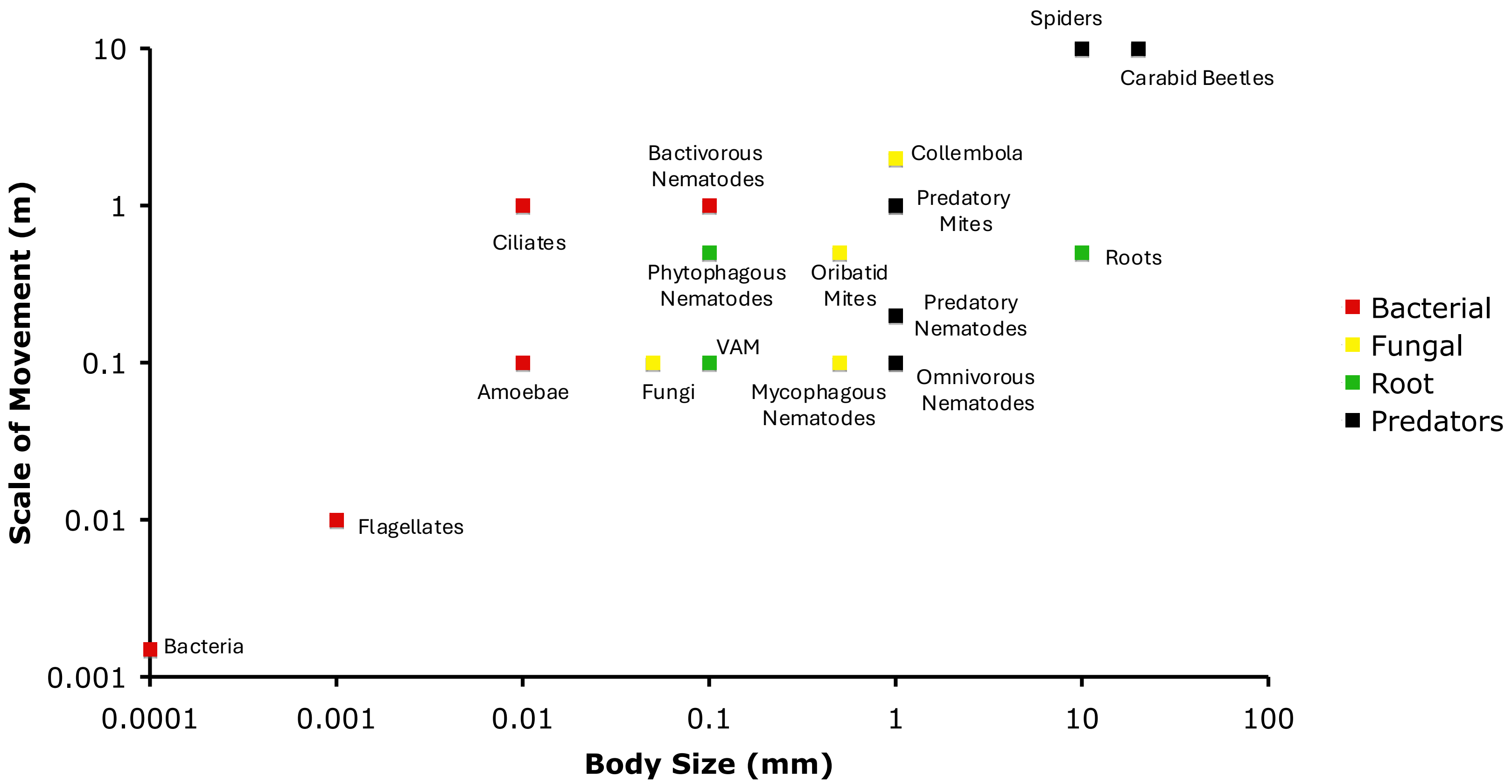
COMMINUTION

- Fragmentation
- Increased surface area
- Leaching of compounds
- C:N

DISSEMINATION

- Dispersal
- Nutrients and Water

Dissemination



Simple models of decay are based on an exponential pattern of loss, where the fraction remaining after 1 year is given by:

$$X/Xo = e^{-k}$$

An alternative, the mass-balance approach, suggests that the annual decomposition should equal the annual input of fresh debris so that the mass of detritus stays constant. Under these assumptions, a constant fraction, k, of the detrital mass decomposes, so that

$$\text{litterfall} = k(\text{detrital mass}),$$

or

$$\text{litterfall}/\text{detrital mass} = k.$$

When the detritus is in steady state, the values for k calculated from the litterbag and mass balance approaches should be equivalent, and mean residence time for plant debris is 1/k (Olson 1963; see also footnote on p. 55).

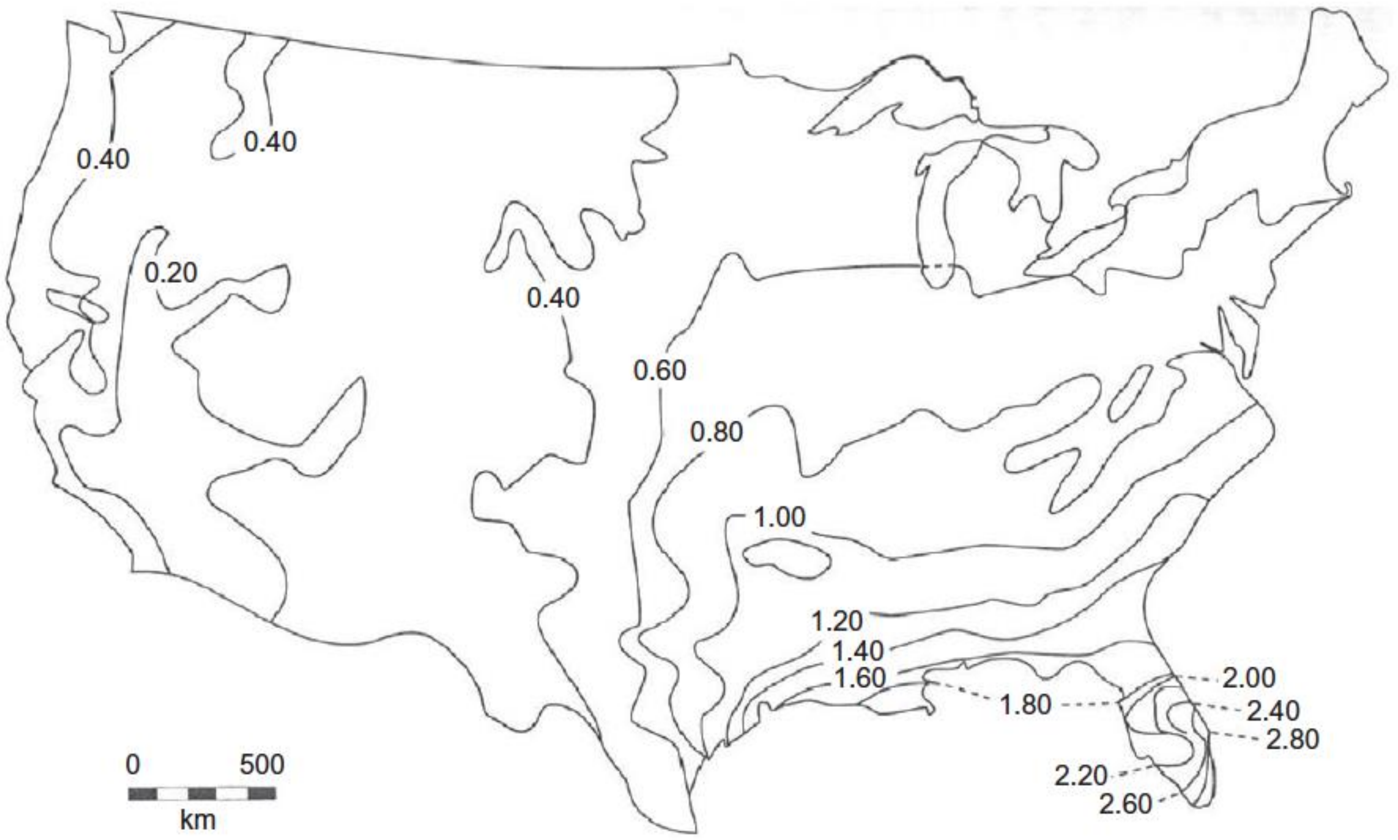
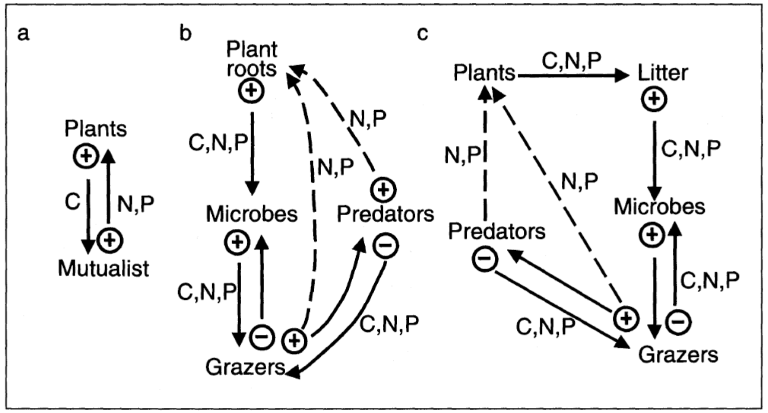
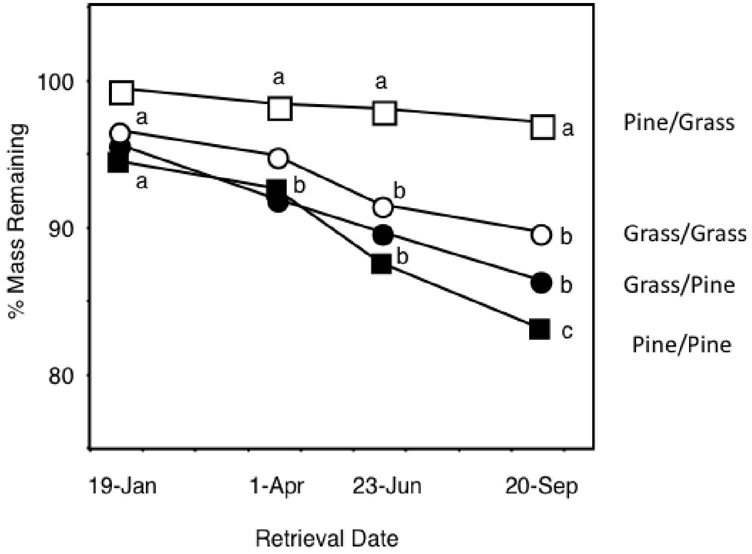


FIGURE 5.17 Rates of decomposition of fresh litter in the United States predicted by a stimulation model using actual evapotranspiration as a predictive variable. Isopleth values are the fractional loss rate (k) of mass from fresh litter during the first year of decomposition. *Source: From Meentemeyer (1978a.)*

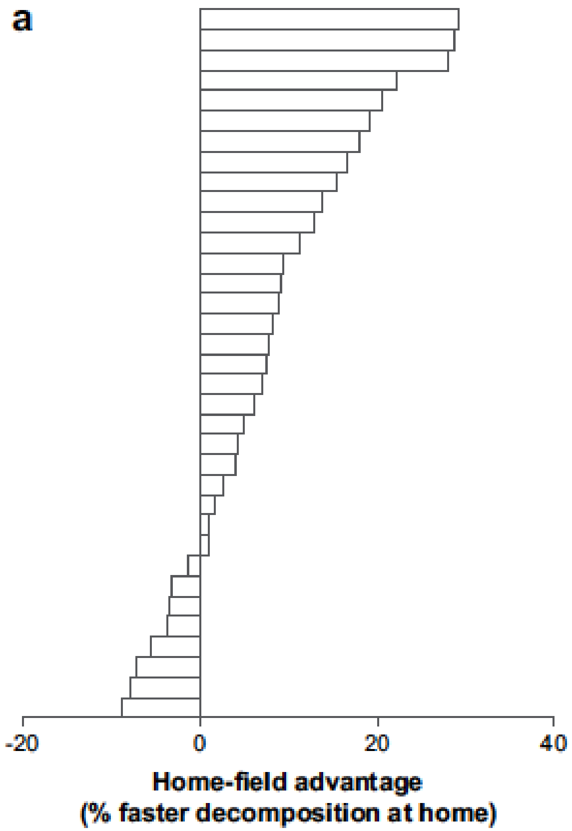
Litter and Decomposition



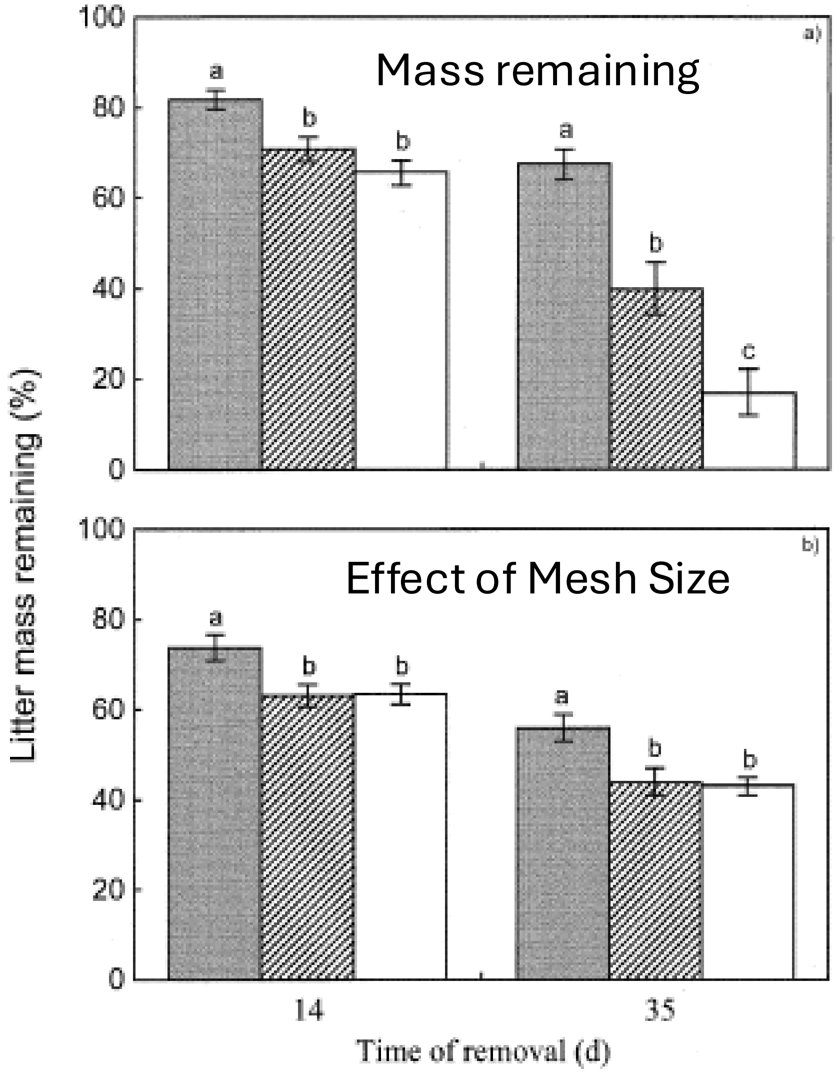
Homecourt Advantage

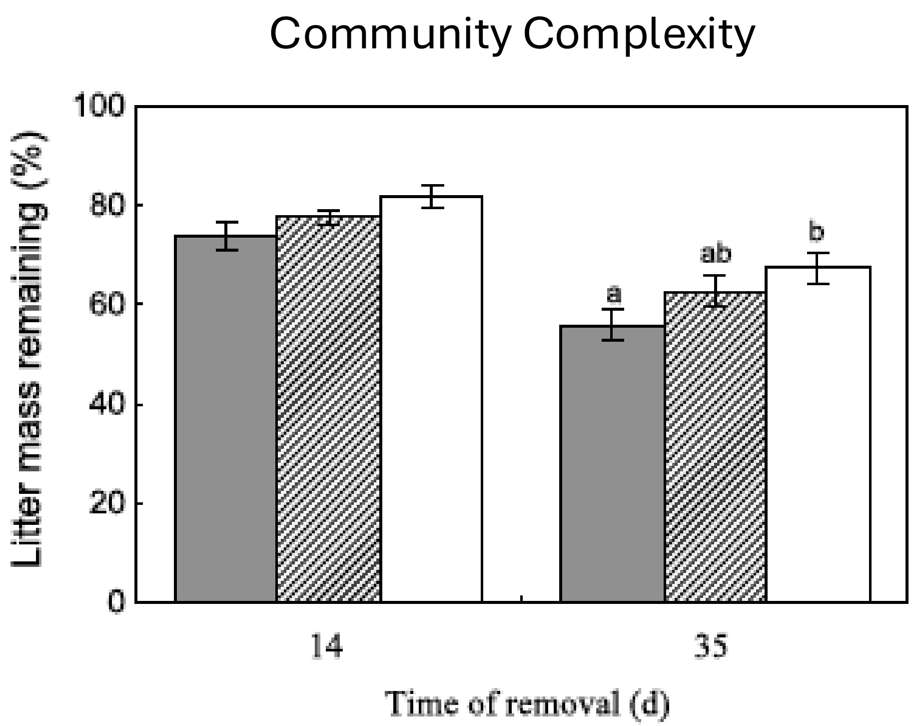


Species Matter



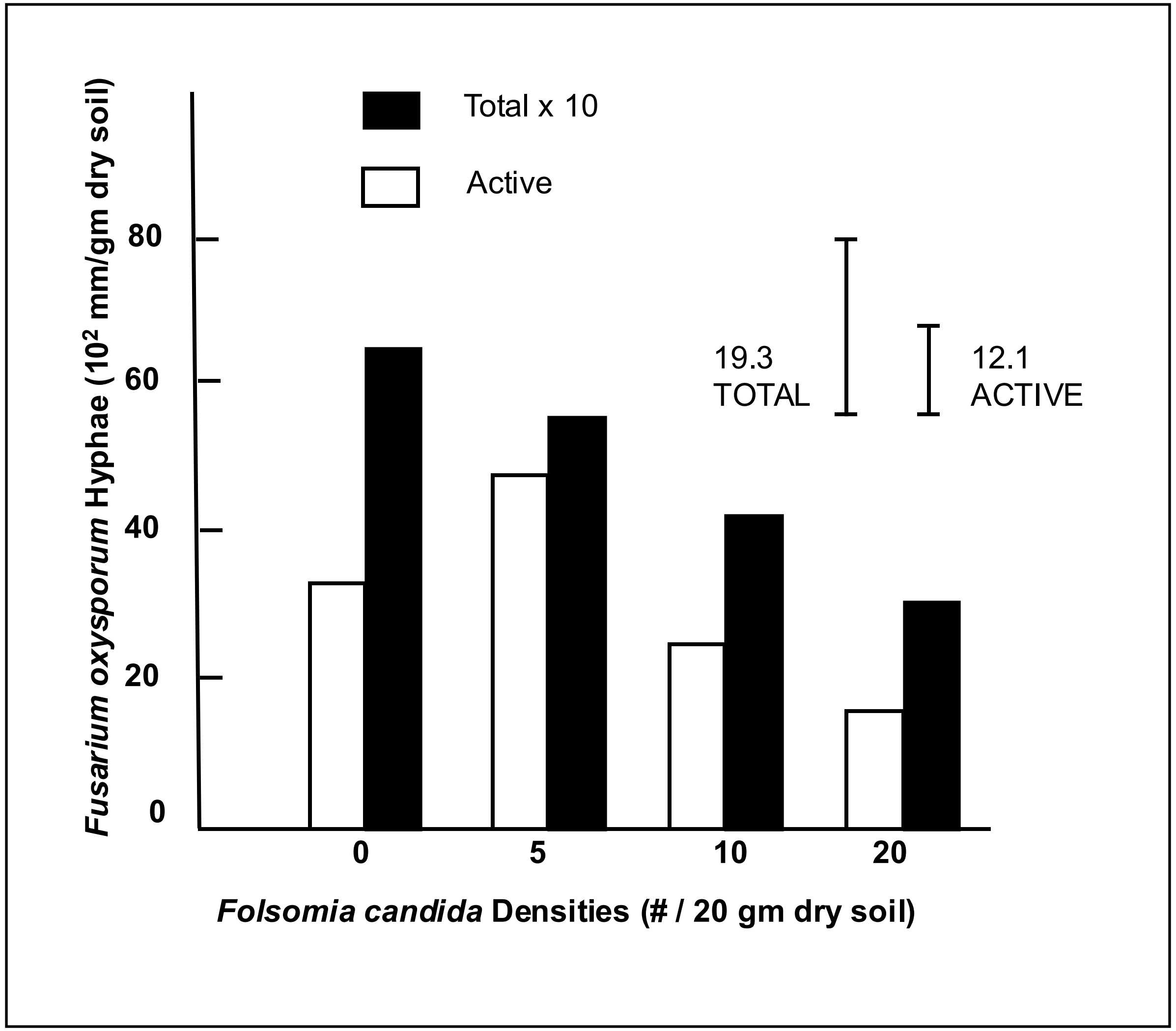
Decomposition

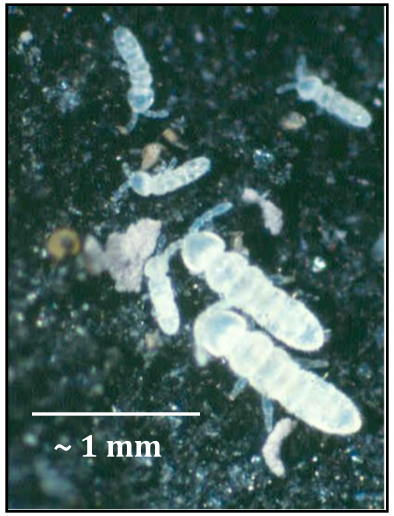




Bradford et al., Oikos 99, 317-323 (2002)

TROPHIC INTERACTIONS





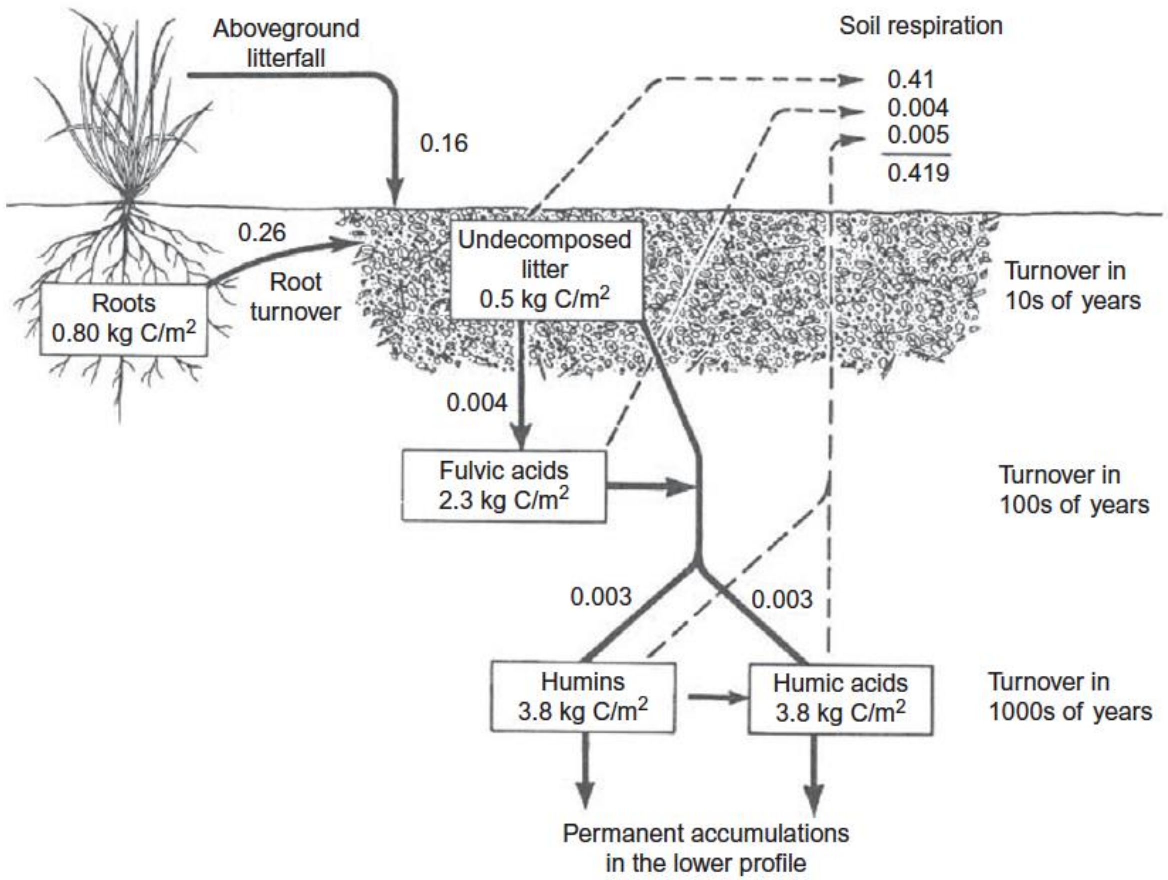
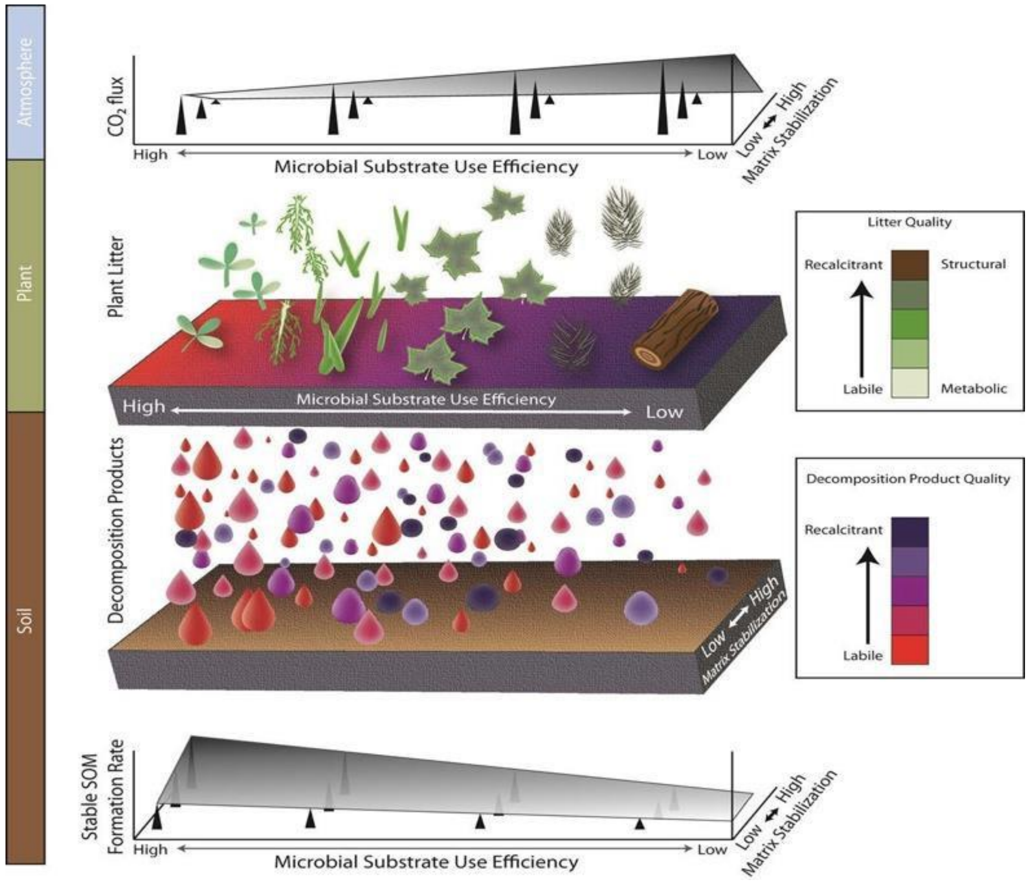


FIGURE 5.19 Turnover of detritus and soil organic fractions in a grassland soil, in units of kgC m^{-2} yr^{-1}. Note that mean residence time can be calculated for each fraction from measurements of the quantity in the soil and the annual production or loss (respiration) from that fraction. *Source: From Schlesinger (1977).*



Cotrufo et al (2013)

TABLE 5.4 Distribution of Soil Organic Matter by Ecosystem Types

Biome	World area (10^6 km^2)	Mean soil profile carbon (kgC/m^2) 0–100 cm	Mean soil profile carbon (kgC/m^2) 0–300 cm	Total soil carbon pool (10^{15} gC) 0–300 cm
Tropical forests				
Deciduous	7.5	15.8	29.1	218
Evergreen	17.0	18.6	27.9	474
Temperate forests				
Deciduous	7	17.4	22.8	160
Evergreen	5	14.5	20.4	102
Boreal forests	12	9.3	12.5	150
Mediterranean shrublands	8.5	8.9	14.6	124
Tropical savannas/grasslands	15	13.2	23.0	345
Temperate grasslands	9	11.7	19.1	172
Deserts	18	6.2	11.5	208*
Arctic tundra	8	14.2	18.0	144
Crops	14	11.2	17.7	248
Extreme desert, rock and ice	15.5			
Total	**136.5**			**2344**

Note: Excludes soil carbonates, which may contain an additional 930 x 10^{15} gC (Schlesinger 1985).
Source: From Jobbágy and Jackson (2000). Used with permission of the Ecological Society of America.

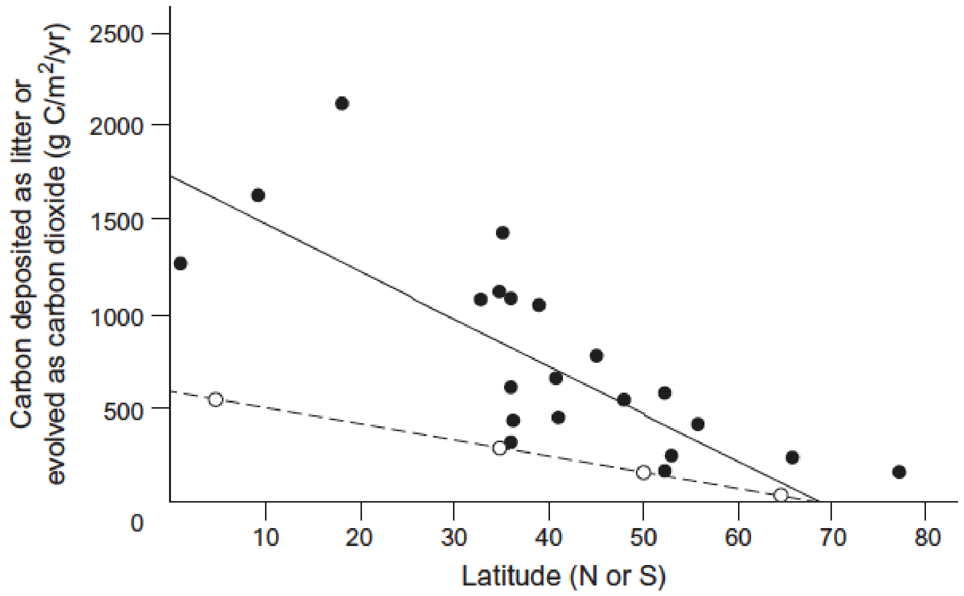


FIGURE 5.20 Latitudinal trends for carbon dynamics in forest and woodland soils of the world. The *dashed line* shows the mean annual input of organic carbon to the soil by litterfall. The *solid line* shows the loss of carbon, measured as the flux CO_2 from the surface. The difference between these lines represents the loss of CO_2 from root and mycorrhizae respiration and from the decomposition of root detritus and exudates. *Source: From Schelesinger (1977).*

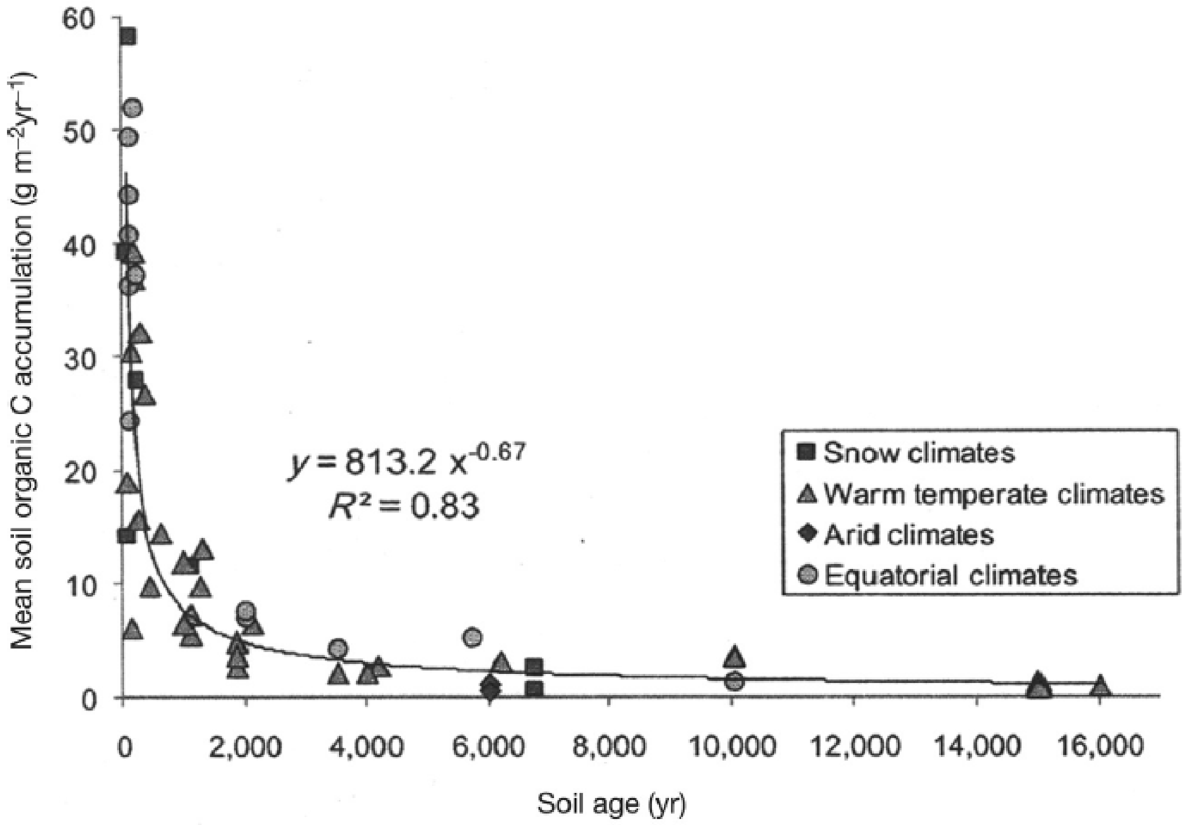


FIGURE 5.21 The rate of accumulation of organic matter in soil chronosequences of different age and climate zones, all derived from volcanic materials. *Source: From Zehetner (2010).*

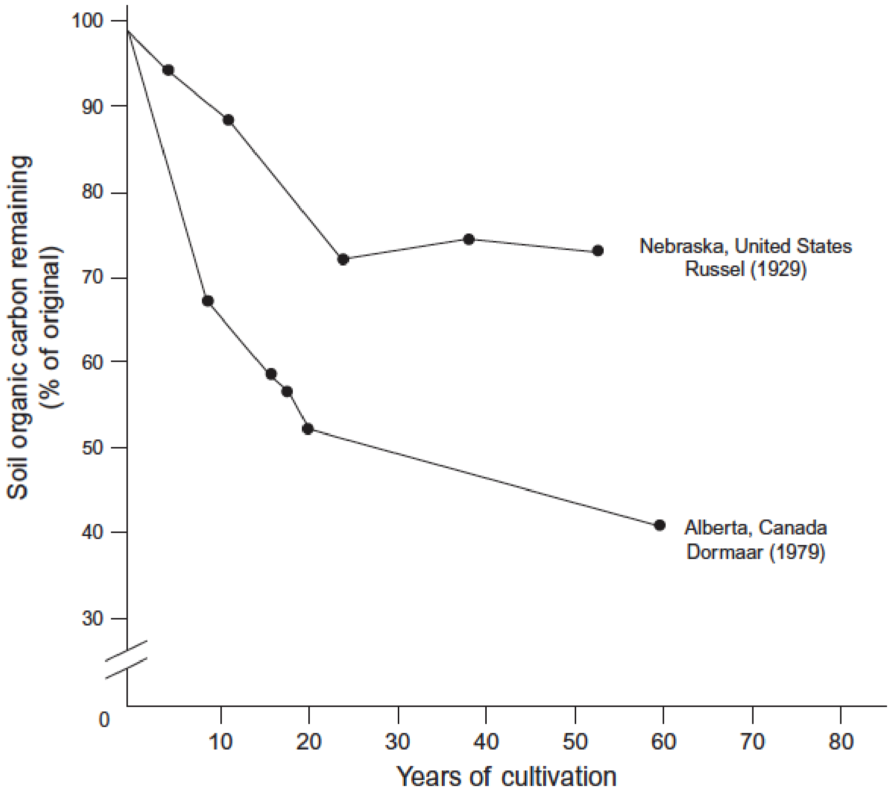
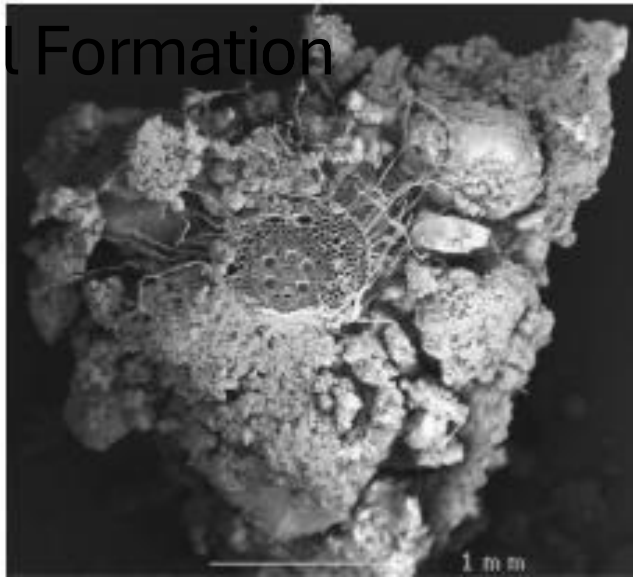
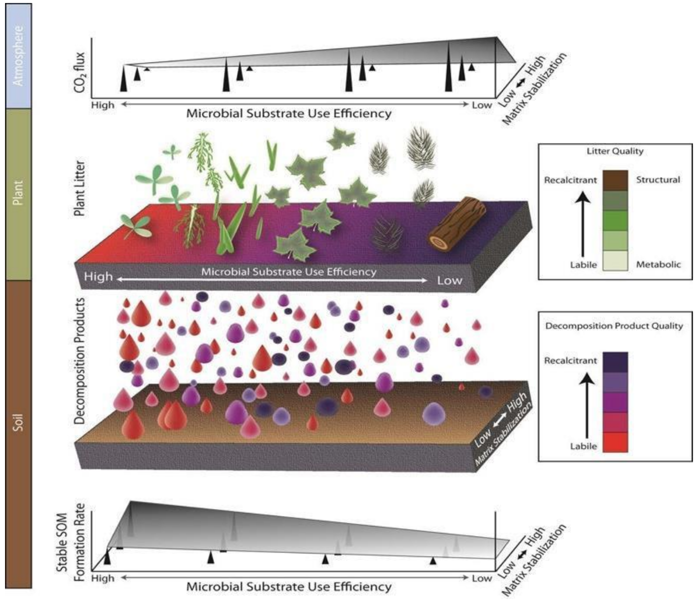
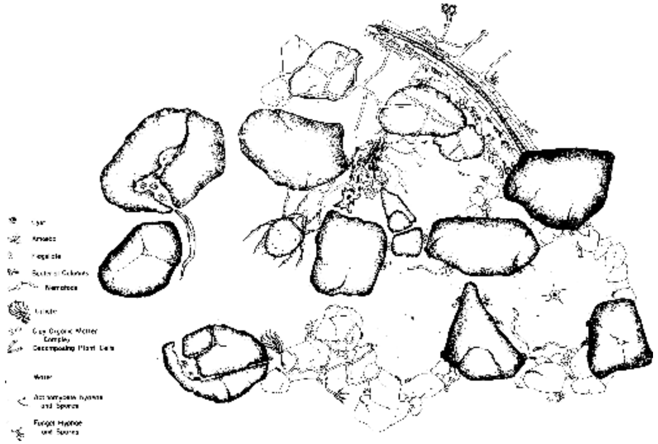


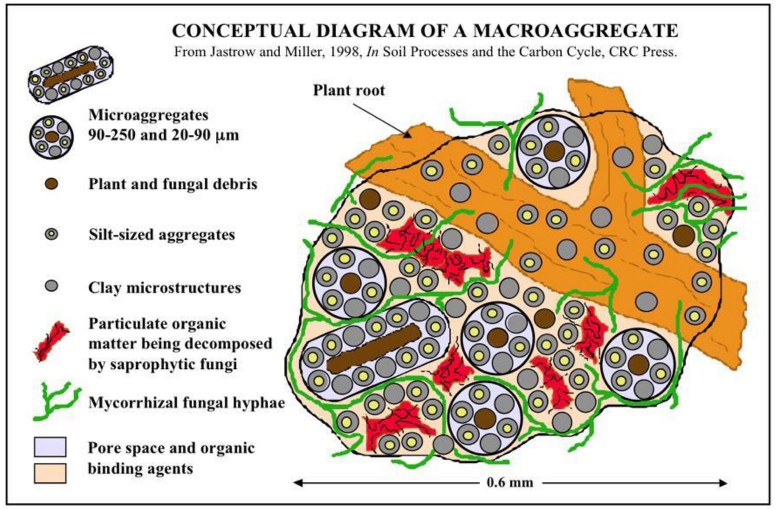
FIGURE 5.22 Decline in soil organic matter following conversation of native soil to agriculture in two grassland soils. *Source: From Schlesinger (1986).*

Soil Formation

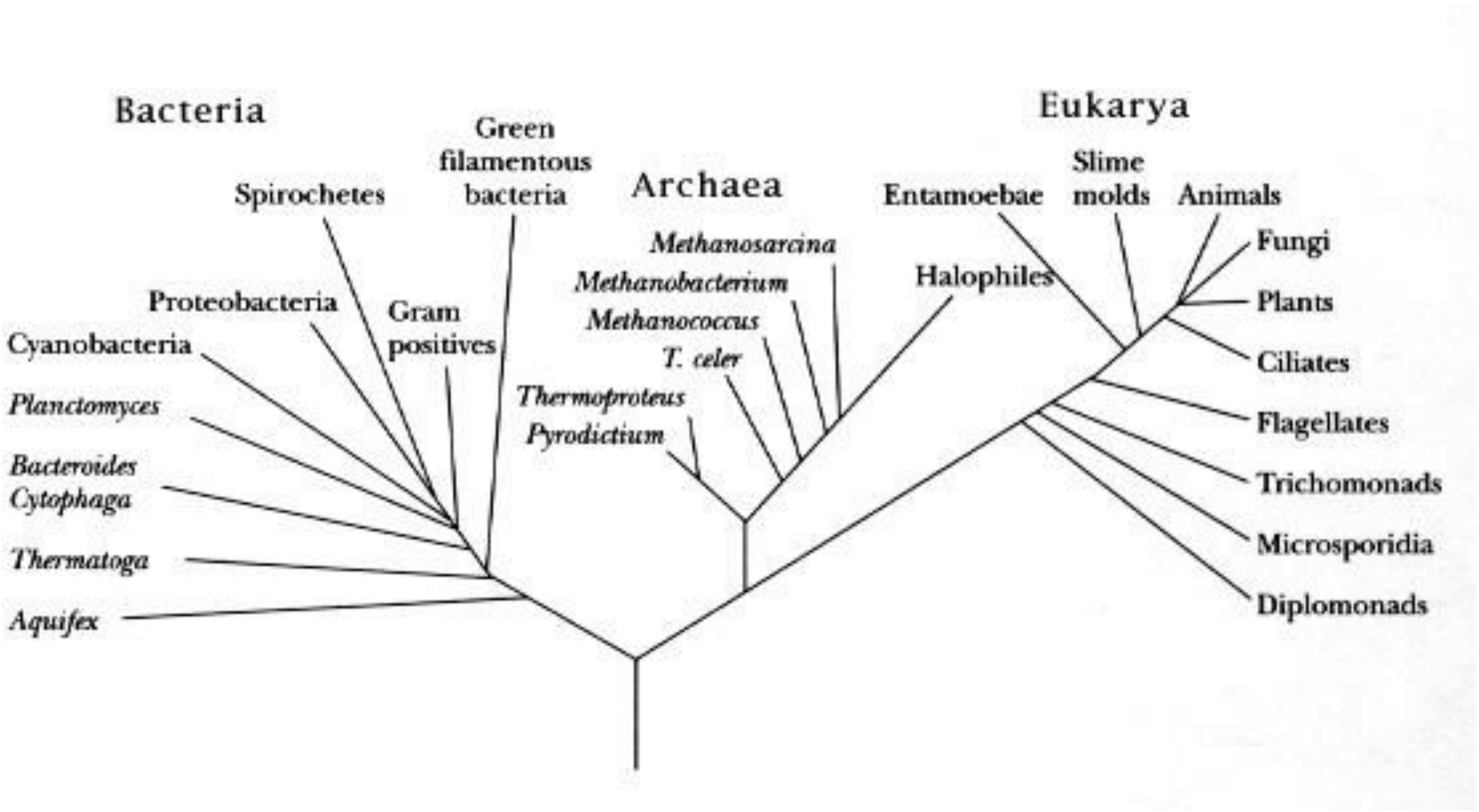




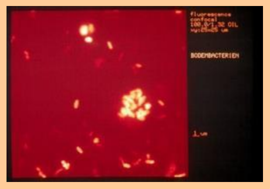


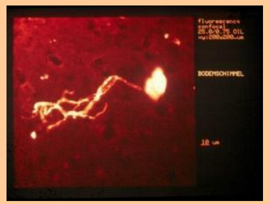


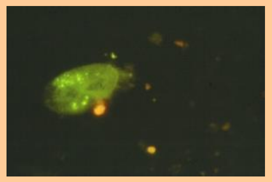
Soil as a Poor Person's Tropics … or maybe a Desert

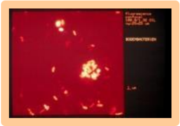
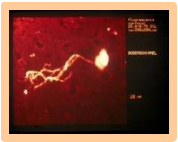
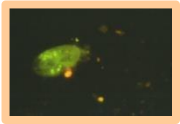
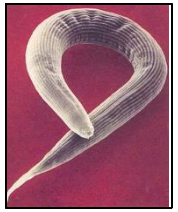


Body width	Taxonomic Group	Percentage of global Described species in soil
1-2 µm	Bacteria	49-66
3-100 µm	Fungi	48
15-100 µm	Protozoa	4
5-120 µm	Nematoda	20
80 µm – 2 mm	Acari	66
150 µm – 2mm	Collembola	>80
300 µm – 1 mm	Diplura	100
500 µm – 4 mm	Symphyla	100
500 µm – 4 mm	Isoptera	61
2-20 mm	Ants	63
	Isopods	50
1-50 mm	Chilopoda	100
	Pauropoda	100
	Diplopoda	100
	Insect Larvae	50
500 µm – 1 mm	Enchytraeidae	100
1-50 mm	Lumbracidae	82

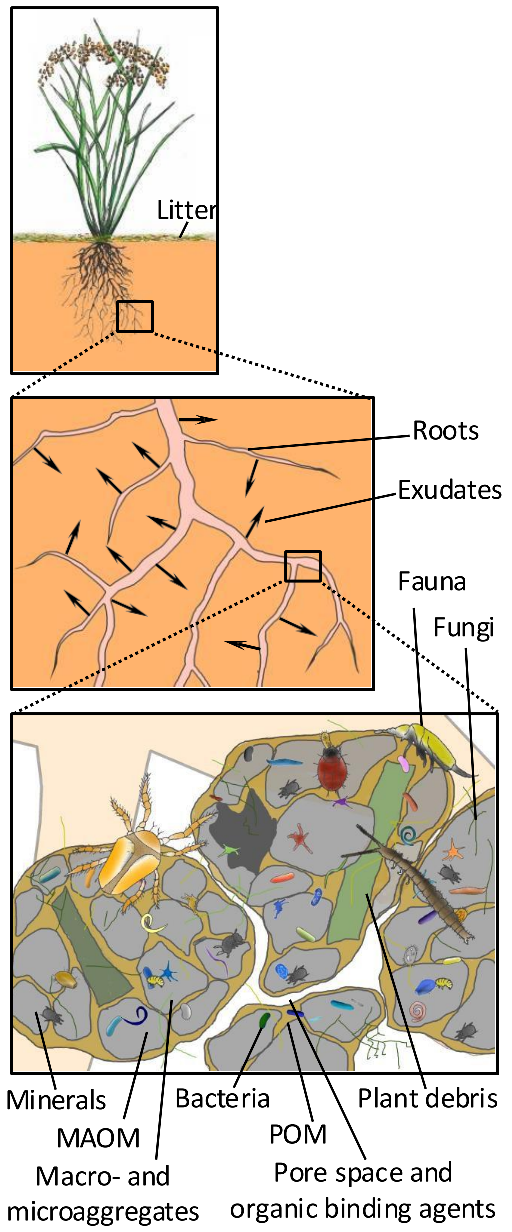




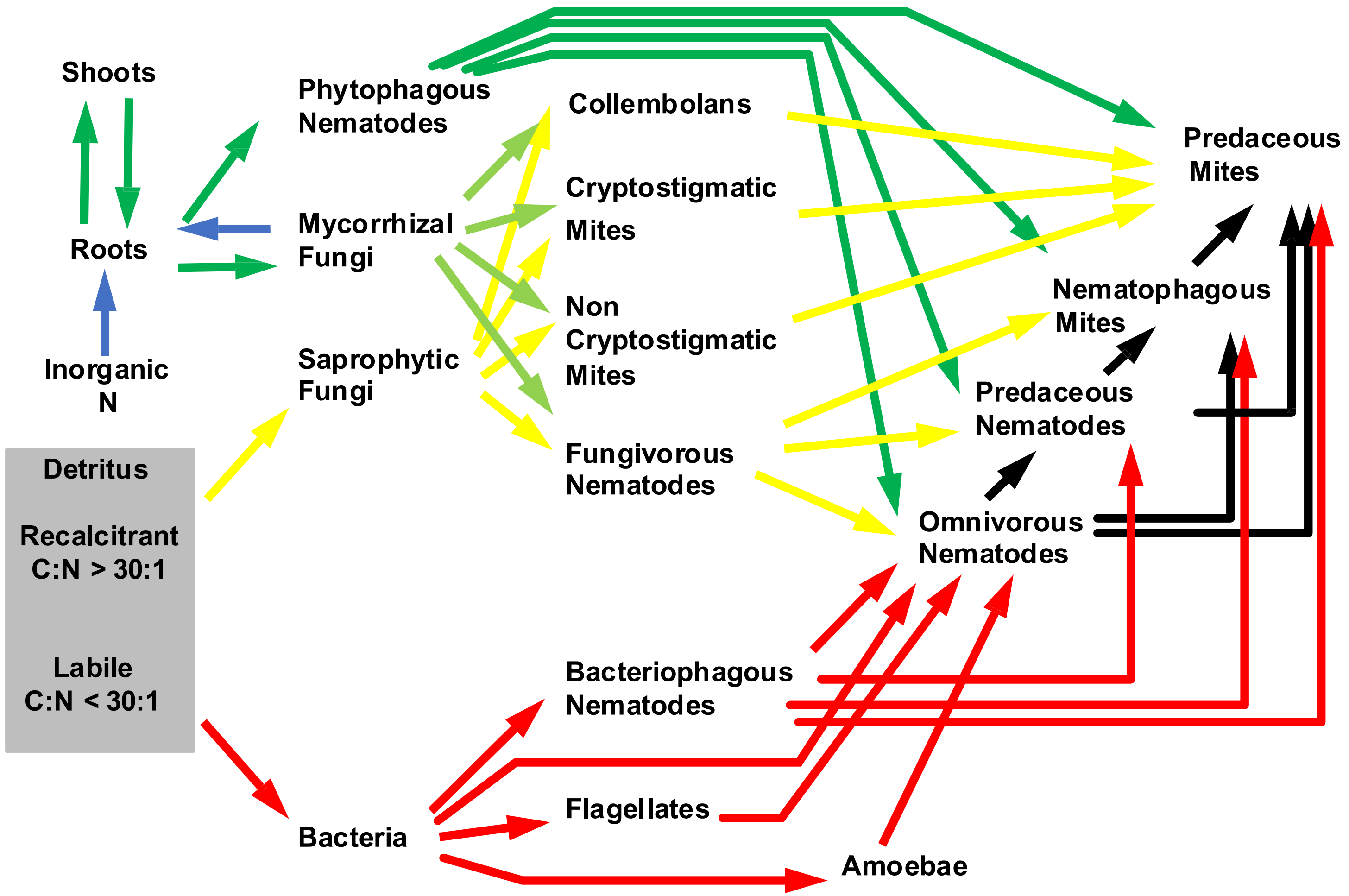


	Bacteria	Fungi	Protozoa	Nematodes	Collembola	Mites
Habitat	Water/ Surfaces	Free Air/ Surfaces	Water/ Surfaces	Water films/ Surfaces	Free Air Spaces	Free Air Spaces
Minimum Generation Time (h)	0.5	4-8	2-4	120	720	720
Turnover Time (season-1)	2-3	0.75	10	2-4	2-3	2-3
Assimilation Efficiency (%)	$100^{\dagger}$	$100^{\dagger}$	0.95	0.38-0.60	0.5	0.3—0.9
Production Efficiency (%)	0.4-0.5	0.4-0.5	0.4	0.37	0.35	0.35-0.40
Body Width	1-2 μm	3-100 μm	15-100 μm	5-120 μm	.150 – 2 mm	.08-2 mm
Biomass (g C indiv.$^{-1}$)						
Functional Response (Type I-III)	NA	NA	I, II	I, II	I, II	I, II

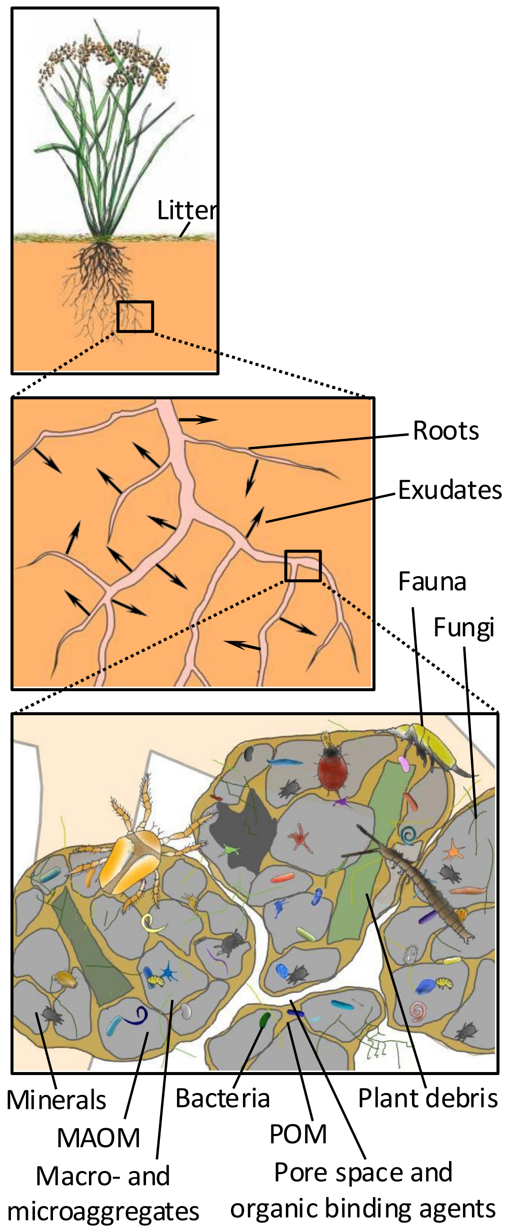


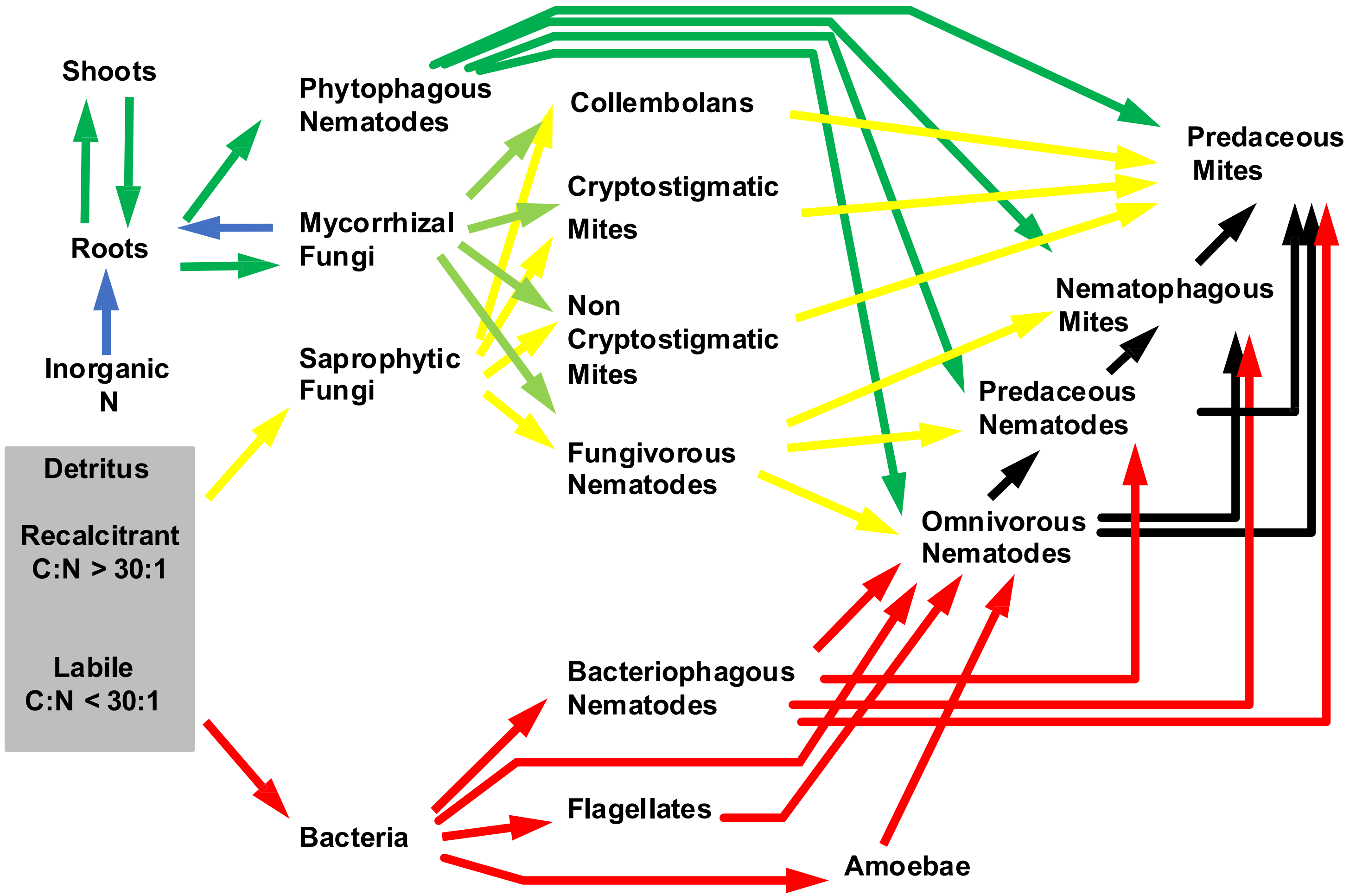
Litter
Roots
Exudates
Fauna
Fungi
Minerals
MAOM
Macro- and microaggregates
Bacteria
POM
Pore space and organic binding agents
Plant debris

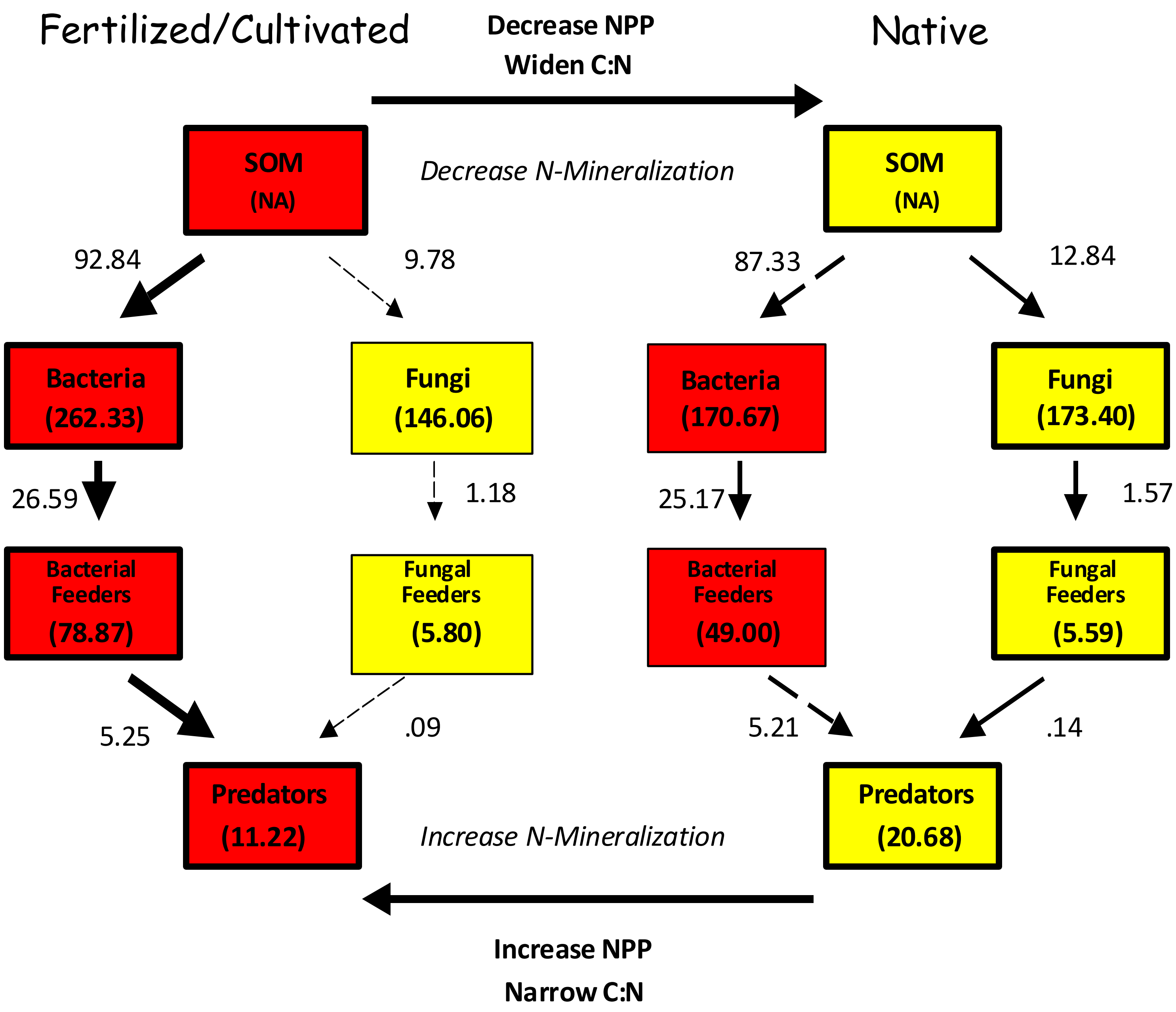


Shoots
Roots
Inorganic N
Detritus
Recalcitrant C:N > 30:1
Labile C:N < 30:1
Phytophagous Nematodes
Mycorrhizal Fungi
Saprophytic Fungi
Bacteria
Collembolans
Cryptostigmatic Mites
Non Cryptostigmatic Mites
Fungivorous Nematodes
Bacteriophagous Nematodes
Flagellates
Amoebae
Predaceous Mites
Nematophagous Mites
Predaceous Nematodes
Omnivorous Nematodes

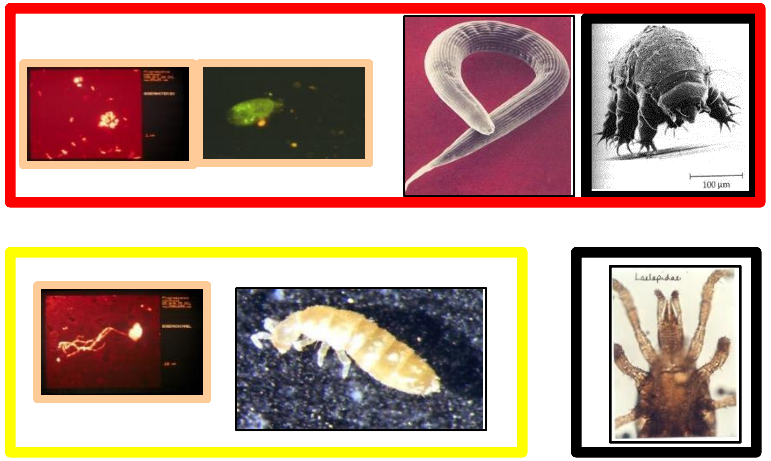
Rewiring – Human Activity







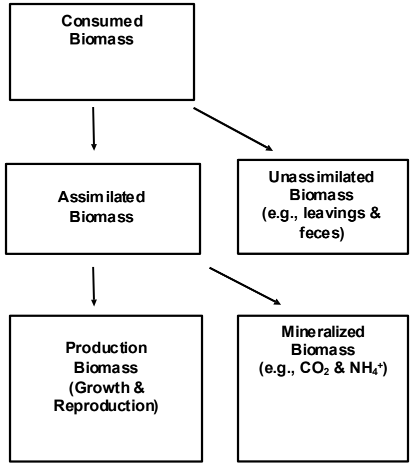
Fertilized/Cultivated
Decrease NPP
Widen C:N
Native
SOM
(NA)
Decrease N-Mineralization
SOM
(NA)
92.84
9.78
87.33
12.84
Bacteria
(262.33)
Fungi
(146.06)
Bacteria
(170.67)
Fungi
(173.40)
26.59
1.18
25.17
1.57
Bacterial Feeders
(78.87)
Fungal Feeders
(5.80)
Bacterial Feeders
(49.00)
Fungal Feeders
(5.59)
5.25
.09
5.21
.14
Predators
(11.22)
Increase N-Mineralization
Predators
(20.68)
Increase NPP
Narrow C:N



$$F_j = \frac{d_j B_j + M_j}{a_j p_j}$$

Prey$_i$ ⟶ *Predator*$_j$

B_i B_j



ODE – based dynamics of a population :

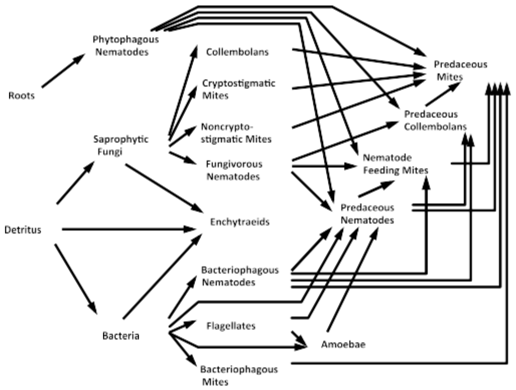
$$X_i = r_i X_i - \Sigma_j c_{ij} X_i X_j$$

$$X_j = -d_j X_j - \Sigma_k c_{jk} X_j X_k + e_j \Sigma_i c_{ij} X_i X_j$$

$$a_{11} = -c_{11} X_1^* \qquad a_{12} = -c_{12} X_1^*$$

$$a_{21} = a_2 p_2 c_{12} X_2^* \qquad a_{22} = 0$$

$$\lambda_{max} = \frac{a_{11} + \sqrt{a_{11}^2 + 4 a_{12} a_{21}}}{2}$$



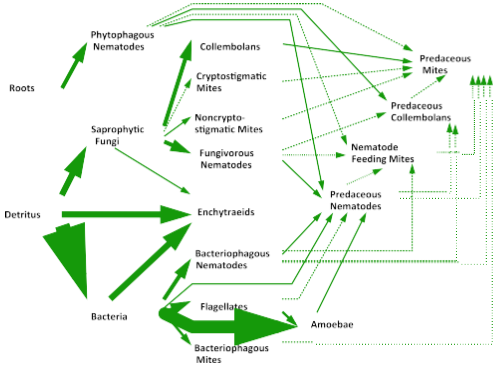
Structure

C

S

FCL

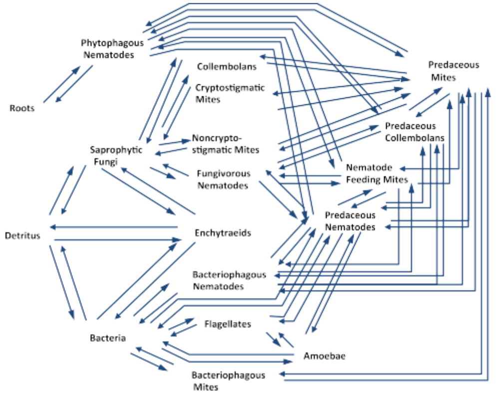
imax



Function

Trophic Interactions

C and N Mineralization



Dynamics

Jacobian Matrix

Stability

Loop weight

Return-Time

Reactivity

nature ecology & evolution

Analysis

https://doi.org/10.1038/s41559-024-02529-y

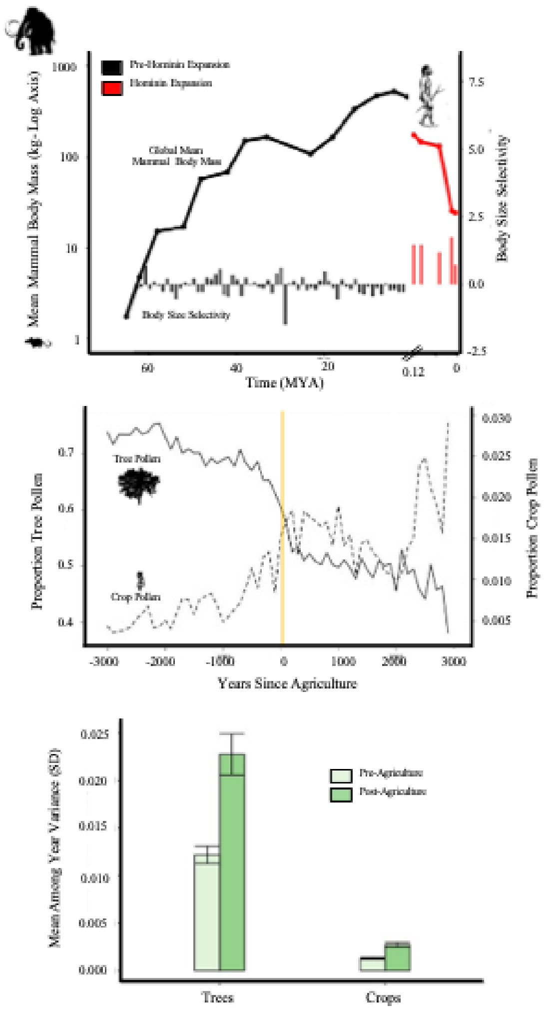
The productivity–stability trade-off in global food systems

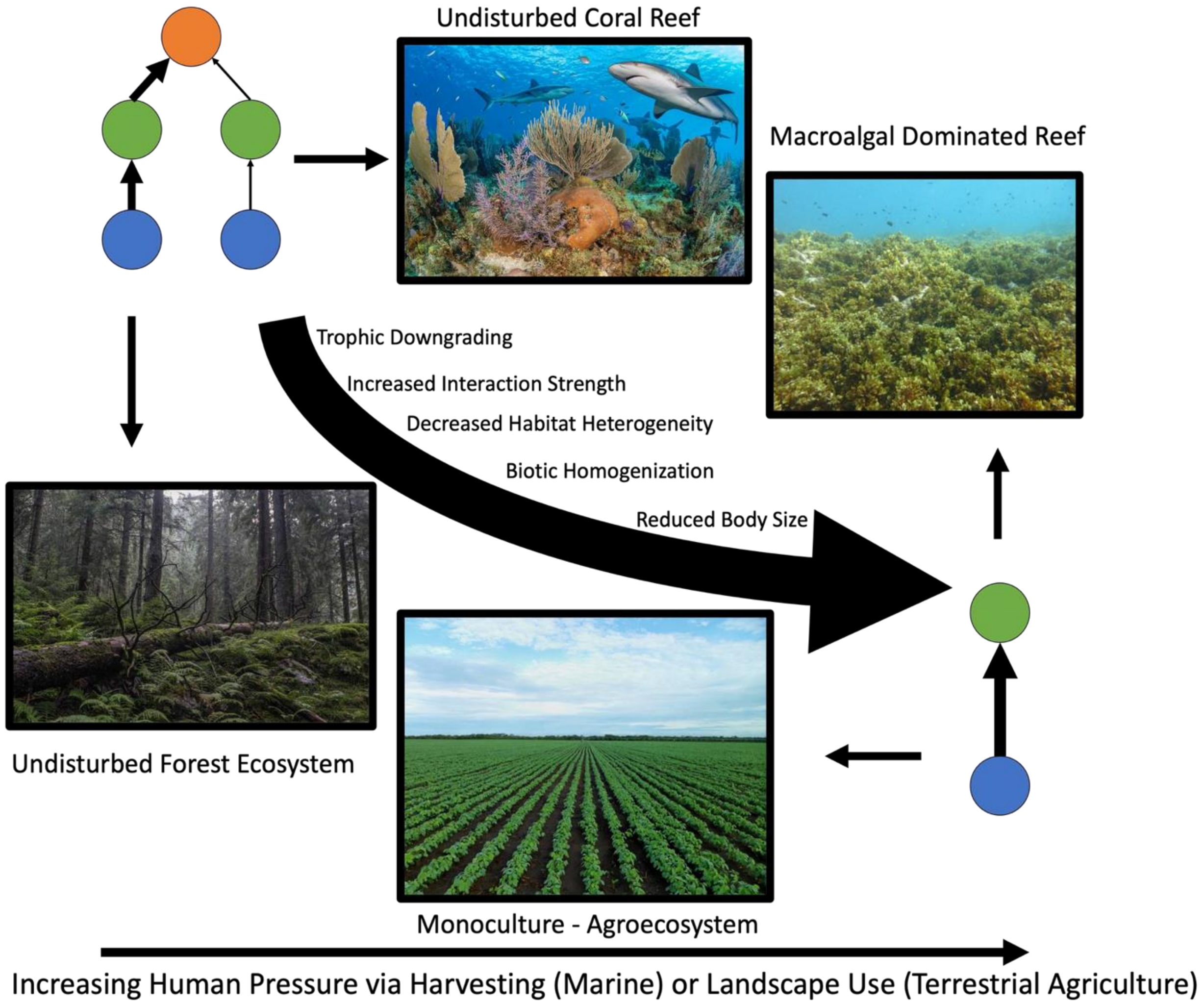
Received: 12 October 2023

Accepted: 29 July 2024

Published online: 03 September 2024

Marie Gutgesell[1,7], Kevin McCann[1,7], Reilly O'Connor[1], Krishna KC[1], Evan D. G. Fraser[1], John C. Moore[2], Bailey McMeans[3], Ian Donohue[4], Carling Bieg[5], Charlotte Ward[1], Brett Pauli[1], Alexa Scott[1], William Gillam[1], Ze'ev Gedalof[1], Robert H. Hanner[1], Tyler Tunney[6] & Neil Rooney[1]





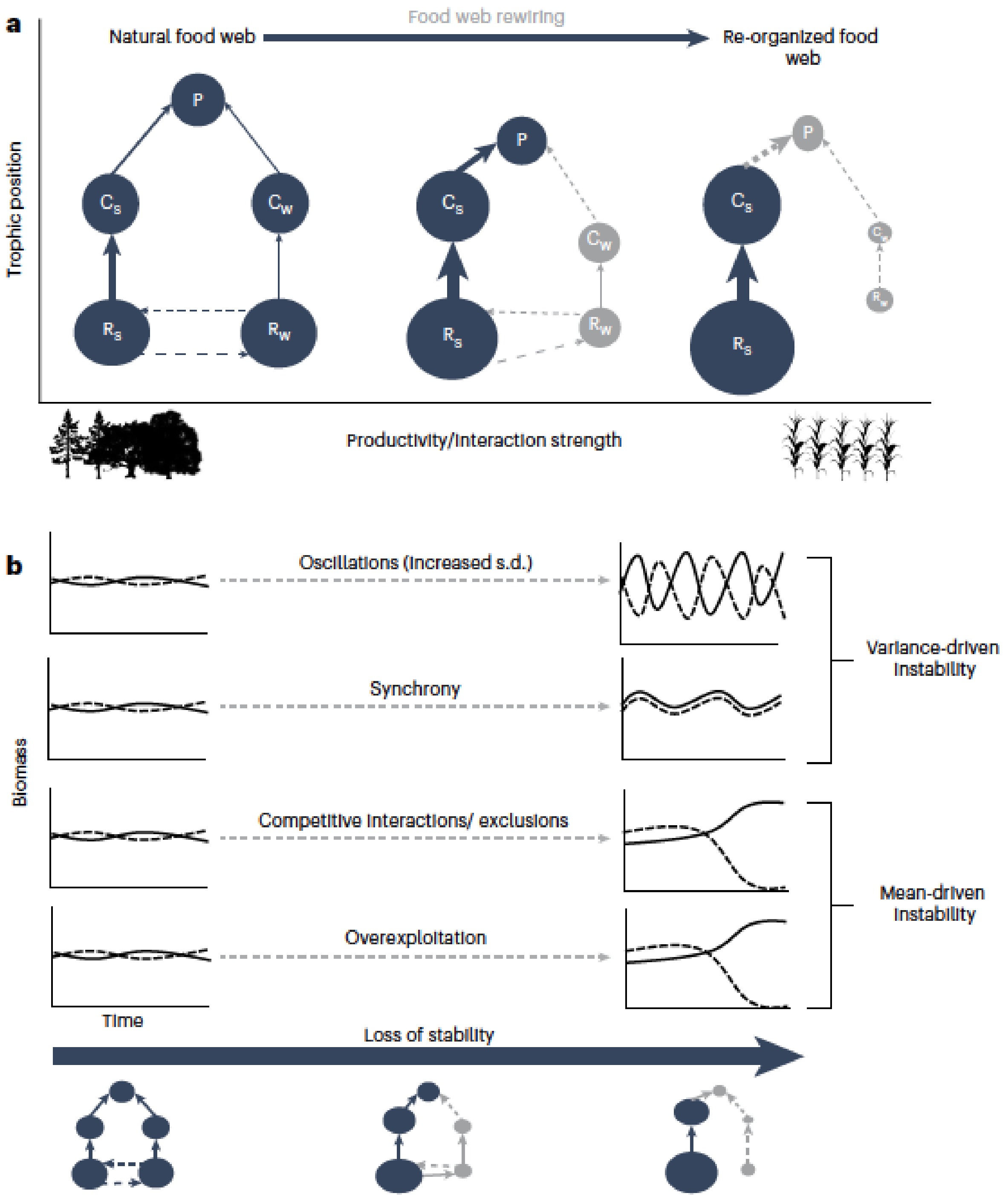
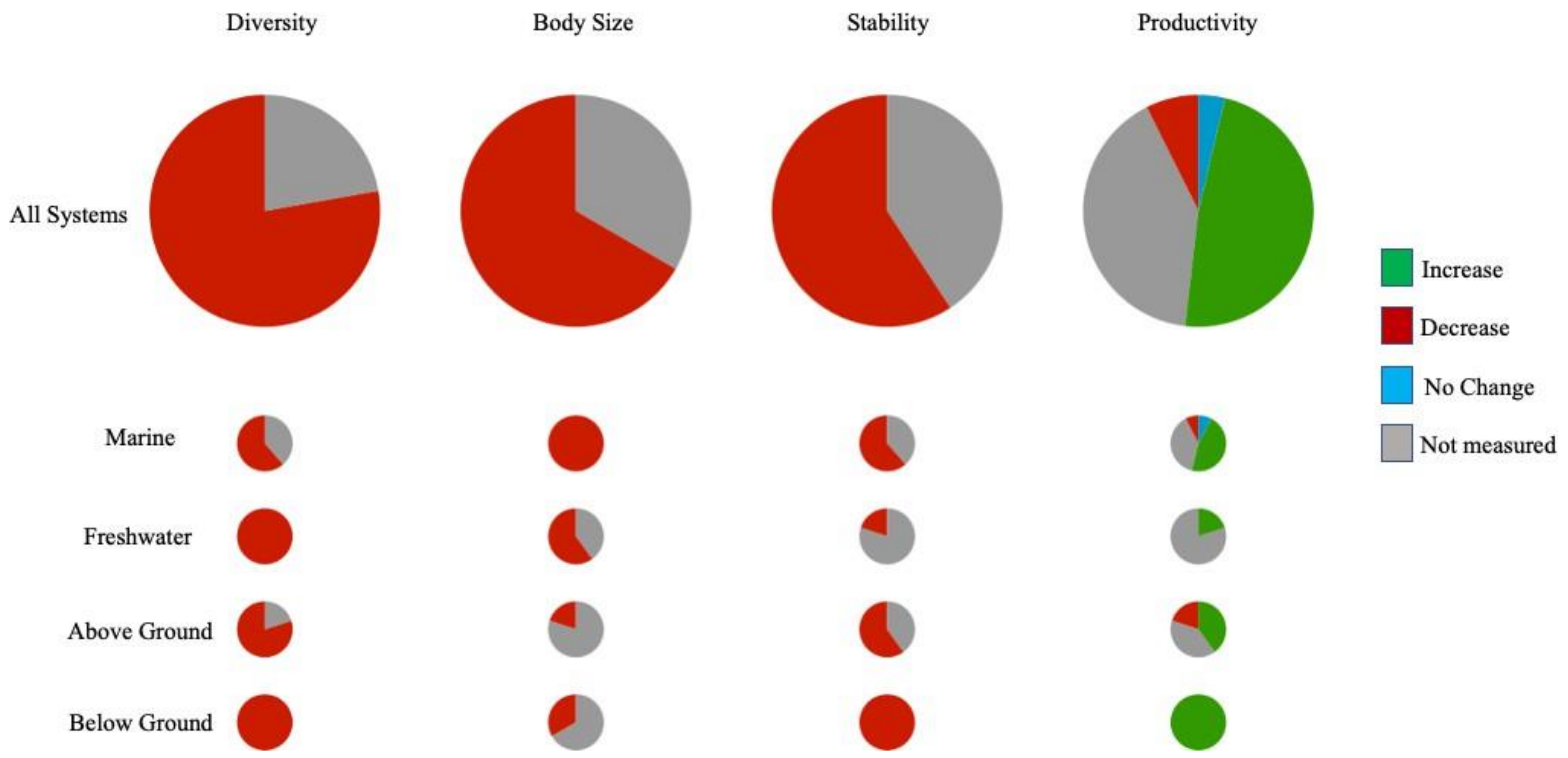

a
Food web rewiring
Natural food web
Re-organized food web
Trophic position
P
C_S
C_W
R_S
R_W
Productivity/interaction strength
b
Oscillations (increased s.d.)
Synchrony
Competitive interactions/ exclusions
Overexploitation
Variance-driven instability
Mean-driven instability
Biomass
Time
Loss of stability

Figure 4 – Empirical literature examples related to food production



Ecology Letters

WILEY

ECOLOGY LETTERS

SYNTHESIS OPEN ACCESS

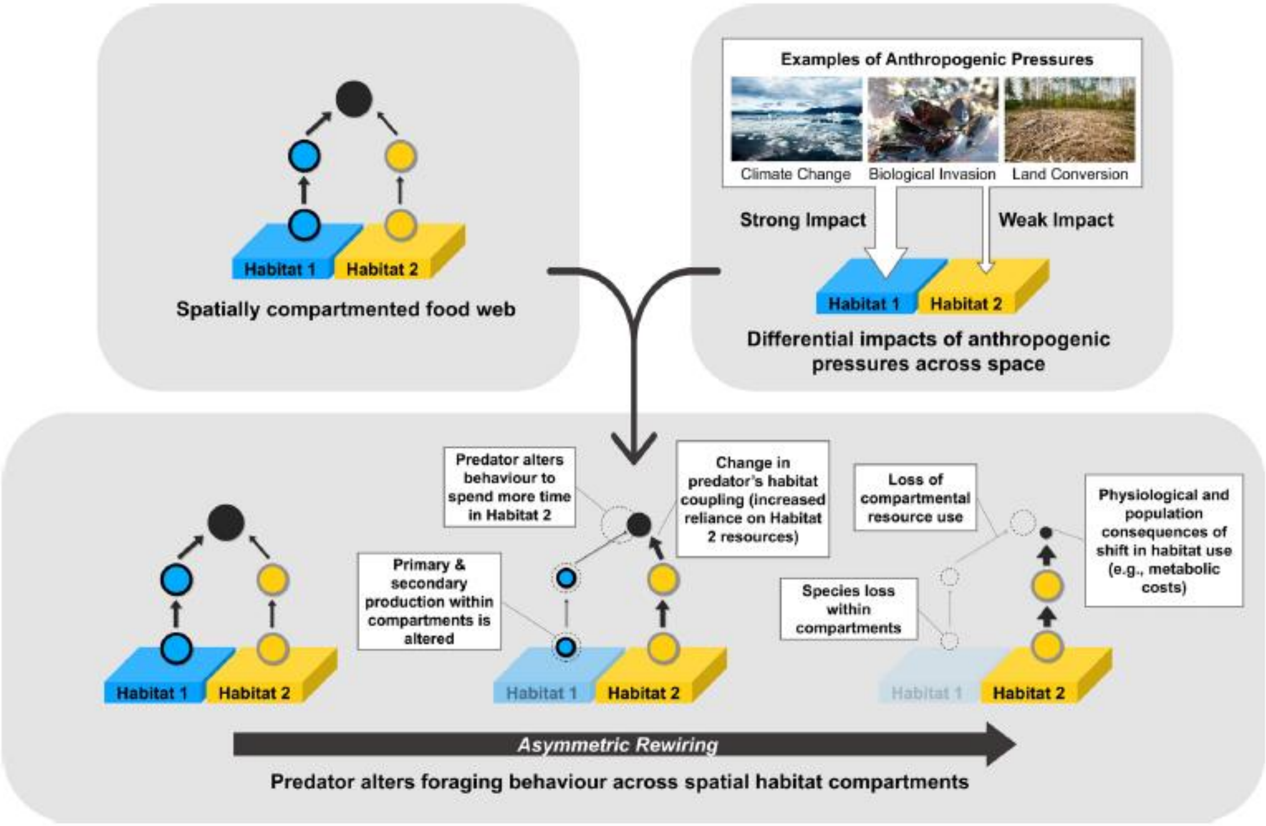
Global Change Asymmetrically Rewires Ecosystems

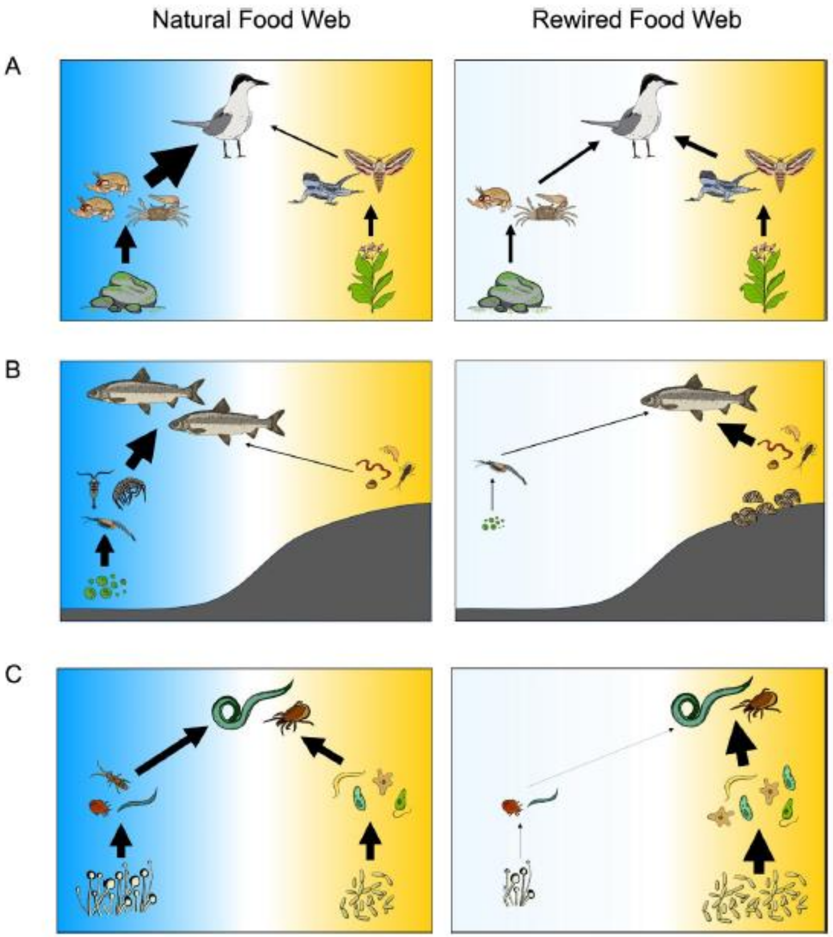
Charlotte A. Ward[1] | Tyler D. Tunney[1,2] | Ian Donohue[3] | Carling Bieg[4] | Kayla R. S. Hale[1] | Bailey C. McMeans[5] | John C. Moore[6] | Kevin S. McCann[1]

[1]University of Guelph, Guelph, Ontario, Canada | [2]Fisheries and Oceans Canada, Moncton, New Brunswick, Canada | [3]Trinity College Dublin, Dublin, Ireland | [4]Case Western Reserve University, Cleveland, Ohio, USA | [5]University of Toronto Mississauga, Mississauga, Toronto, Canada | [6]Colorado State University, Fort Collins, Colorado, USA

Correspondence: Charlotte A. Ward (cward@uoguelph.ca)

Received: 30 January 2025 | **Revised:** 18 June 2025 | **Accepted:** 20 June 2025





Ecology Letters

WILEY

ECOLOGY LETTERS

SYNTHESIS OPEN ACCESS

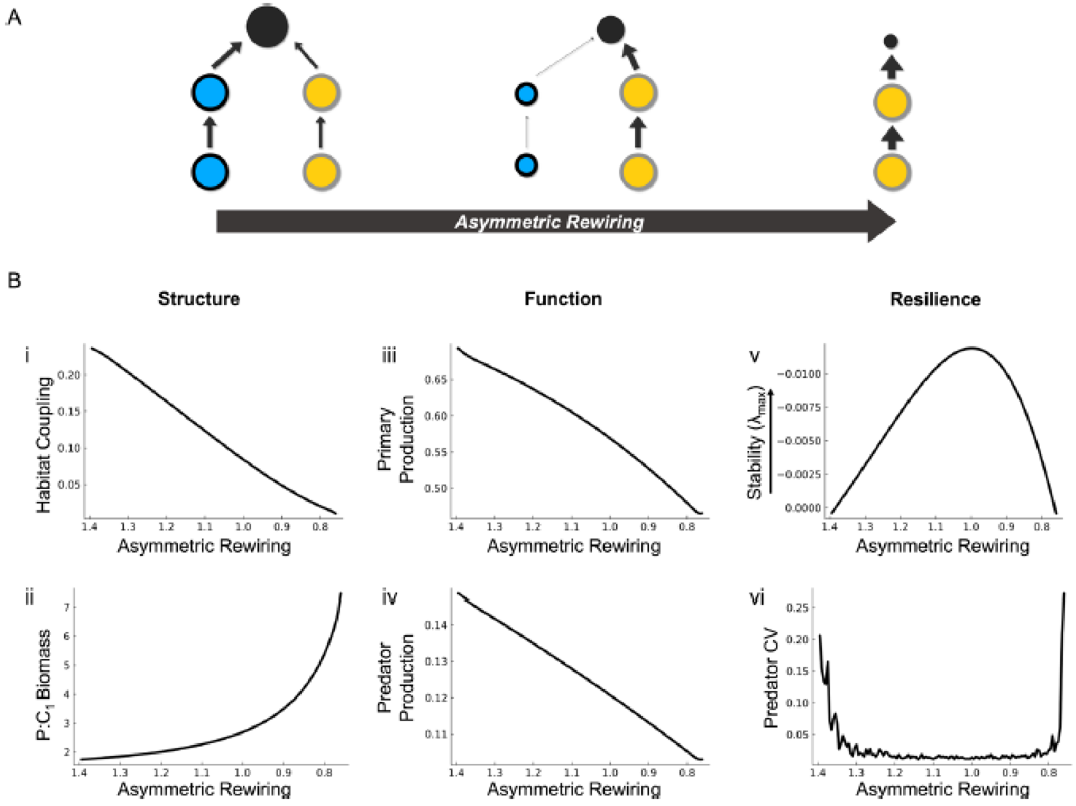
Global Change Asymmetrically Rewires Ecosystems

Charlotte A. Ward[1] | Tyler D. Tunney[1,2] | Ian Donohue[3] | Carling Bieg[4] | Kayla R. S. Hale[1] | Bailey C. McMeans[5] | John C. Moore[6] | Kevin S. McCann[1]

[1]University of Guelph, Guelph, Ontario, Canada | [2]Fisheries and Oceans Canada, Moncton, New Brunswick, Canada | [3]Trinity College Dublin, Dublin, Ireland | [4]Case Western Reserve University, Cleveland, Ohio, USA | [5]University of Toronto Mississauga, Mississauga, Toronto, Canada | [6]Colorado State University, Fort Collins, Colorado, USA

Correspondence: Charlotte A. Ward (cward@uoguelph.ca)

Received: 30 January 2025 | **Revised:** 18 June 2025 | **Accepted:** 20 June 2025



Ward et al. 2025