

General Instructions. This is a closed book exam. Please turn off and put away all cell phones, iPods, and other electronic devices. Answer all of questions 1-4, then pick **either** essay 5 **or** 6 to answer. Don't miss the extra credit on the last page.

Part 1. Short answer. Answer questions 1-4. Pay attention to all components of the questions to get full credit.

1.a. (10 points) Based on fig. 11.7 from Chapin, Matson and Mooney, below, describe the factors a, b, and c (below) and how they combine to determine the efficiency of energy transfer from one trophic level to the next.

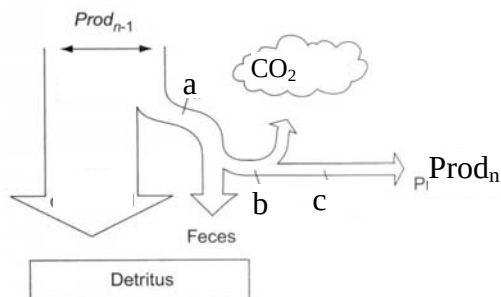


Fig. 11.7 CMM

- a. (2.5 pts.) Consumption efficiency (C_n/P_{n-1}) – the amount of production at a given trophic level that is consumed by the next highest trophic level.
- b. (2.5 pts.) Assimilation efficiency (A_n/C_n) – the amount of energy consumed that is digested.
- c. (2.5 pts.) Production efficiency (P_n/A_n) – the amount of energy that goes into growth (new biomass) from what was assimilated.
- (2.5 pts) These steps determine trophic efficiency (the amount of production at a given trophic level that is converted to production at the next highest trophic level) by the following formula: $P_n/P_{n-1} = C_n/P_{n-1} * A_n/C_n * P_n/A_n$.
- I also accepted the formula $P_n = C_n - \text{feces} - \text{urine} - \text{respiration}$

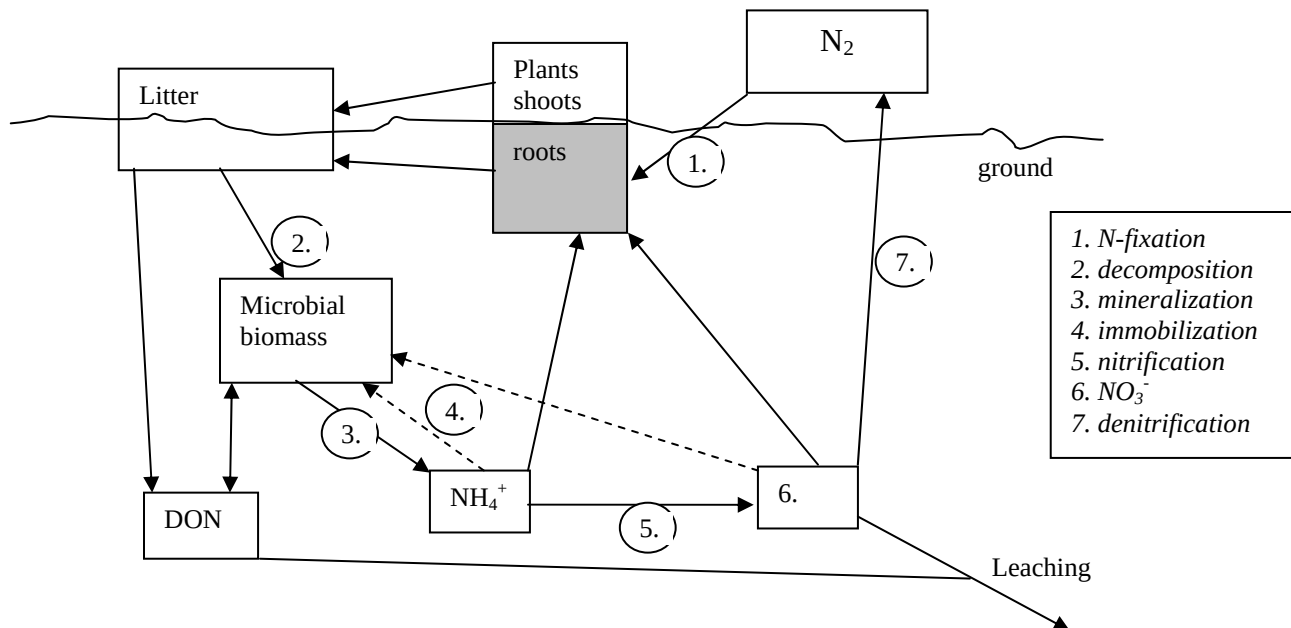
b. (4 points) How would you expect overall trophic efficiency to differ (in relative terms) for an invertebrate, poikilothermic herbivore compared to an homeothermic predator feeding on that herbivore? Briefly explain.

Overall trophic efficiency (P_n/P_{n-1}) should be higher for the invertebrate poikilotherm herbivore than the homeothermic predator. One could argue that the consumption and assimilation efficiencies would be higher for the homeotherm predator because a greater proportion of animal than plant production is edible (consumption efficiency) and higher, more constant gut temperature and more digestible food (assimilation efficiency). However, the poikilotherm herbivore will have a much higher production efficiency due to lower losses in respiration than in the endotherm, which must expend a lot of energy to maintain constant body temperature.

2. (8 points) Briefly describe how mycorrhizae are different from and similar to N-fixing mutualisms in terms of a) what organisms are involved, b) the primary nutrients taken up and sources of those nutrients, and c) the costs and benefits of the association (i.e., who gets what from whom). (You can do this in table form rather than essay form if you want, just so long as your descriptions are clear).

	<i>N-fixing mutualisms</i>	<i>Mycorrhizae</i>
a. organisms	Rhizobium bacteria associate with legume plant; Actinomycete bacteria (e.g., Frankia) associate with some non-legume shrubs and trees	Fungi – either Zygomycetes in endomycorrhizae or Basidiomycetes in ecto's. Most plants (~80% of species) form these associations.
b. nutrients	Bacteria convert atmospheric N_2 into available NH_4^+	Fungal hyphae take up nutrients, especially P, from soil and decomposing organic matter.
c. costs/benefits	Bacteria get fixed C (carbohydrates) from plant, plant gets fixed N (NH_4^+) from bacteria.	Fungi get fixed C (carbohydrates) from plant, plant gets P, and some N and water, from fungi.

3. (12 points) Label the pools and fluxes of the nitrogen cycle in the figure below, and state brief answers to the questions.



Which of the numbered fluxes is (are) partly or completely mediated by bacteria? 1, 2, 3, 4, 5, 7

Which of these fluxes primarily take(s) place under anaerobic conditions? 7, (I also took 1, since nitrogenase is inhibited by O_2 , though generally N-fixation requires O_2 for cellular respiration to generate all the ATP necessary).

Which of these fluxes is (are) chemoautotrophic? 5

Of all the fluxes shown, which one(s) compete(s) with plants for available nitrogen? 4, 7, and leaching

Of all the fluxes shown, which one(s) result(s) in a net loss of available nitrogen from the ecosystem? 7 and leaching

Which of these nitrogen pools is the largest? Atmospheric N_2

Which of these nitrogen pools turns over the quickest? NH_4^+ and NO_3^-

0.5 point each for the numbered pool & fluxes, 1 pt each for the questions

4. (6 points) Your book argues that LAI and season length are better predictors of NPP across biomes than is the daily photosynthesis rate per unit leaf area. Why might this be so, given what we've learned about photosynthetic responses to leaf N, plant responses to increased N availability, and plant allocation strategies?

Increased leaf N generally leads to increased rates of photosynthesis, greater growth and higher leaf area index (LAI). Therefore, across biomes, higher plant nitrogen in more fertile sites is often "diluted" by greater growth. This relates to plant allocation strategies in that plants will invest abundant nutrients to get more limiting resources (e.g., fixed C). Across biomes, increased growing season length also leads to increased growth and LAI. In both cases, more leaf area correlates best with ecosystem NPP.

Part 2. (20 pts.) Answer **one** of the essay questions, below. BE SURE TO INDICATE WHICH ONE YOU ARE ANSWERING, and be sure to address ALL components of the question to get full credit. Don't miss the extra credit question at the bottom of the last page.

5. (10 points) Given the data shown below (Fig. 3a from Finzi et al. 2002), how do you expect elevated CO₂ to affect total ecosystem decomposition rates, based on its effects on lignin concentration of leaves? Why? Name two other direct or indirect effects of elevated CO₂ that might influence ecosystem decomposition and briefly describe the mechanism.

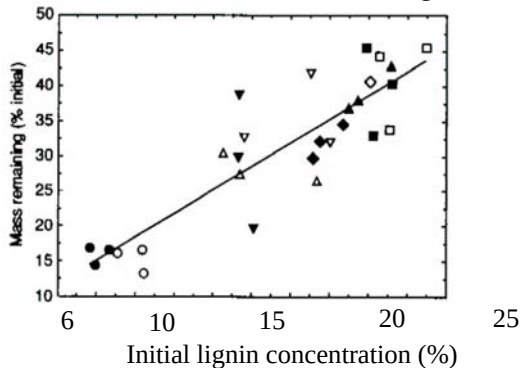


Fig. 3a from Finzi et al. 2002, showing percent of initial mass remaining following 24 months of decomposition for litter of different species. The different symbol styles represent different species, with filled symbols being from ambient CO₂ and dark symbols from elevated CO₂ (3 replicates per species from each treatment).

6. A) Explain the concept “you are what you eat, isotopically speaking” for ¹³C and how that relates to a food web isotopic mixing model. B) How does ¹⁵N differ from ¹³C in this regard? C) Using this background, explain how trout influenced the feeding relationships of *Rana muscosa*, using the data from Table 3 of Finlay and Vredenburg (2007), below.

TABLE 3. Mixing-model results for mean proportion of diet sources contributing to predator growth in uninvaded and trout-occupied lakes.

Lake	<i>R. muscosa</i>			Trout		
	Benthic prey	Pelagic or terrestrial prey	SE	Benthic prey	Pelagic prey	SE
8	1.14	-0.14	0.18			
29	0.80	0.20	0.16	1.09	-0.09	0.19
31	1.18	-0.18	0.08			
2	1.20	-0.20	0.12			
11	1.00	0.00	0.15			
13	0.88	0.12	0.05			
9	0.65	0.35	0.19	1.04	-0.04	0.26
51	1.07	-0.07	0.12			
10	0.94	0.06	0.20			
5	0.79	0.21	0.05	1.05	-0.05	0.13
48	0.88	0.12	0.08			
1	1.03	-0.03	0.11			

Notes: The $\delta^{13}\text{C}$ of pelagic and terrestrial prey overlapped so we could not distinguish their respective contributions to frog growth. We assumed only aquatic prey sources for trout in lakes, and thus only benthic and pelagic end-members were used. Results for trout-occupied lakes are shown in boldface. Contributions significantly above 1.0 for *R. muscosa* observed in the three smallest fishless lakes (i.e., 2, 8, and 31) are discussed in Results: Stable-isotope ratios.

5. A. (10 pts) i. Finzi and Schlesinger (2002) hypothesized that under higher CO₂, leaf litter quality would decrease (higher lignin) and decomposition rates would slow, also slowing rates of nutrient regeneration.

ii. From fig. 3a, we indeed see a correlation of higher lignin content with decreased decomposition rates (greater % mass remaining). This relationship is mostly driven by differences among species in leaf lignin content.

iii. However, the figure shows no consistent effect of increased CO₂ on % lignin or decomposition on a species-by-species basis (i.e., comparing dark symbols with unfilled symbols). Sometimes dark symbols show higher lignin and lower decomp (upward triangles), sometimes lower lignin and higher decomp (diamonds), and sometimes no difference in decomp no matter what difference in lignin (circles and squares).

iv. Overall, then, these data show no support for a litter chemistry feedback to decomposition and nutrient availability.

B. (5 pts.) One alternative, indirect mechanism that could affect ecosystem- level decomposition is hinted at in the data shown in fig. 3a and was discussed explicitly in the paper. Shifts in species composition resulting from different competitive abilities under elevated CO₂ could lead to large changes in ecosystem rates of decomposition if new dominant species differ greatly in litter quality from old dominant species. Given the data shown, this could result in a much greater shift in overall litter quality than chemical effects caused by elevated CO₂.

C. (5 pts.) Another alternative, indirect mechanism was also discussed in the Finzi & Schlesinger paper. If increased CO₂ causes increased plant production and litterfall, then more nitrogen immobilization could result from the higher inputs of high C:N material. If there is not enough available N to fulfill the microbial needs for nitrogen, then decomposition would slow. Eventually, however, even slow decomposition is expected to lead to lower C:N ratios in the decomposing organic matter, such that N mineralized will roughly equal demand.

I also accepted indirect effects of elevated CO₂ on climate (temperature and/or moisture) if these were explained adequately and with ecological consistency in the arguments.

6. A) You are what you eat, isotopically speaking” means that consumers quite closely reflect the $\delta^{13}\text{C}$ value of their food, with very little fractionation. This is useful in figuring out food sources from mixing models, in those cases where there are two food sources with very different $\delta^{13}\text{C}$ signatures. In this case, the $\delta^{13}\text{C}$ signature of the consumer will reflect the weighted average of the $\delta^{13}\text{C}$ signatures of the food sources: $\delta^{13}\text{C}_{\text{sample}} = f_1 * \delta^{13}\text{C}_{s1} + f_2 * \delta^{13}\text{C}_{s2}$, where f_1 and f_2 are the fractions of total diet that come from food sources s_1 and s_2 ($f_1 + f_2 = 1$). This gives two equations with 2 unknowns, which can be solved for f_1 and f_2 .

B) If you have three food sources instead of just two, you can use ^{15}N in mixing models in concert with ^{13}C , with one exception: there is significant fractionation with ^{15}N because N is in so many metabolically active compounds and the lighter isotope ^{14}N tends to get excreted more in feces and urine (“you are what you eat minus what you excrete”). On average, there is a +3.4‰ (per mil) shift in $\delta^{15}\text{N}$ with each trophic level. This can be useful in trophic studies to determine the average trophic level of the consumer.

C) The data in Table 3 from Finlay and Vredenburg (2007) illustrate that presence of trout effectively shifts the diet of frogs from benthic to more pelagic prey. The mixing model with benthic vs. pelagic prey as end members shows that trout diets are completely benthic prey (fractions of benthic prey are not significantly different from 1). This is true for frogs in lakes without trout as well, where the fraction of benthic prey ranges from 0.88-1.2. However, in lakes with trout, the fraction of benthic prey decreased to 0.65-0.80, indicating increase reliance on pelagic or terrestrial prey, likely due to competition with trout for benthic prey. (Data not shown here indicate that emergence of adult mayflies and stoneflies was much lower in lakes with than without trout.)

EXTRA CREDIT (2 points). Kirchoff (2002) shows a map with ~22.5 km of spawning streams in the watersheds studied by Helfield & Naiman (2001) (H&N). H&N estimate that salmon deposit a total of ~ 11,000 kg of marine-derived nitrogen per year in both of these watersheds combined. Using these data, estimate the amount of MDN deposited in g/m²/yr, assuming, for simplicity, equal deposition from the stream to 100 m away. (Note this is a “back of the envelope” estimate – you shouldn’t need a calculator.) Is this enough to fertilize trees?