Symbioses

April 13, 2021

Figures and tables from Lambers book unless otherwise noted

Ice-breaker review questions

1. What is a symbiosis? What are the different types?
2. Why would a plant establish a symbiosis?
3. How would a scientist identify a symbiosis?
4. What are some examples of symbioses involving plants?

Today's symbioses

1. Mycorrhizae
2. N-fixing bacteria
3. Fungal endophytes

Today’s symbioses

1. Mycorrhizae
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Mycorrhizae Basics

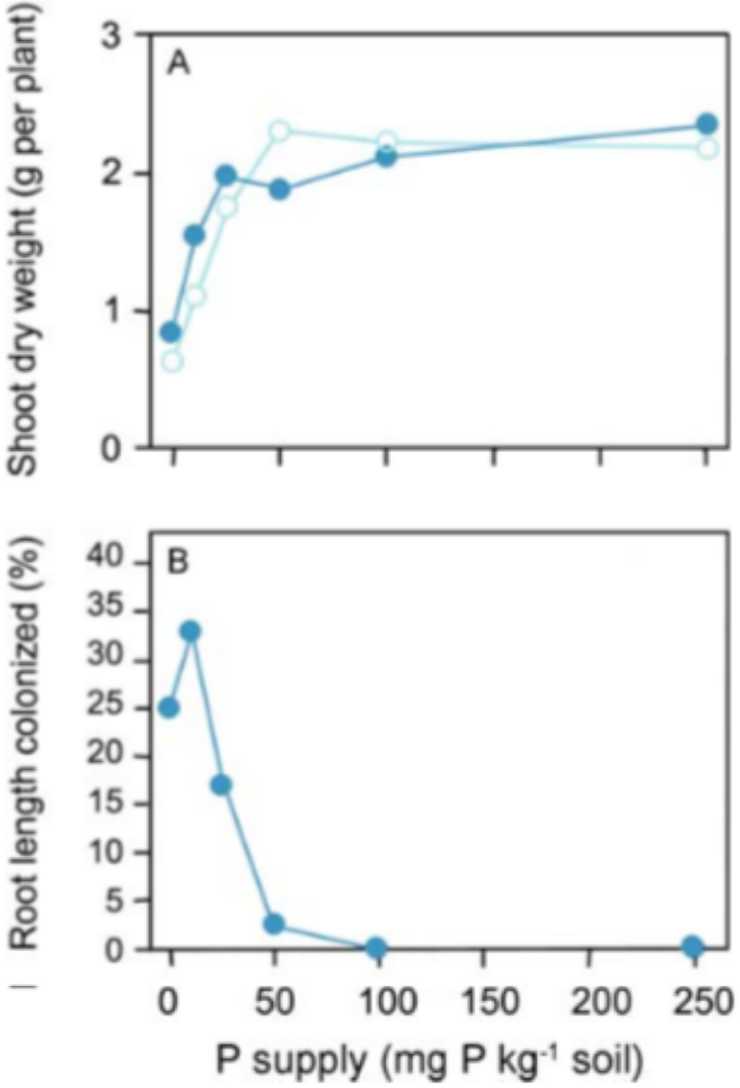
- Associated with plant roots
  - 82% of plant species
- Increase root surface area
  - Similar to root hairs
  - Increase absorptive surface
- Increases nutrient uptake
  - Primarily N and P

TABLE 1. The length of mycorrhizal hyphae per unit colonized root length as measured for a number of plant species, infected with different arbuscular mycorrhiza-forming fungal species.

Fungus	Host	Hyphal length (m cm^{-1} root)
Glomus mosseae	*Allium cepa* (onion)	0.79–2.5
Glomus mosseae	*Allium cepa*	0.71
Glomus macrocarpum	*Allium cepa*	0.71
Glomus microcarpum	*Allium cepa*	0.71
Glomus sp.	*Trifolium* sp. (clover)	1.29
Glomus sp.	*Lolium* sp. (ryegrass)	1.36
Glomus fasciculatum	*Trifolium* sp.	2.50
Glomus tenue	*Trifolium* sp.	14.20
Gigaspora calospora	*Allium cepa*	0.71
Gigaspora calospora	*Trifolium* sp.	12.30
Acaulospora laevis	*Trifolium* sp.	10.55

Source: Various authors, as cited in Smith & Gianinazzi-Pearson (1988).

Plants help regulate the symbiosis



Types of Mycorrhizae

1. Arbuscular Mycorrhiza
2. Ectomycorrhiza
3. Ericoid Mycorrhiza
4. Orchid Mycorrhiza

Types of Mycorrhizae

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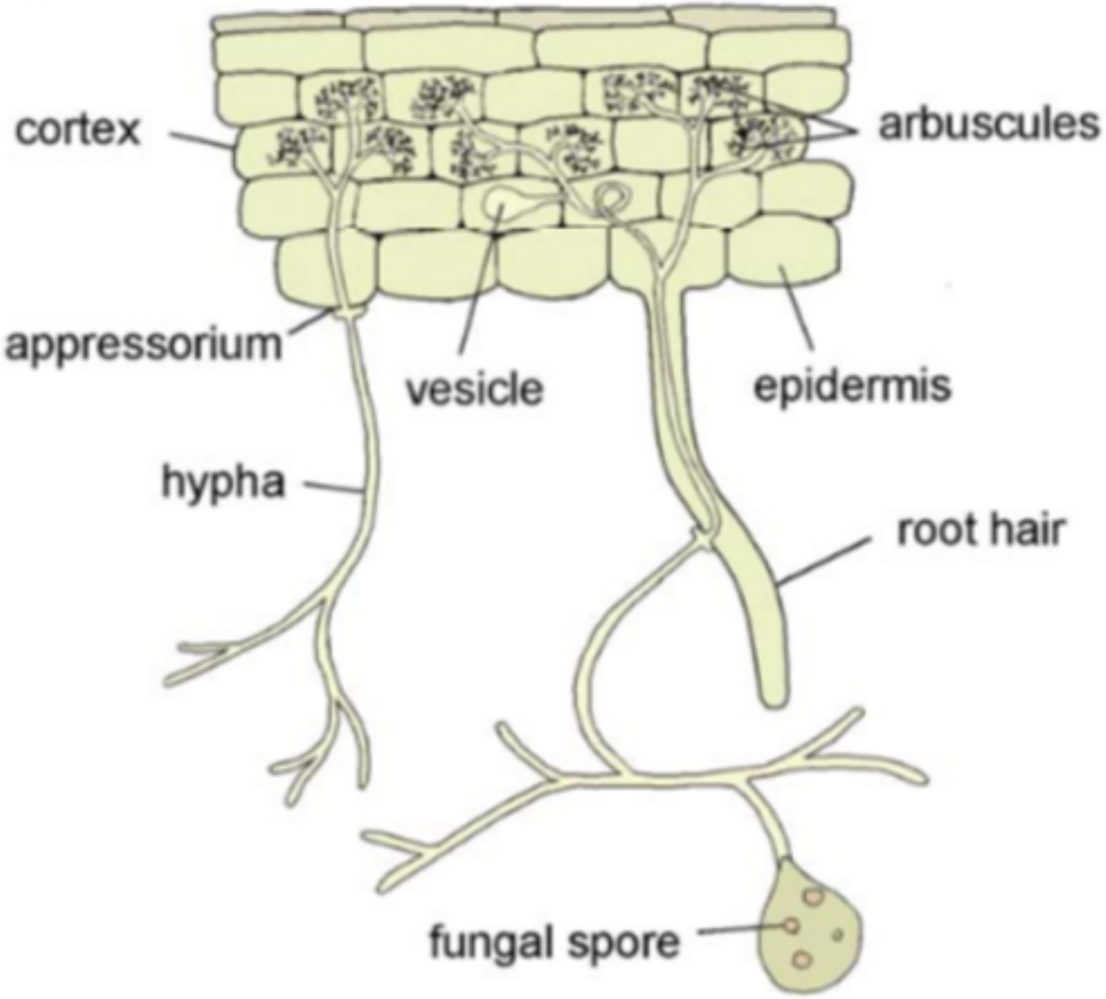
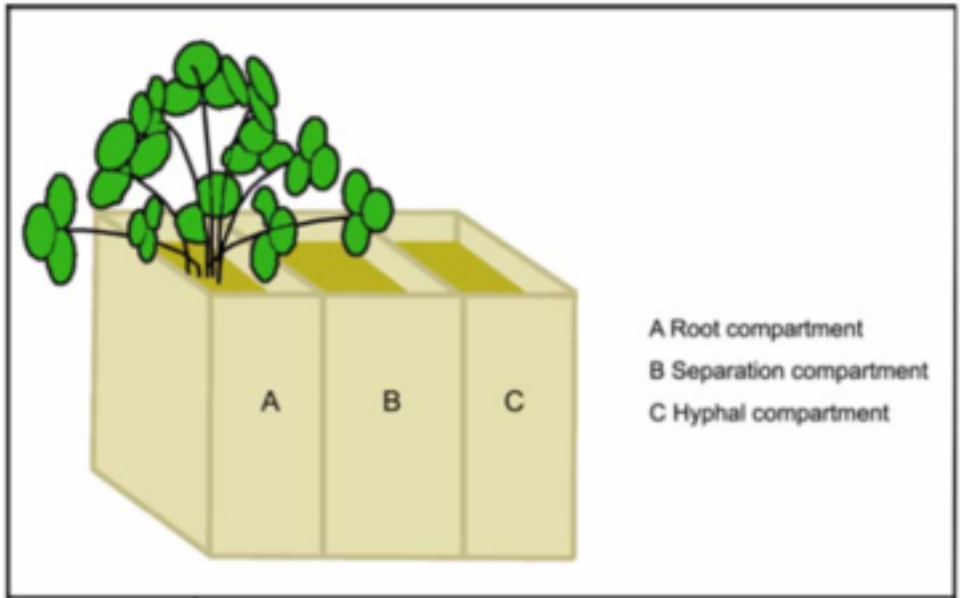
Arbuscular Mycorrhiza (AM)

- Most widespread association
  - 92% of all plant families
- Trade nutrients for Carbon via arbuscules
- Use vesicles for storage
- Increase inorganic N and P acquisition



AM: Primary benefit is increased access to nutrients (not access to new nutrients)



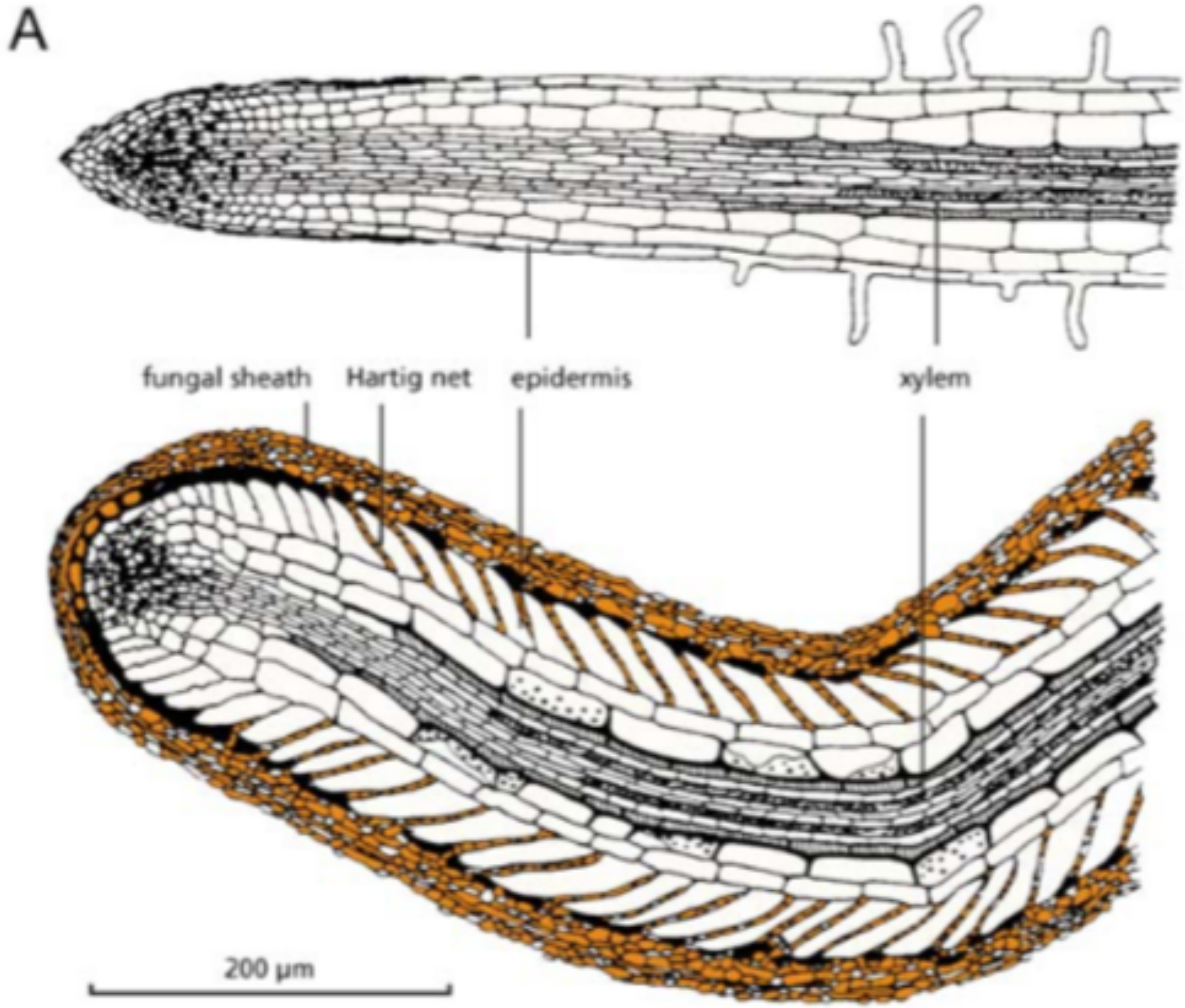
P source	Shoot ^{32}P content as a percentage of total P uptake (%)	
	Nonmycorrhizal	Mycorrhizal
Ca_2-P	0.2	18.5
Ca_8-P	0.9	13.2
Ca_{10}P	0.7	0.8
A1-P	1.2	14.0

Figure 7. Diagram showing the design of the rhizoboxes used to assess which chemical forms of P can be accessed by arbuscular mycorrhizal hyphae. The ^{32}P-labeled P source is added to the hyphal compartment only. The ^{32}P content is expressed as a proportion of the total P content of the shoots of *Trifolium pratense* (red clover) (Yao et al. 2001).

Mycorrhizae getting more P

Ectomycorrhiza

- Associations are more limited
  - Mainly trees: e.g., *Pinus, Quercus, Salix, Fagus, Eucalyptus, Betula, Populus, Alnus, Fraxinus, Cupressus*
- Do not penetrate host cells
- Exchange occurs in the intercellular spaces
- Can access organic nutrient sources



Organic vs. Inorganic nutrient acquisition

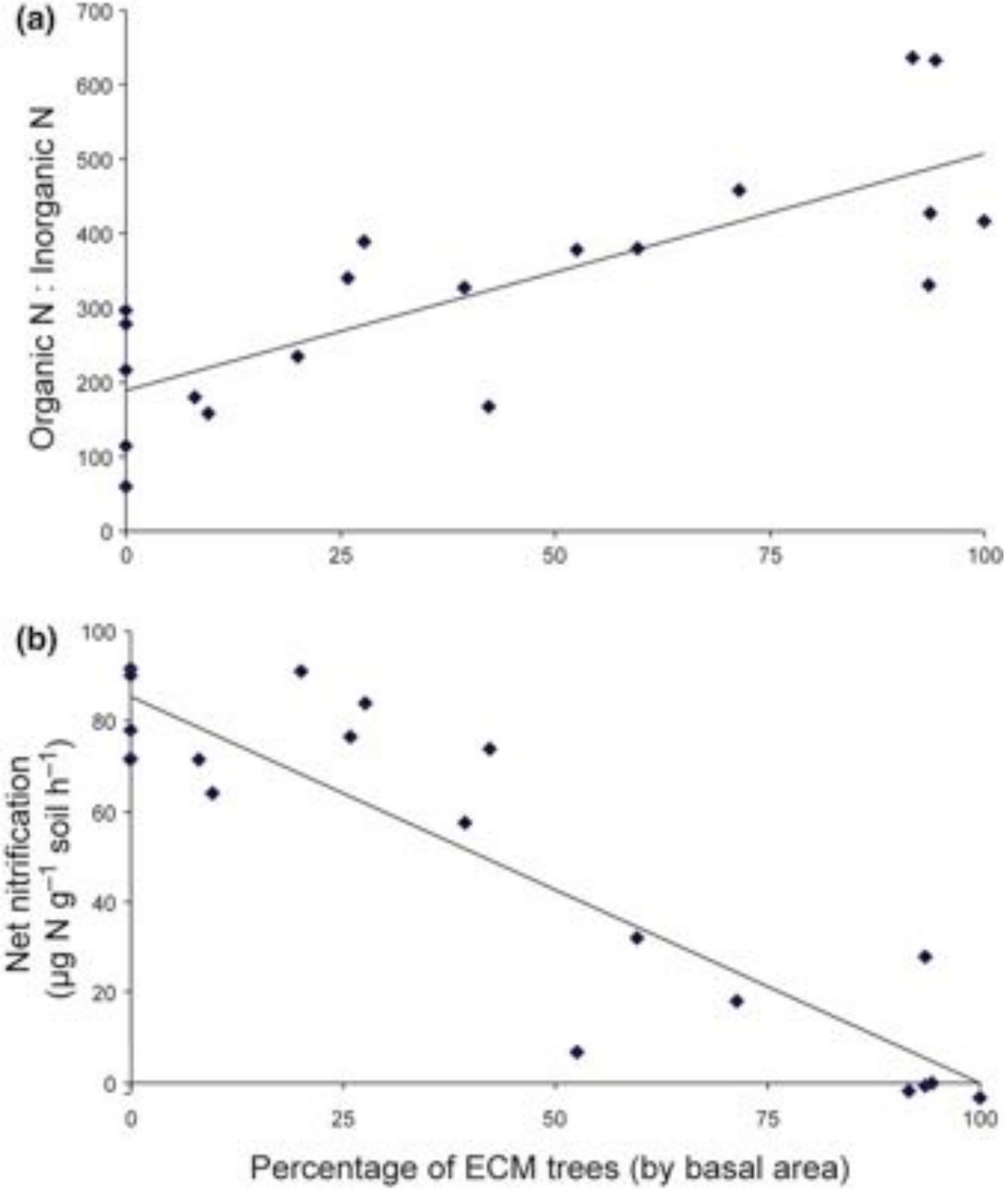
TABLE 2. ^{15}N abundance of leaf samples collected in different years in Tanzania.*

Species	Symbiotic status	$\delta^{15}N$ 1980	1981	1984
Brachystegia boehmii	EC	1.64	1.32	1.23
B. microphylla	EC	1.53	1.51	1.73
Julbernardia globiflora	EC	2.81	1.63	1.60
Pterocarpus angolensis	AM+NO	−0.81	−0.87	−0.93
Diplorynchus condylocarpon	AM	–	−0.36	−0.60
Xeroderris stuhlmannii	AM+NO	–	0.01	0.62
Dichrostachys cinerea	AM+NO	–	0.45	−0.38

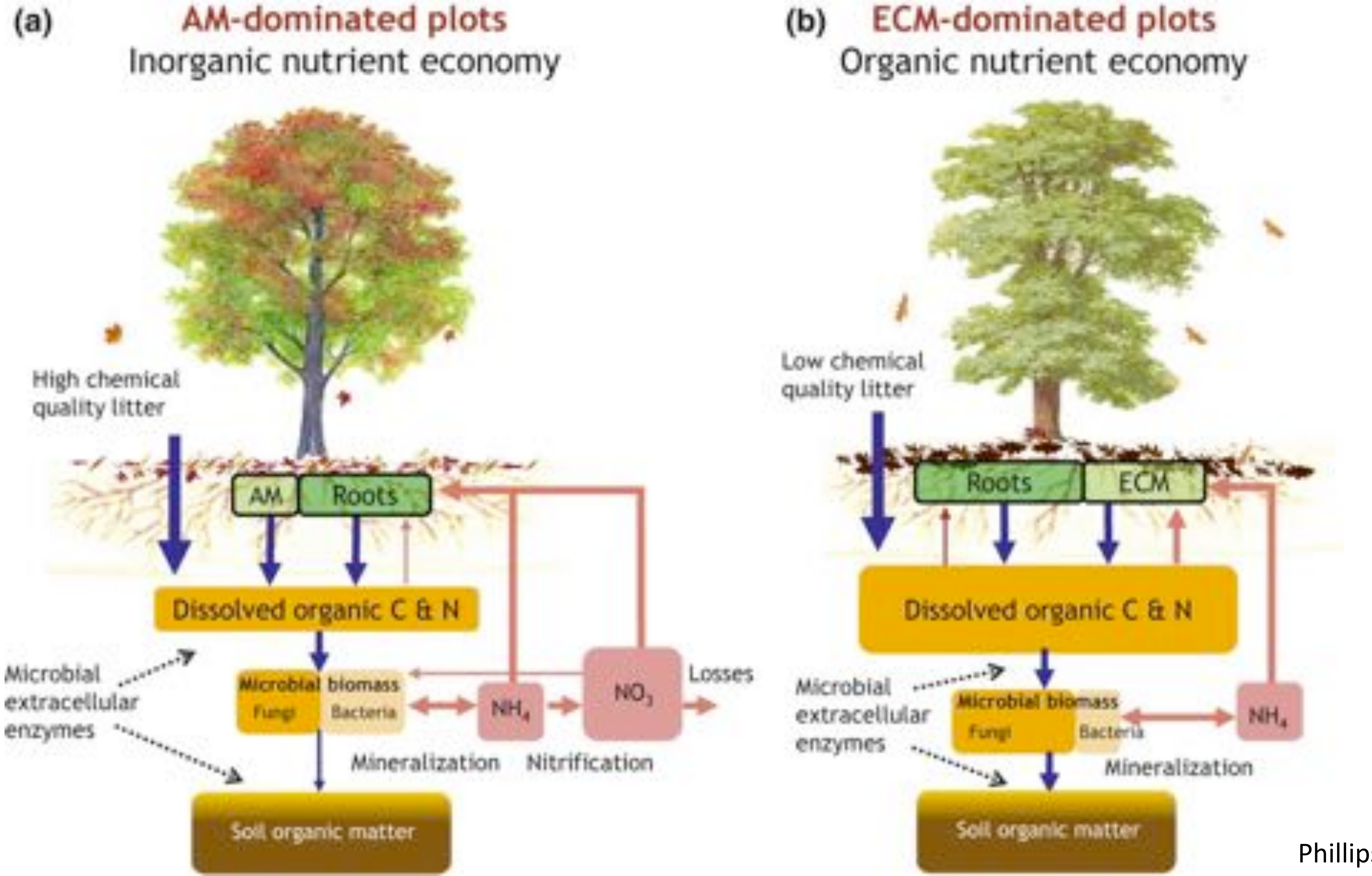
Source: Högberg (1990).

* EC = ectomycorrhizal; AM = arbuscular mycorrhizal; NO = nodulated. The experiments summarized here were actually carried out with the aim to determine the extent of symbiotic N_2 fixation of the nodulated plants. Since nodulated plants have access to dinitrogen from the atmosphere, they are expected to have $\delta^{15}N$‰ values closer to atmospheric N_2 than do plants that do not fix dinitrogen. The data presented here stress that control plants need to be sampled to allow a proper comparison. This table shows that the choice of the control plants is highly critical (see also Sect. 3 of this chapter).

Ectomycorrhizae have different signature, suggesting acquisition from different source (organic in this case)



Phillips et al. (2013)



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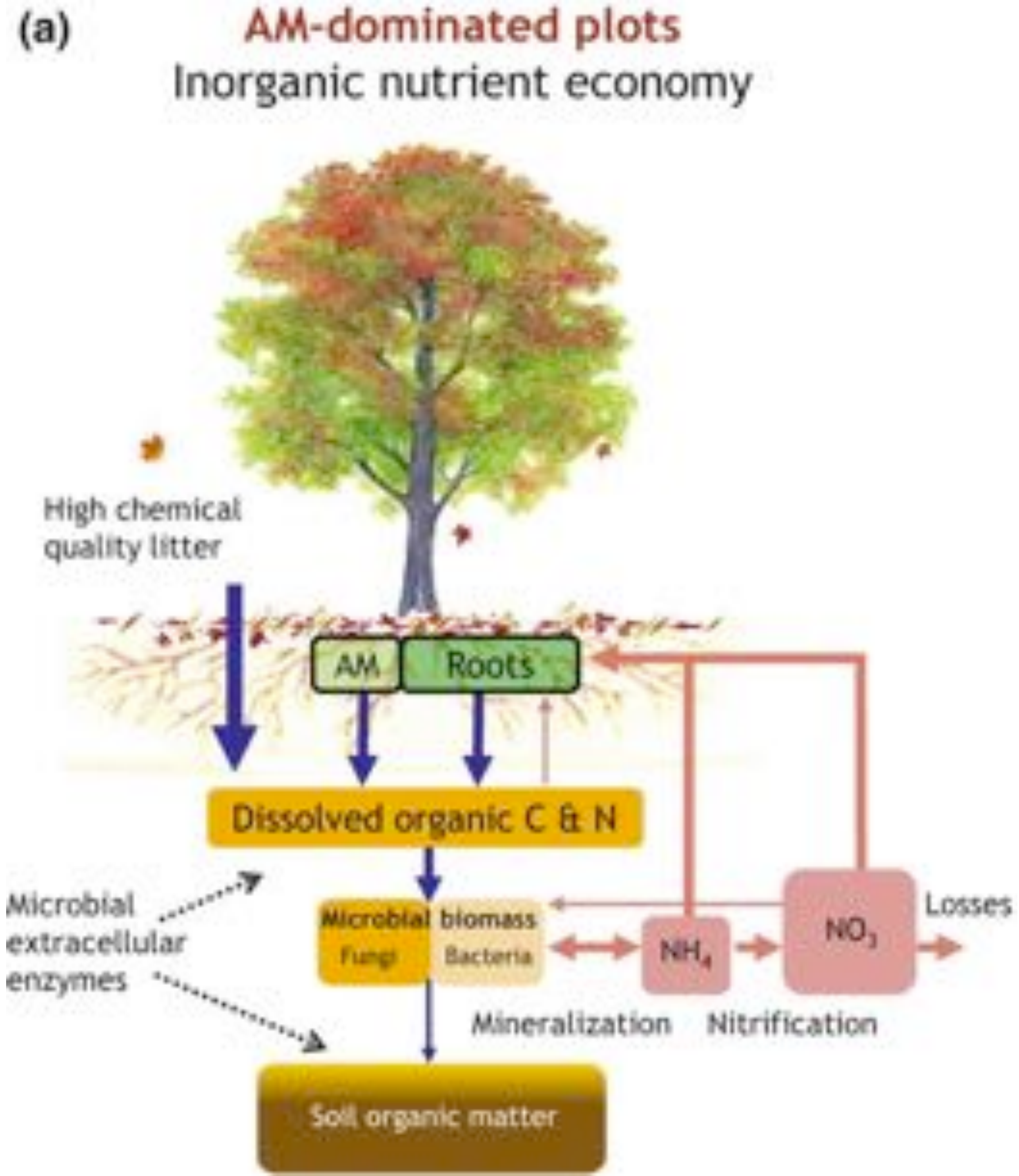

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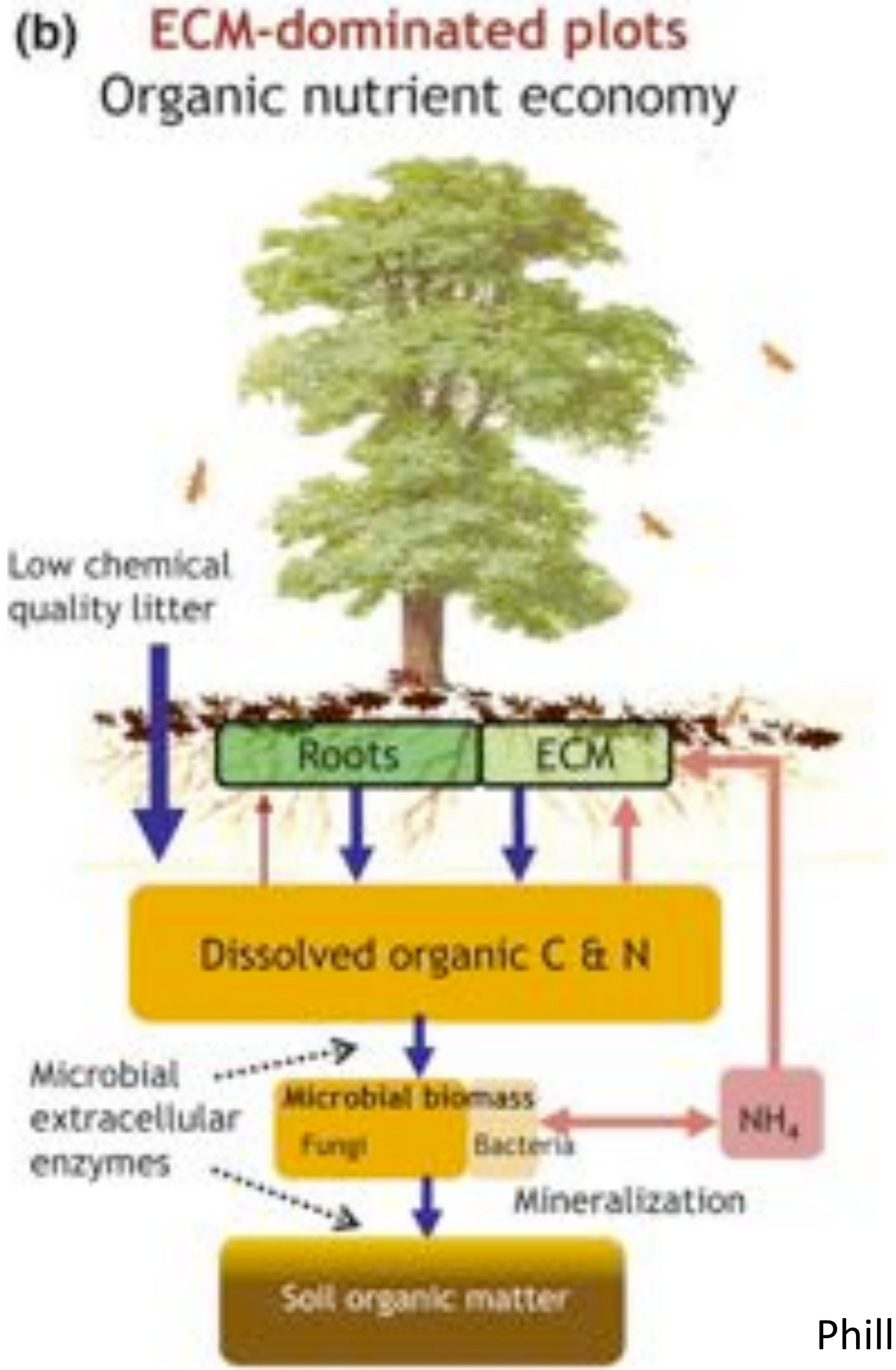

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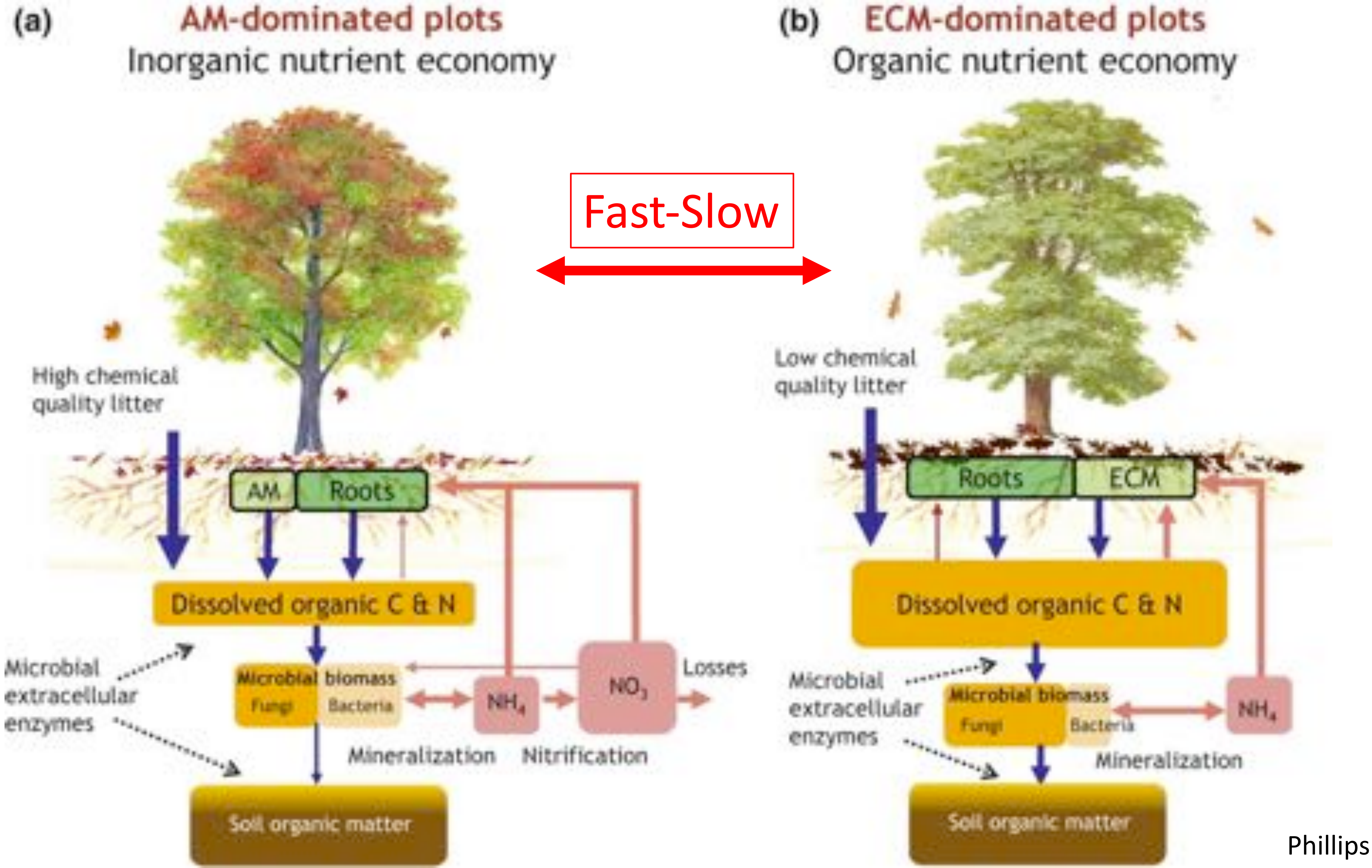

Phillips et al. (2013)

Carbon costs of mycorrhizal symbioses

- 4-20% of the carbon fixed by photosynthesis goes to mycorrhizae

TABLE 3. Comparison of accumulated ^{14}C and fresh mass in mycorrhizal and nonmycorrhizal halves of root system of two citrus cultivars.*

	^{14}C recovered from below-ground tissue dpm g^{-1}		Fresh mass mg $plant^{-1}$	
Species	+	–	+	–
Sour orange	66.4	33.6	1580	1240NS
Carrizo citrange	67.7	32.3	1990	1520NS

Source: Koch & Johnson (1984).

*+ and – denote mycorrhizal and nonmycorrhizal plants, respectively; NS indicates that there was no significant difference.

Today’s symbioses

1. Mycorrhizae
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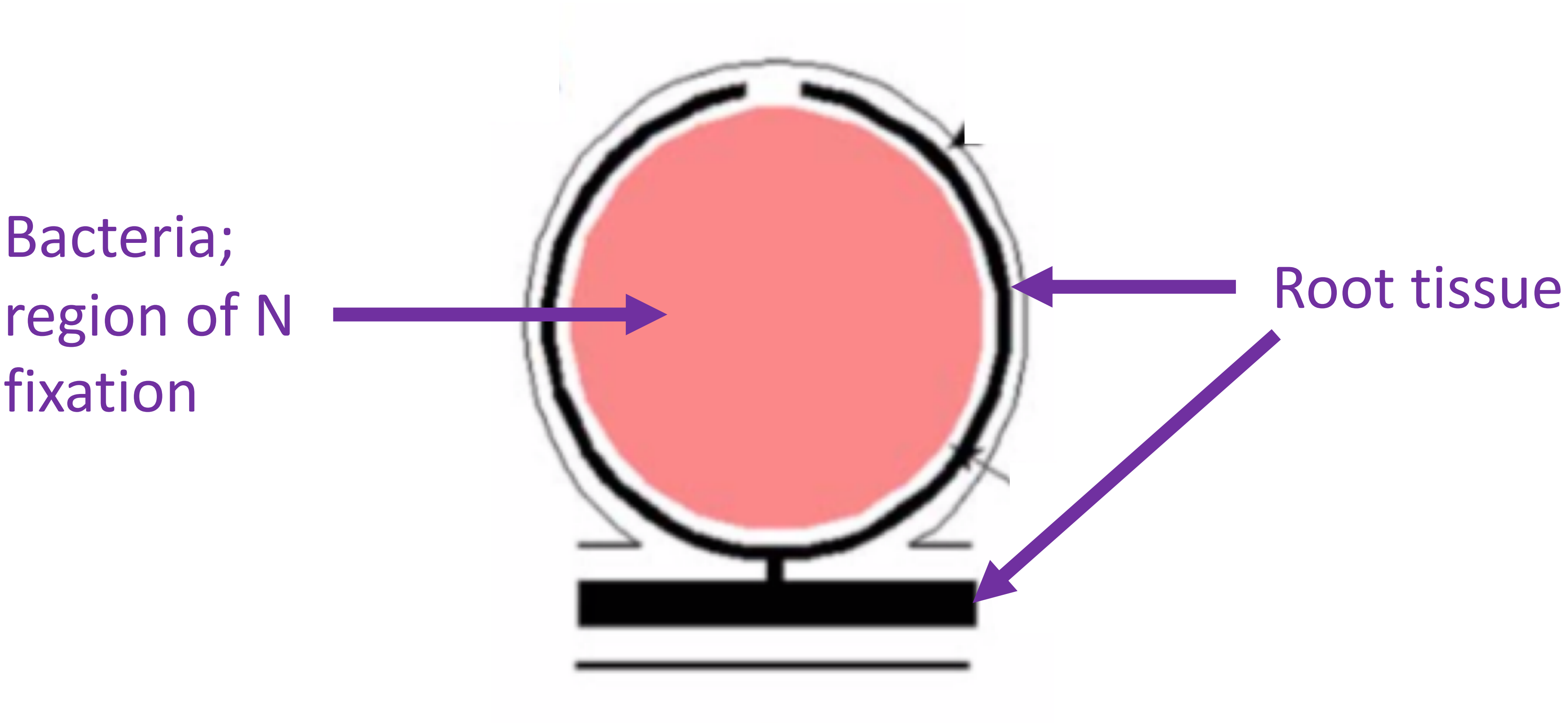
3. Fungal endophytes

Nodule Forming Rhizobia

- Convert N_2 gas into ammonia (NH_3)
- Process plants can't perform on their own
- Form nodules on roots to exchange NH_3 with carbon

FIGURE 13. N_2-fixing symbiotic systems. (*Top, left*) Legume–rhizobium symbiosis on the South African *Chamaecrista mimosoides* (fishbone dwarf cassia) (photo H. Lambers). (*Bottom, left*) Symbiotic structure (rhizothamnia) between the Western Australian *Allocasuarina humilis* and an Actinobacteria (*Frankia*) (courtesy M.W. Shane, School of Plant Biology, The University of Western Australia, Australia). (*Right*) Symbiotic structure between *Macrozamia riedlii* and cyanobacteria (courtesy M.W. Shane, School of Plant Biology, The University of Western Australia, Crawley, Australia).

Nodule Forming Rhizobia



Nodule Forming Rhizobia

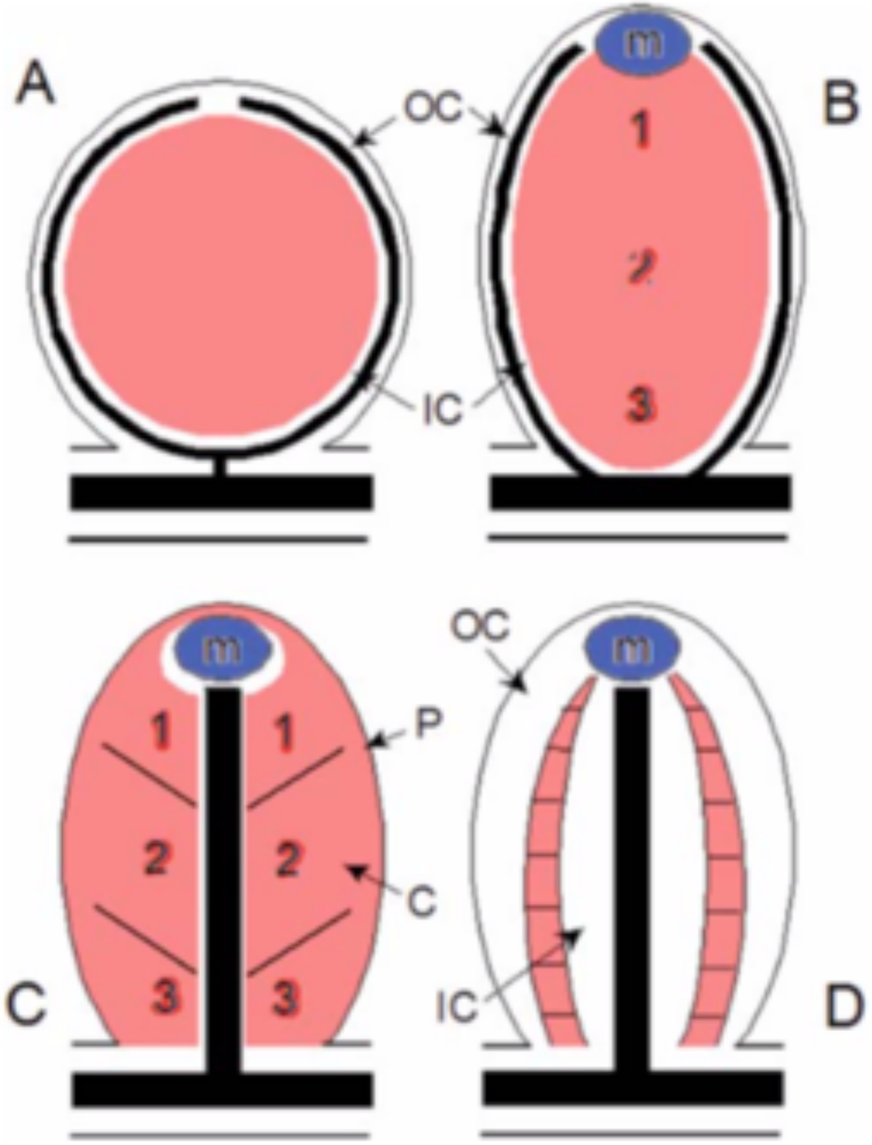


FIGURE 14. Diagrammatic representation of longitudinal sections through (A) an indeterminate legume nodule, (B) a determinate legume nodule, (C) an actinorhizal nodule, and (D) a lobe of a symbiotic coralloid root cluster. The red colored regions represent the infected zones. The dark, thick lines represent vascular tissues. Outer cortical (OC) tissue, inner cortical (IC) tissue, and meristems (m, blue) are indicated. In the indeterminate legume nodule (B) and the actinorhizal nodule (C), the zones of infection (1), N_2 fixation (2), and senescence (3) are indicated (Vessey et al. 2005).

Fabaceae

- The legumes!
  - Soybean
  - Alfalfa
  - Clover
  - Peas
  - Lentils
  - Mesquite
  - Peanuts
  - Tamarind

Fabaceae…and some other things

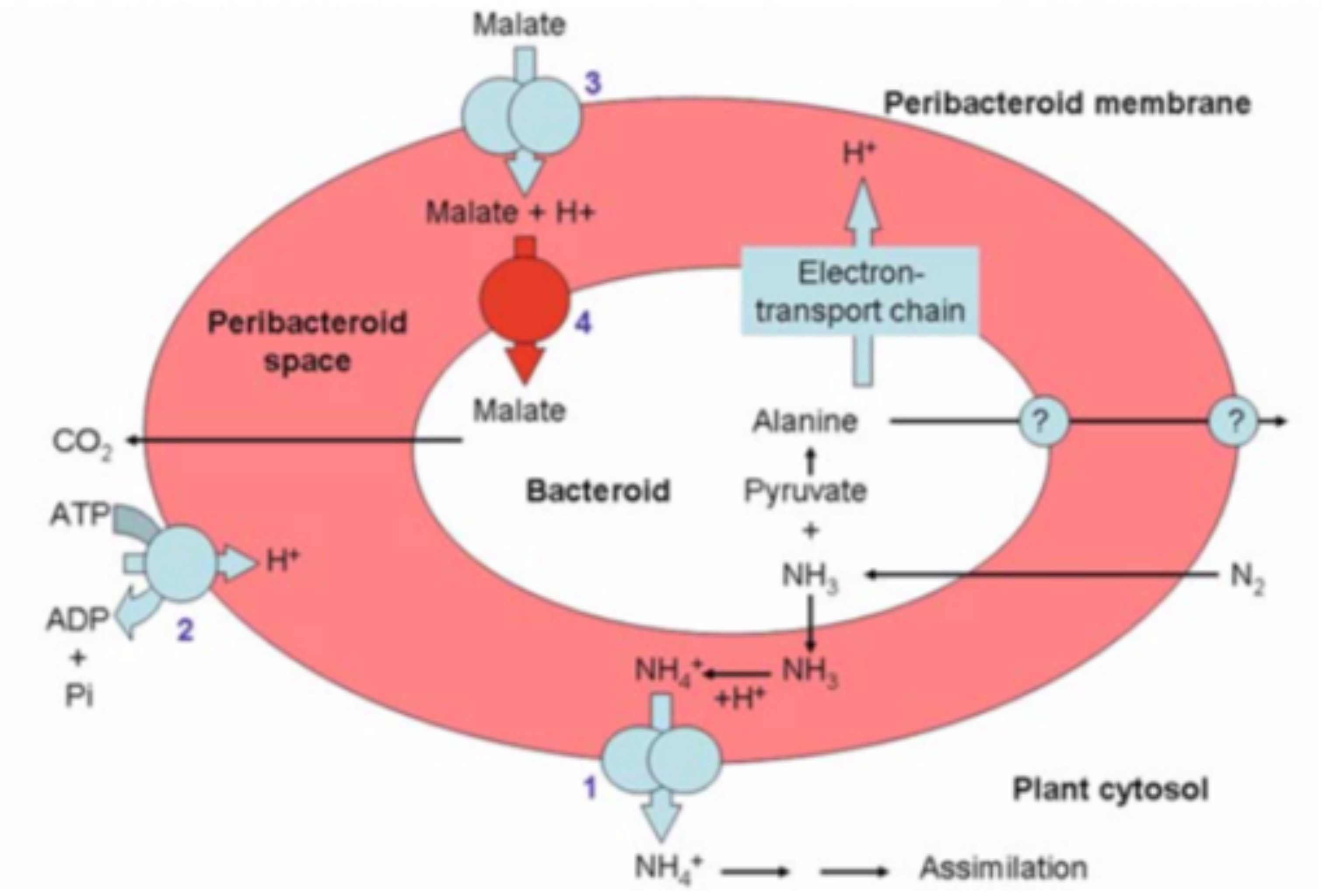
Table 4. Symbiotic associations between plants and microorganisms capable of fixing atmospheric N_2.*

Plant type	Genus	Microorganism	Location	Amount of N_2 fixed (kg N ha^{-1} $season^{-1}$)
Fabaceae	*Pisum*	*Rhizobium*	Root nodules	10–350
	Glycine	*Bradyrhizobium*	Root nodules	15–250
	Medicago	*Sinorhizobium*	Root nodules	440–790
	Sesbania	*Azorhizobium* *Mesorhizobium*	Stem nodules	7–324
Ulmaceae	*Parasponia*	*Bradyrhizobium*	Root nodules	20–70
Betulaceae	*Alnus*	*Frankia*	Root nodules	15–300
Casuarinaceae	*Casuarina*	*(Actinobacteria)*	Root nodules	9–440
Eleagnaceae	*Eleagnus*	*(Actinobacteria)*	Root nodules	nd
Rosaceae	*Rubus*	*(Actinobacteria)*	Root nodules	nd
Pteridophytes	*Azolla*	*Anabaena*	Heterocysts in cavities of dorsal leaf lobes	40–120
Cycads	*Ceratozamia*	*Nostoc*	Coralloid roots	19–60
Lichens	*Collema*	*Nostoc*	Interspersed between fungal hyphae	nd

Source: Kwon & Beevers (1992), Gault et al. (1995), Peoples et al. (1995), Vance (2002).

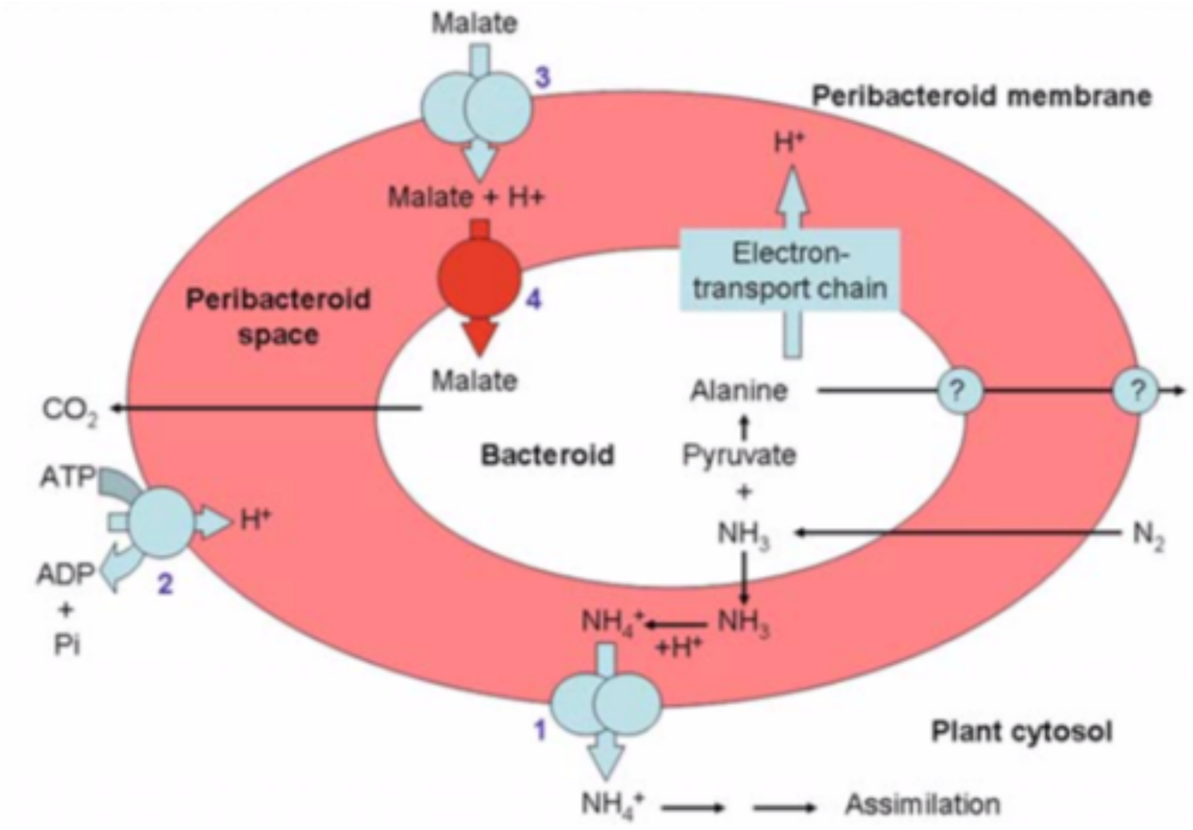
* Only a limited number of species are listed, just to provide an example; nd is not determined.

Carbon cost of the rhizobia symbiosis



Carbon cost of the rhizobia symbiosis

- 4-13% of photosynthate when soil N is high
- 25% or higher when soil N is low



Suppression of rhizobia symbiosis

- Presence of N reduces plant-mediated bacterial activity

TABLE 9. Apparent nitrogenase activity and the O_2-limitation coefficient, 2 days after addition of NO_3^- to the root environment of nodulated 21-day-old plants of *Pisum sativum* (pea).*

$[NO_3]$ (mM)	Apparent nitrogenase activity [nmol H_2 g^{-1} (nodule dry mass) s^{-1}]
0	45
5	38
10	22
15	24

Source: Kaiser et al. (1997).

* The apparent nitrogenase activity was measured as the rate of H_2 evolution. As explained in Sect. 3.4, nitrogenase activity leads to the production of H_2. There is normally no net evolution of H_2, because rhizobia have a hydrogenase (i.e., an enzyme that uses H_2 as an electron donor). In the present experiment, a rhizobium strain was used that lacks hydrogenase so that the evolution of H_2 could be measured. The O_2 limitation coefficient is calculated as the ratio between total nitrogenase activity (H_2 evolution in the absence of N_2) and potential nitrogenase activity (H_2 evolution in the absence of N_2 at an optimum concentration of O_2).

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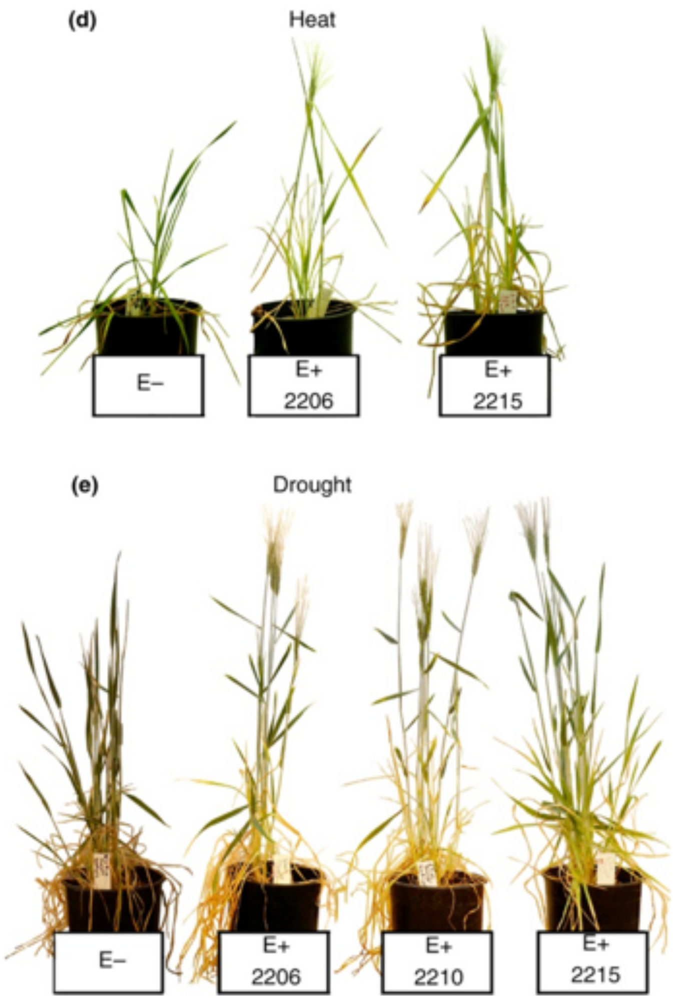
Fungal endophytes can harm herbivores

Table 10. Antiherbivore effects of fungal endophytes that infect grasses.

Animal	Host genus grass	Fungal endophyte genus	Comments
Mammals			
Cattle, horses	*Festuca*	*Acremonium*	Reduced mass gain, gangrene, spontaneous abortion
Cattle, sheep, deer	*Lolium*	*Acremonium*	Reduced mass gain, tremors, staggers, death
Cattle, goats	*Andropogon*	*Balansia*	Reduced milk production, death
Cattle	*Paspalum*	*Myriogenospora*	Reduced mass gain, tremors gangrene
Insects			
Fall armyworm	*Cenchrus*	*Balansia*	Avoidance, reduced survival, reduced growth, increased development time
	Cyperus	*Balansia*	
	Festuca	*Acremonium*	
	Lolium	*Acremonium*	
	Paspalum	*Myriogenospora*	
	Stipa	*Atkinsonella*	
Aphids	*Festuca*	*Acremonium*	Avoidance
Billbugs	*Lolium*	*Acremonium*	Reduced feeding and oviposition
Crickets	*Lolium*	*Acremonium*	Complete mortality
Cutworms	*Dactylis*	*Epichloe*	Reduced survival and mass gain
Flour beetles	*Lolium*	*Acremonium*	Reduced population growth
Sod webworms	*Lolium*	*Acremonium*	Reduced feeding and oviposition
Stem weevils	*Lolium*	*Acremonium*	Reduced feeding and oviposition

Source: Clay (1988).
Note: The examples are representative but not exhaustive.

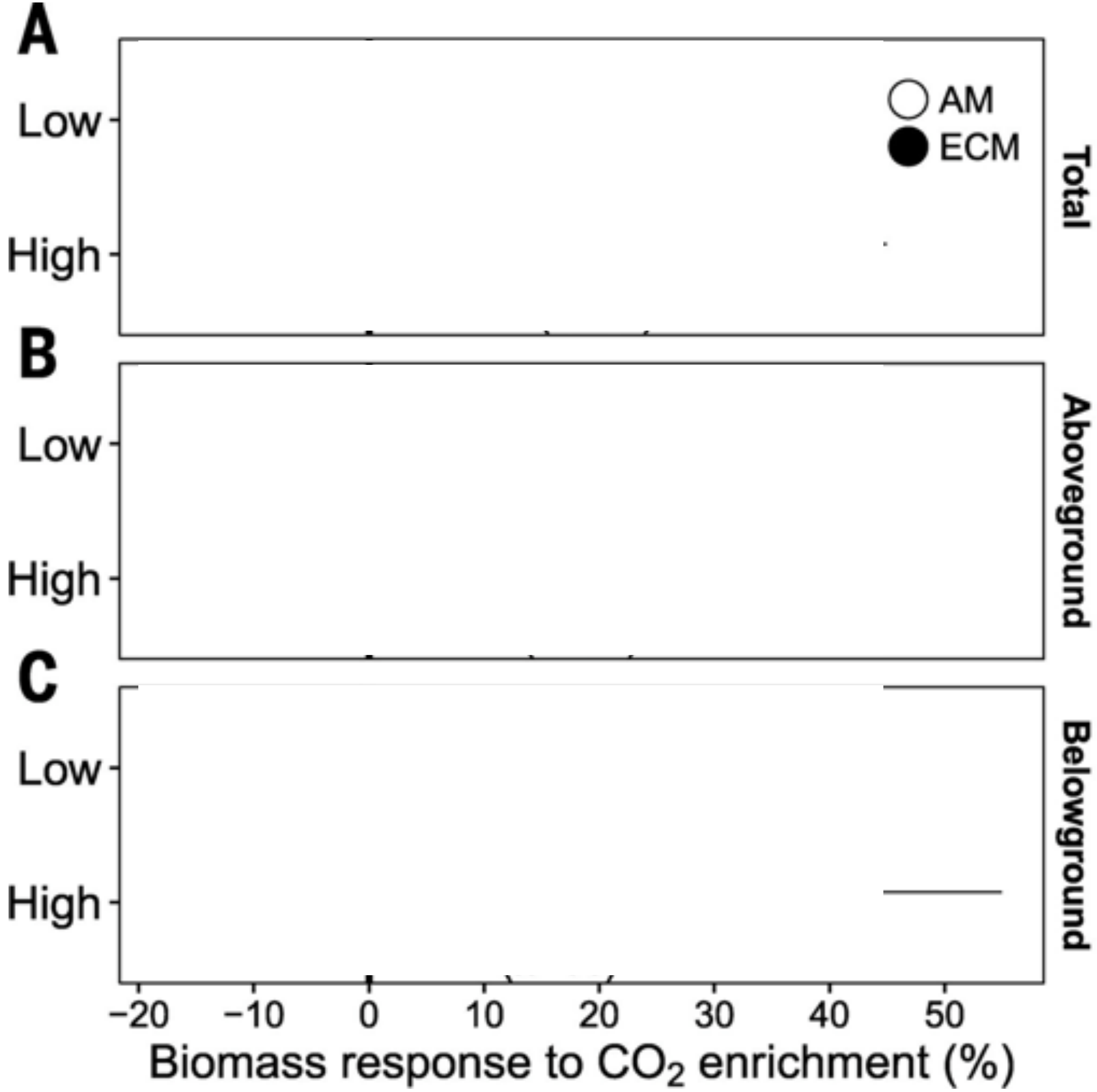
Fungal endophytes can increase stress tolerance



Hubbard et al. (2013)

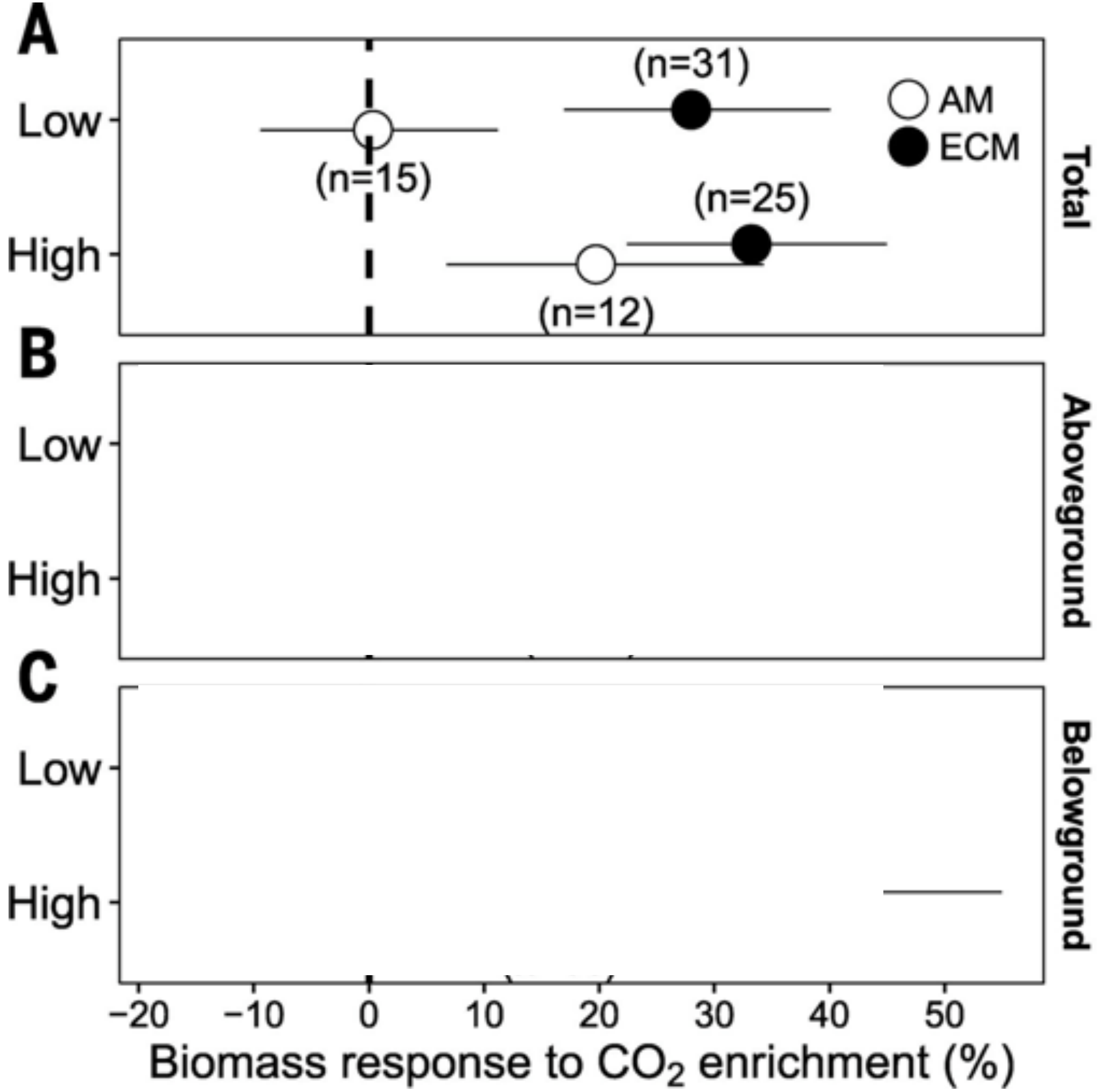
Consequences for global change

Elevated CO_2



Low = low Nitrogen
High = high
Nitrogen

Terrer et al. (2016)



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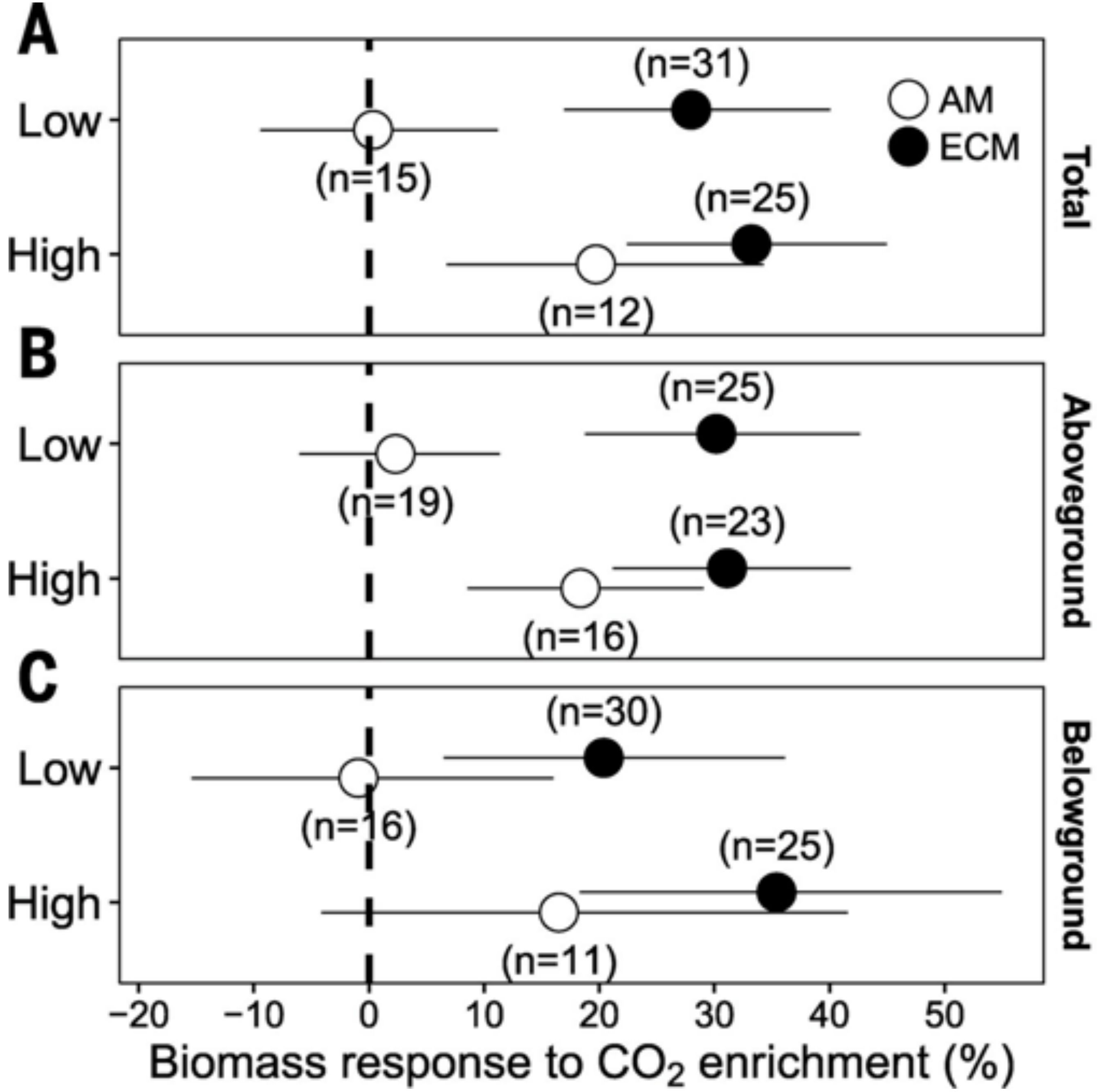

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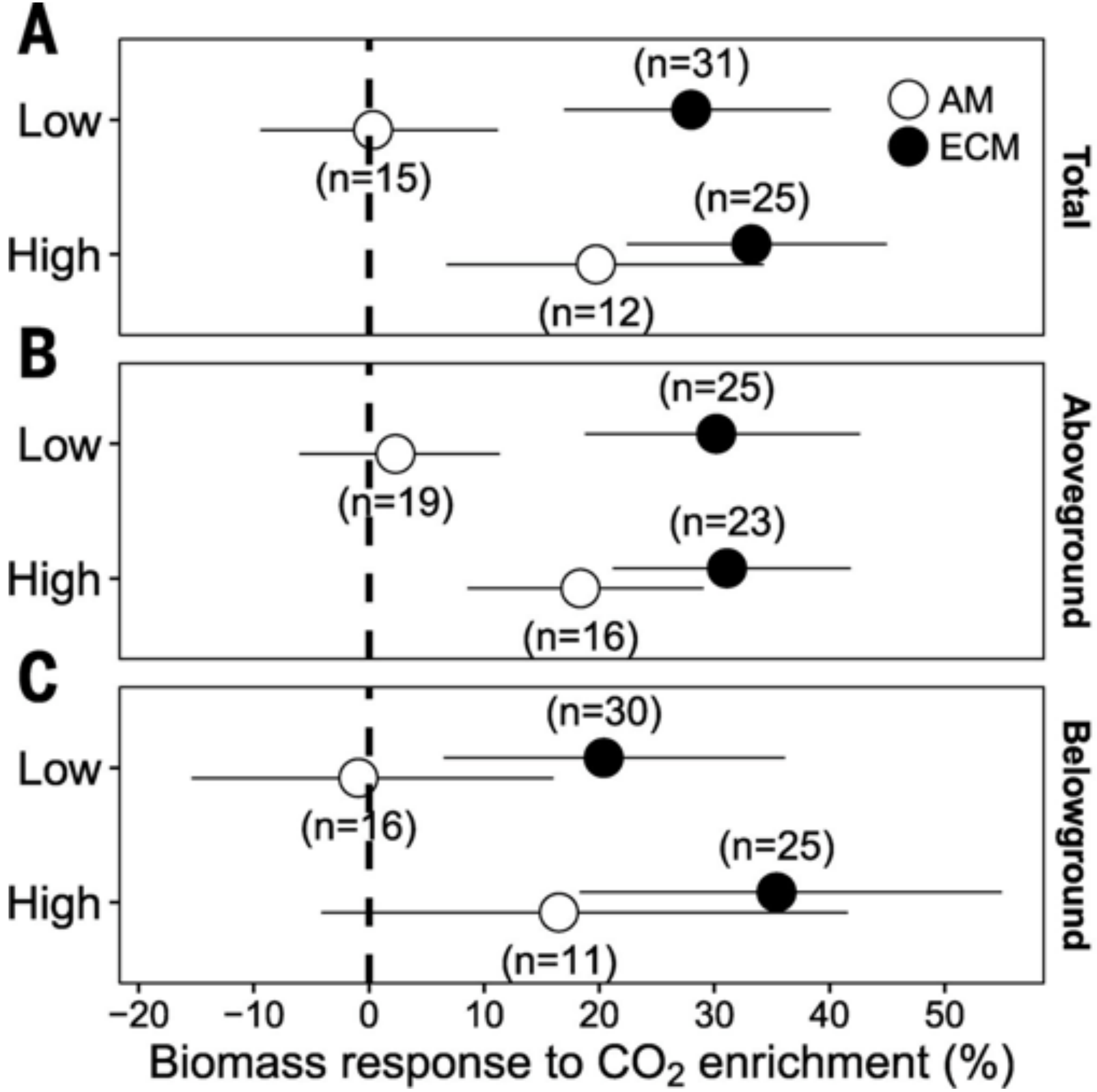

Low = low Nitrogen
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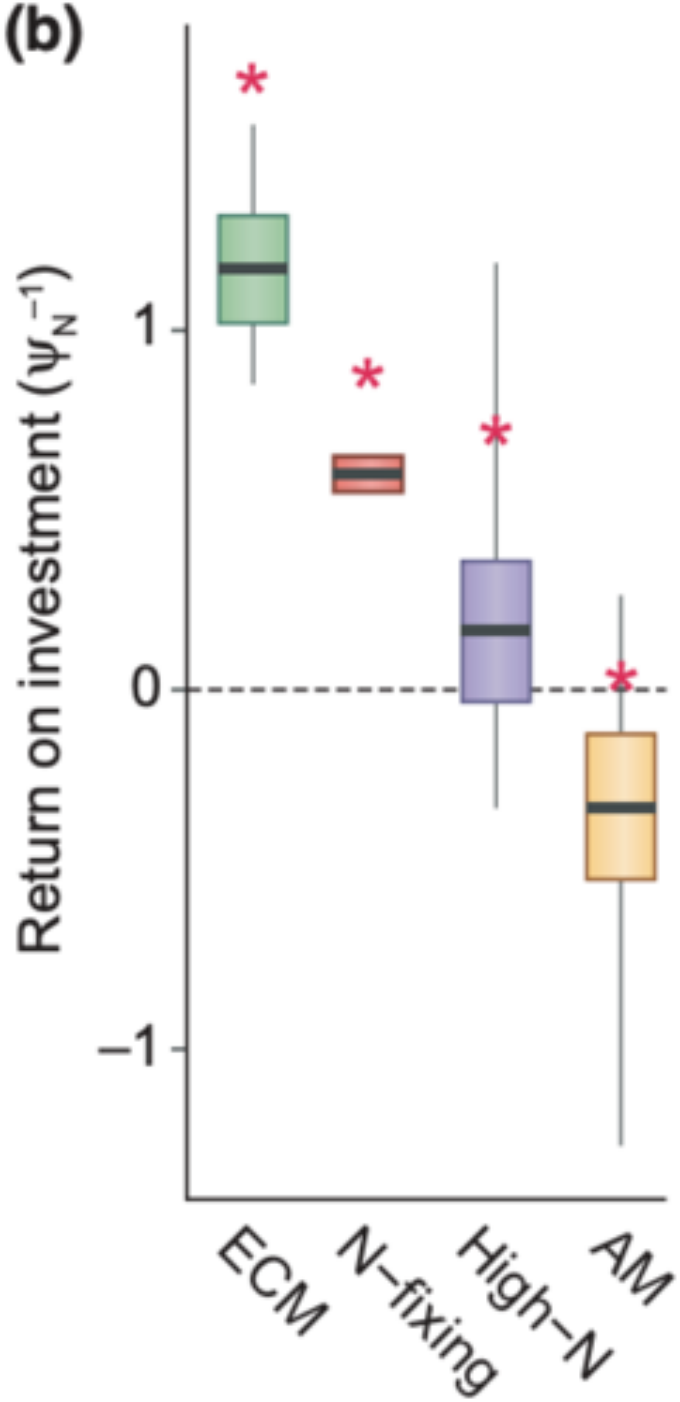
Why would there be a difference between AM and ECM?

Terrer et al. (2016)



Higher N return per C invested in ECM than AM species

Terrer et al. (2018)

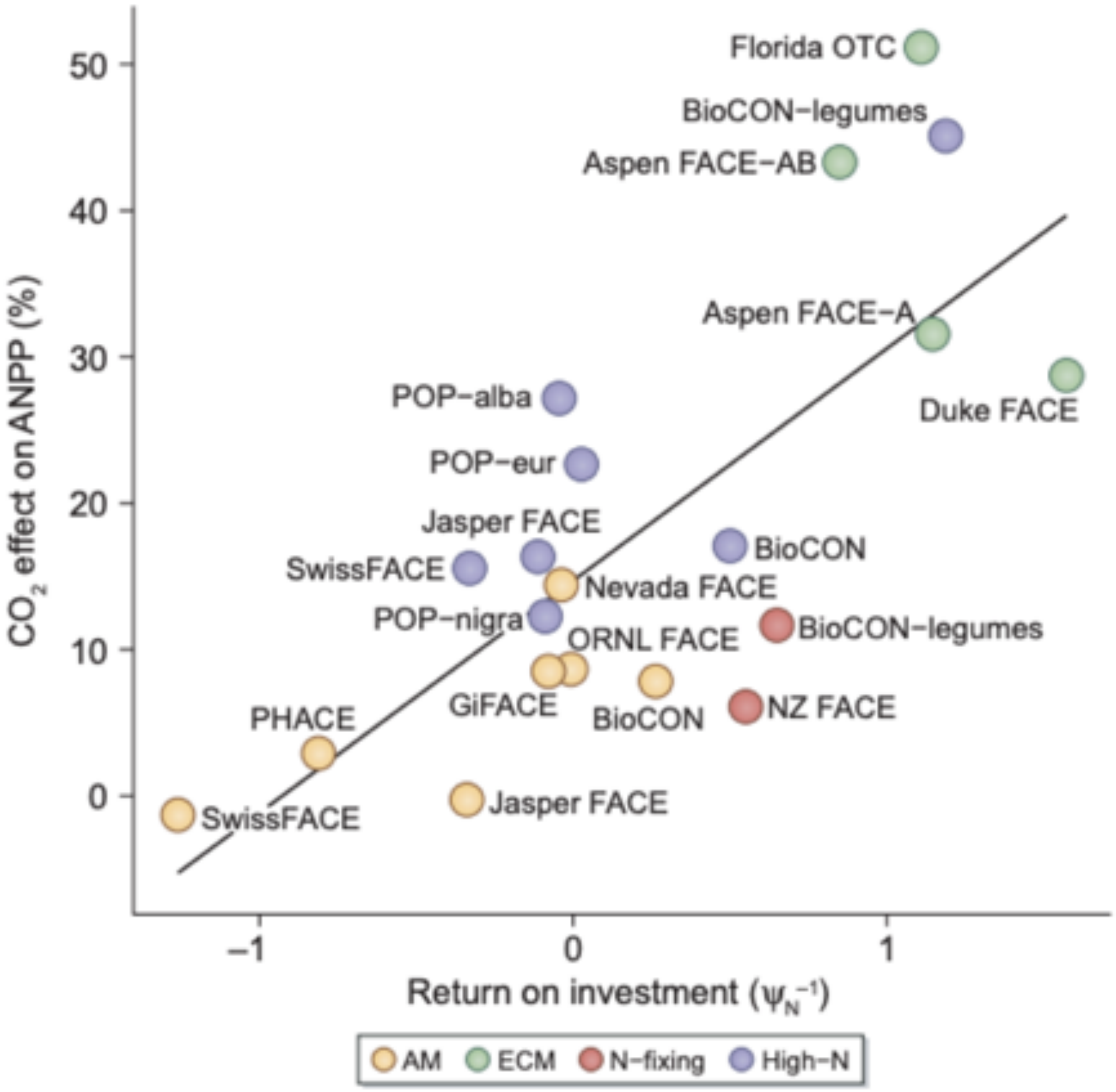
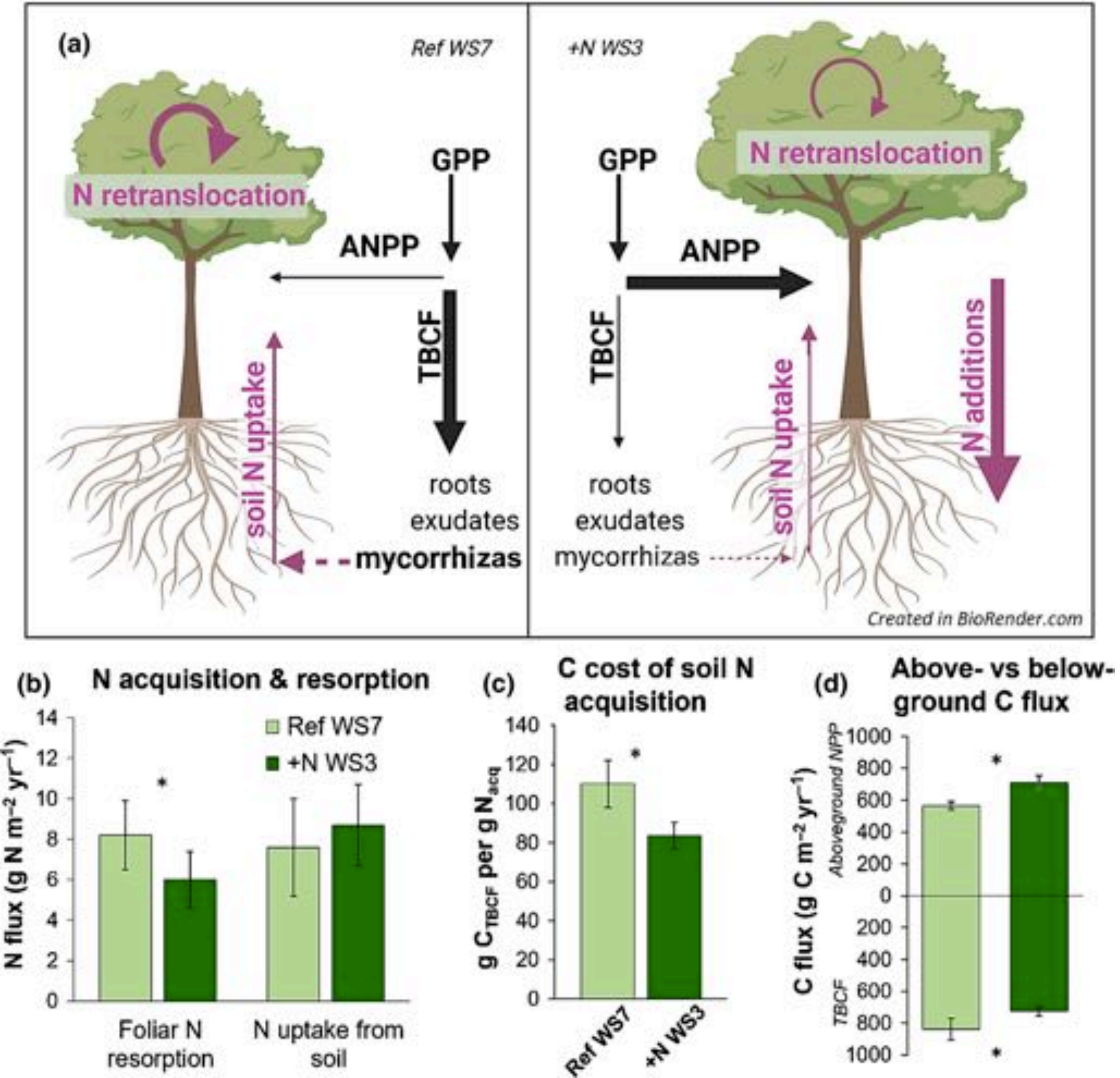


Fig. 3 Relationship between the effect of elevated CO_2 on aboveground biomass production (ANPP) and the nitrogen (N) return on investment (ψ_N^{-1}, Eqn 1). Sources of site-level data are given in Table 1.

Terrer et al. (2018)

Global change: Nitrogen deposition



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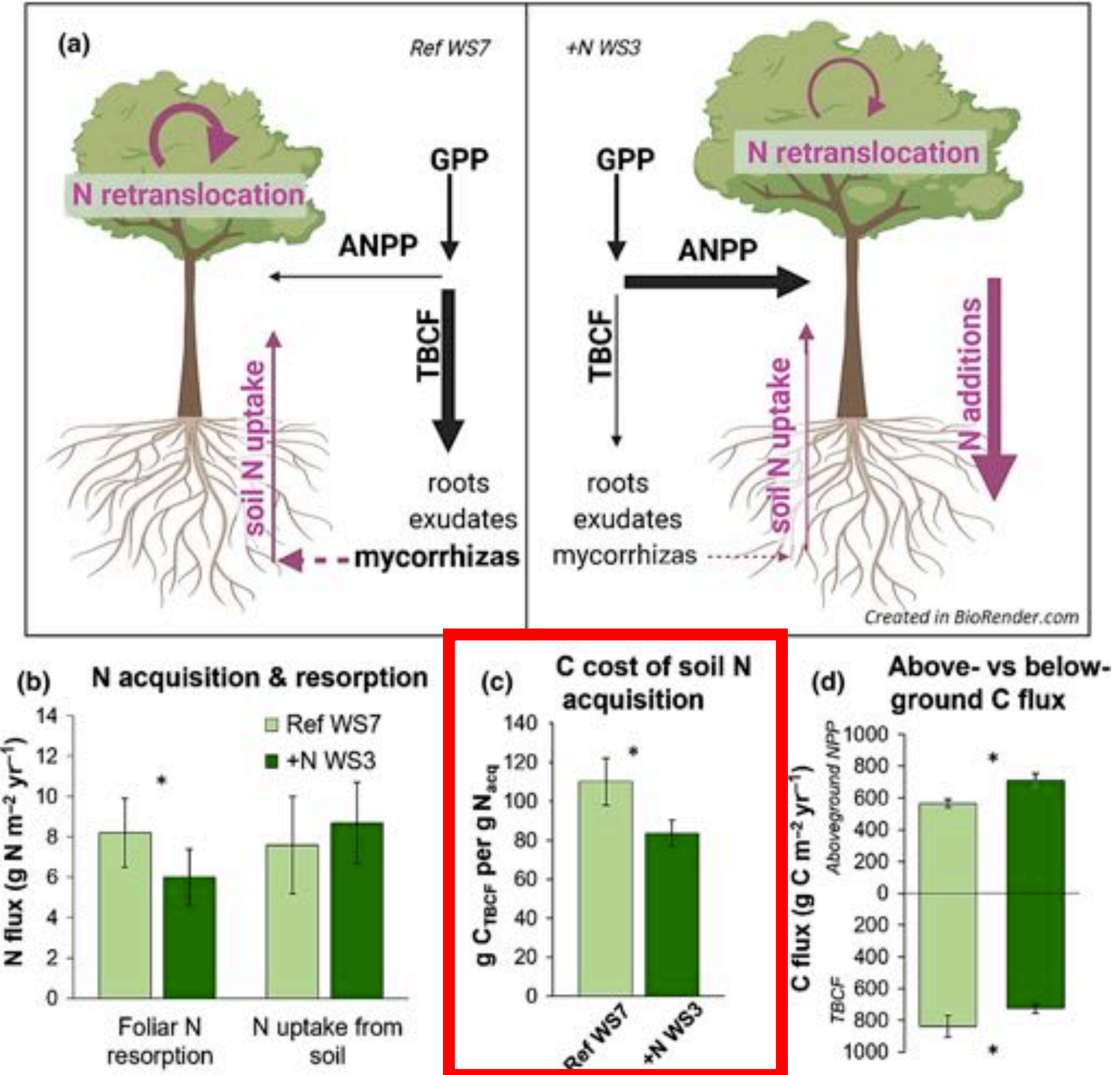

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Add soil N reduces C cost of N acquisition, because of reduced symbiotic interaction