PLANT ECOPHYSIOLOGY **Lecture topic 14**

Mycorrhizal fungi: plant biology, physiology, and ecology

Definition of a mycorrhiza: a structure in which a symbiotic union between a fungus and the roots of a plant confers increases in fitness to one or both partners (Read 1999).

1. ***Types of Mycorrhizas***

A. There are a number of different mycorrhizal morphologies depending on the plant and fungal species involved in the symbiosis:

- Vesicular-Arbuscular (VA) mycorrhizas: Fungi: Glomalean (130 spp.), Plant: Gymnosperms, Angiosperms, Pterophtyes, Bryophytes, generally low host specificity
- Ectomycorrhizas (ECM): Fungi: Basidiomycete and Ascomycete (6000 sp.), Plant: Gymnosperms and Angiosperms, low to moderate host specificity
- Arbutoid mycorrhizas: Fungi: Basidiomycete, Plant: Ericales
- Ericoid mycorrhizas (ERM): Fungi: Ascomycete, Plant: Ericales and Byrophytes
- Monotropoid mycorrhizas: Fungi: Basidiomycete, Plant: Monotropaceae (Ericales), high fungal specificity
- Orchid mycorrhizas: Fungi: Basidiomycete, Plant: Orchidaceae

B. Although the structural forms of mycorrhizas vary considerably, their main functions are similar (see below).

2. ***Occurrence of Mycorrhizas in Nature***

A. 90% of all land plants belong to families that are commonly mycorrhizal (Trappe 1987)

- Mycorrhizas have been described in 83-85% of dicots, 79% of monocots, and most conifers (95% of Pinaceae)
- Easier to identify non-mycorrhizal families, typically dominated by ruderal species (Brassiacaceae) or having different root structures (Proteaceae)

B. Widely distributed across nearly all major biomes (see Read 1993 figures):

- VA typically dominate in grasslands, shrublands, tropical rainforests, typically areas with P limitation, ~80% of all plant species are VA.
- ECM dominate in temperate forests, particularly coniferous forests, typically areas with N limitation, lower % of plant species, but high % of land coverage
- ERM dominate in heathlands, alpine environments.

C. The mycorrhizal symbiosis has a *long* history (VA - 500 mya; ECM – 130 mya) and was probably key in allowing plants to colonize land (Pirozynski and Malloch 1975; Redecker 2000)

3. ***Functional Aspects of the Mycorrhizal Symbiosis***

A. The mycorrhizal symbiosis is a trading system:

- Fungi have extensive mycelial networks for nutrient and water uptake, but need a source of carbon, while plants have an autogenic source of carbon, but need to get nutrients and water from the soil, therefore, plants give the fungus carbon (typically as a sugar) and fungus passes nutrients to plant (see Smith and Read 1997 figure).

- Mycorrhizal fungi have been shown to have other functional attributes aside from facilitating nutrient and water uptake, such as protecting plants from root pathogens and soil heavy metal concentrations.

4. ***Mycorrhizas and Plant Nutrition***

A. Mycorrhizal plants typically have much higher nutrient contents than non-mycorrhizal plants.

Particularly evident with major limiting nutrients such as N and P (for both VA and ECM).

B. Why do mycorrhizal plants have such a nutritional advantage? (possible mechanisms)

- Extension of root system allows mycorrhizal plants to access a much larger soil area (movement of nutrients through the fungus is typically much faster than through the soil) (See Read 1991 and Giovanetti et al. 2001 figures). Fungal hyphae also have smaller diameters than roots and therefore can access smaller soil pores (which effectively increases the volume of soil exploited) (good evidence for this mechanism).

- Fungi may be more effective nutrient competitors against free-living soil microbes than roots (evidence for this mechanism is inconclusive) or fungi may alter the rhizosphere bacterial community in ways that facilitate nutrient capture (evidence small but possible).

- Fungi may have different uptake kinetics than roots, leading to more effective uptake at lower nutrient concentrations (evidence suggests not true). Fungi also have much higher surface-to-volume ratio than roots, which may increase the rate at which nutrients are absorbed.

- Fungi have enzymes (e.g. phosphotases, proteases) and chelating compounds to capture nutrients from soil organic and inorganic material that are not normally accessible to plants (good evidence for this, although some conflicting results VA uptake of P).

5. ***Mycorrhizas and Plant Water Relations***

A. Mycorrhizal fungi can alter plant water relations in a number of ways, which typically result in increased water capture (See Parke et al. 1983 and Duan et al. 1996 figures).

B. How do mycorrhizas affect plant water relations? (mechanisms not mutually exclusive)

Plant Size:

- The root systems of mycorrhizal plants are often larger and more finely divided than non-mycorrhizal plants, which access to more of the water in the soil.

Unrelated to Plant size:

- Nutritional – P starvation can affect stomatal conductance.

- Physiological – Rates of transpiration can also be altered by mycorrhizal fungi (See Auge 2001 for details with AM).

- Environmental – Soil structure can be altered by mycorrhizal fungi in ways that increase soil water content.

6. ***Mycorrhizas and Plant Growth***

There is conflicting evidence about the effects of mycorrhizas on plant growth. Many studies have shown positive growth (See Boucher et al 1990 figure), while others have shown neutral or negative growth.

It is important to note:

- Most of the studies of mycorrhizas and plant growth have been done under laboratory conditions where the effects of growth may be affected by other factors.

- The life stage of the plant may also affect whether growth is positive or negative. Seedlings with small carbon quantities may be negatively affected by mycorrhizas, while larger plants may be positively affected due to a more positive carbon balance.

- Although growth is often correlated with fitness and therefore used in many studies to indicate the importance of a certain factor, survival is essential to fitness, and by amending water and nutrient conditions, mycorrhizal effects may have a greater impact on survival than growth (see Perry et al. 1989).

7. ***Mycorrhizas and Plant Ecology***

A. Aside from their role in plant nutrition and water relations, mycorrhizal fungi can have major ecological impacts on:

- Plant Establishment and Succession (see Nara and Hogetsu 2004 figures)
- Plant Community Diversity (see Van der Heijden et al. 1998 figures)
- Ecosystem Biogeochemistry

8. ***Cost of the Mycorrhizal Symbiosis***

A. Range of Estimates: 4 – 20% of total plant Carbon is transferred to the fungus, multiple studies using independent methods have estimated ~15% (see Smith and Read 1997)

B. Environmental conditions have a large impact on whether the symbiosis has a positive or negative outcome (see Johnson 1997 and Zhou and Sharik 1997 figures)

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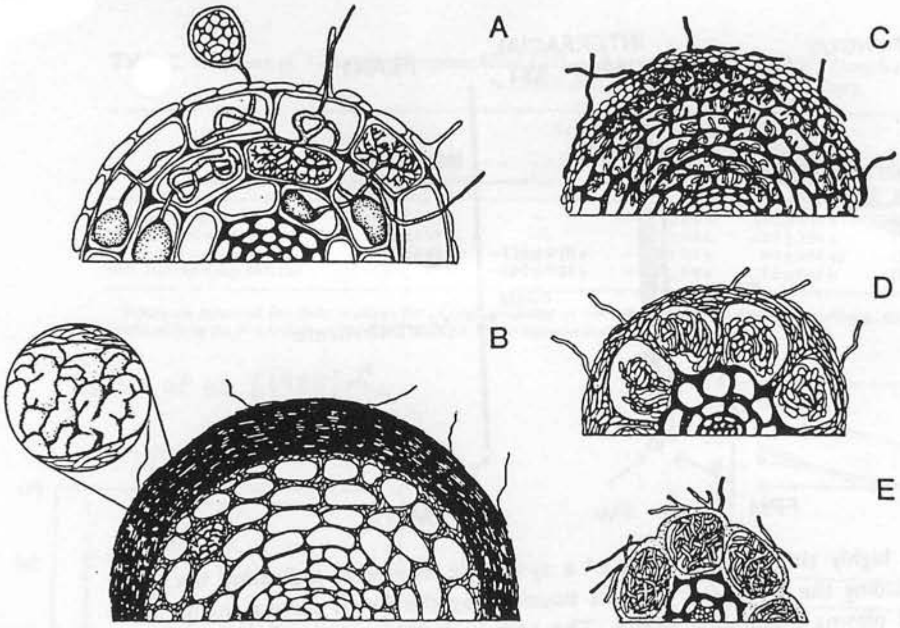
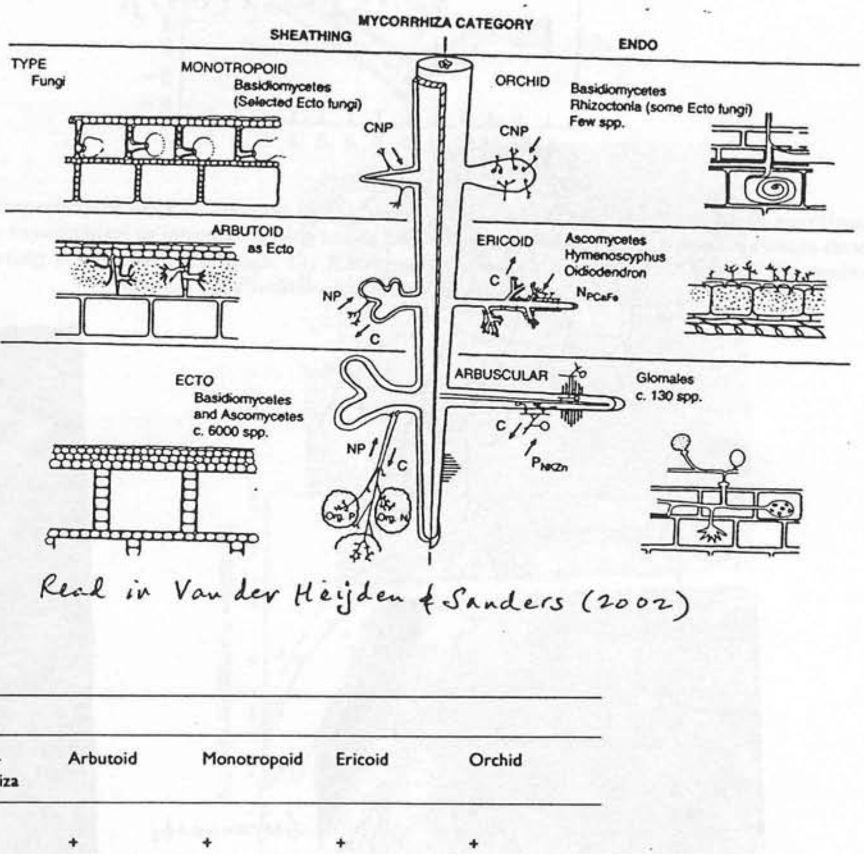


Figure 11.1. Classes of mycorrhizal associations. Shown are the vesicular-arbuscular mycorrhiza (A), ectomycorrhiza (B), ectendomycorrhiza (C), arbutoid mycorrhiza (D), and ericoid mycorrhiza (E). Each of these classes of mycorrhizae has varying levels of specificity.

Molina et al. (1992)



Read in Van der Heijden & Sanders (2002)

Smith & Read (1997)

Table 1 The characteristics of the important mycorrhizal types

	Kinds of mycorrhiza						
	VA	Ectomycorrhiza	Ectendo-mycorrhiza	Arbutoid	Monotropoid	Ericoid	Orchid
Fungi							
septate	–	+	+	+	+	+	+
aseptate	+	–	–	–	–	–	–
Intracellular colonization	+	–	+	+	+	+	+
Fungal sheath	–	+	+ or –	+ or –	+	–	–
Hartig net	–	+	+	+	+	–	–
Vesicles	+ or –	–	–	–	–	–	–
Achlorophylly	– (?+)	–	–	–	+	–	+*
Fungal taxa	Zygo	Basidio/Asco (Zygo)	Basidio/Asco	Basidio	Basidio	Asco	Basidio
Plant taxa	Bryo Pterido Gymno Angio	Gymno Angio	Gymno Angio	Ericales	Monotropaceae	Ericales Bryo	Orchidaceae

* All orchids are achlorophyllous in the early seedling stages. Most orchid species are green as adults.
The structural characters given relate to the mature state, not the developing or senescent states. Entries in brackets indicate rare conditions.
The fungal taxa are abbreviated from Zygomycetes, Ascomycetes and Basidiomycetes; the plant taxa from Bryophyta, Pteridophyta, Gymnospermae and Angiospermae.

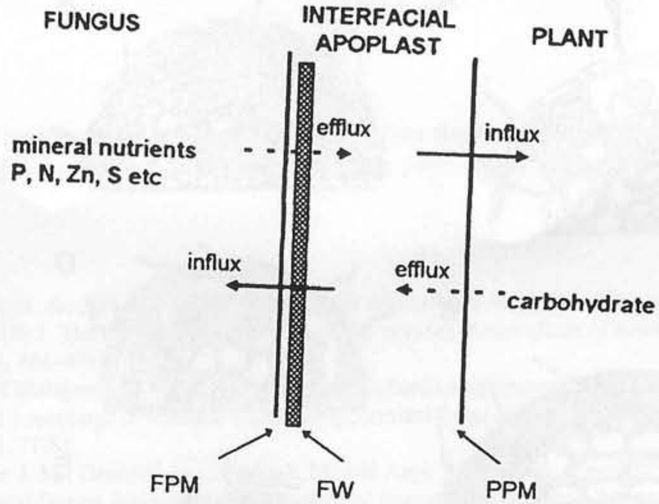
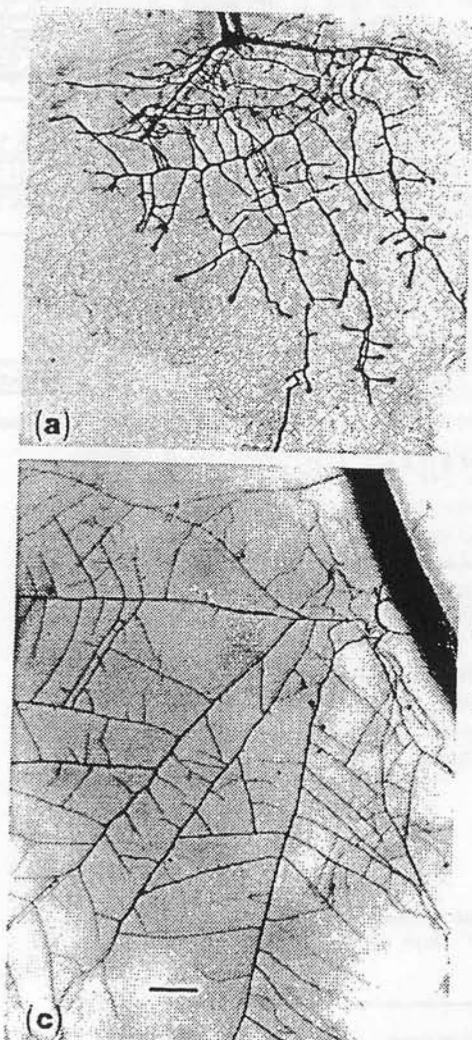


Figure 14.6 A highly simplified diagram of a symbiotic interface, indicating the key components including the interfacial apoplast bounded by the fungal plasma membrane (FPM) and plant plasma membrane (PPM). The arrows indicate membrane transport processes involved in transfer of carbohydrate and soil-derived nutrients. Dashed lines, efflux; solid lines, influx. Wall of the fungus is indicated by shading, but plant wall and wall-like components not shown.

Smith & Read (1997)

Read (1991)



Giovannetti et al. (2001)

Table 1 Root length, arbuscular mycorrhizal colonization and extension of *Glomus mosseae* extraradical mycelial networks in three different mycorrhizal plants

	Allium porrum	*Thymus vulgaris*	*Prunus cerasifera*
Root length (mm)	201.9 ± 29.4b	516.4 ± 35.6a	465.5 ± 58.8a
AM colonization (% root length)	54.4 ± 3.6b	46.7 ± 2.6b	64.4 ± 3.1a
Total hyphal length (mm)	7471 ± 1356a	5169 ± 441a	7096 ± 897a
Area covered by the extraradical mycelium (mm^2)	2755 ± 453a	2525 ± 161a	2898 ± 254a
Hyphal length per total root length ($mm\ mm^{-1}$)	40.2 ± 7.2a	10.1 ± 0.7b	15.9 ± 1.7b
Hyphal length per mycorrhizal root length ($mm\ mm^{-1}$)	73.7 ± 12.2a	21.9 ± 1.4b	24.93 ± 2.9b

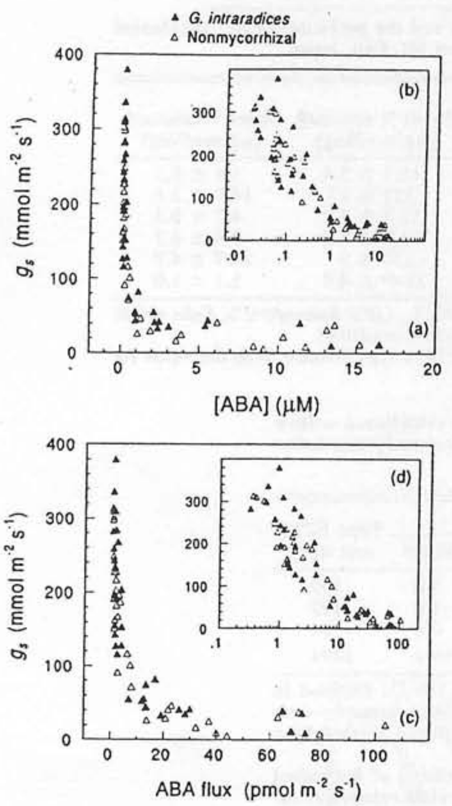
Values, means ± SE; $n = 8$. Values followed by the same letters within the same row are not significantly different ($P < 0.05$; Duncan's test).

Table 2. *Response of 7-month-old mycorrhizal (M) and non-mycorrhizal (NM) Douglas-fir seedlings watered daily or subjected to cyclic drought (watered every fifth day).*

Treatments	Net photosynthesis ($mg\ CO_2\ dm^{-2}\ h^{-1}$)	Leaf potential (bars) Max	Leaf potential (bars) Min	Needle area (cm^2)	Root dry weight (mg)	Shoot dry weight (mg)	Shoot:root dry weight
M, watered daily	11·07±0·95 a	—	−10·7±0·6 a	10·2±1·32 a	408±23 a	287±20 a	0·72±0·058 ab
NM, watered daily	7·55±1·07 a	—	−10·6±0·6 a	11·2±2·04 a	337±32 ab	268±44 a	0·76±0·075 ab
M, watered every fifth day	8·95±1·48 a	−12·0±0·50 a	−19·8±1·3 b	8·4±0·87 ab	253±27 bc	237±20 ab	0·96±0·041 b
NM, watered every fifth day	0·87±1·02 b	−12·3±0·31 a	−12·8±0·8 a	3·3±0·31 b	182±14 c	118±10 b	0·65±0·025 a

Values are means of five daily readings for 11 (watered daily) or seven (watered every fifth day) seedlings. ±s.e. Values not followed by the same letter differ significantly at the $P < 0·05$ level (Scheffe's Multiple Range Comparison).

Parke et al. (1983) ↗



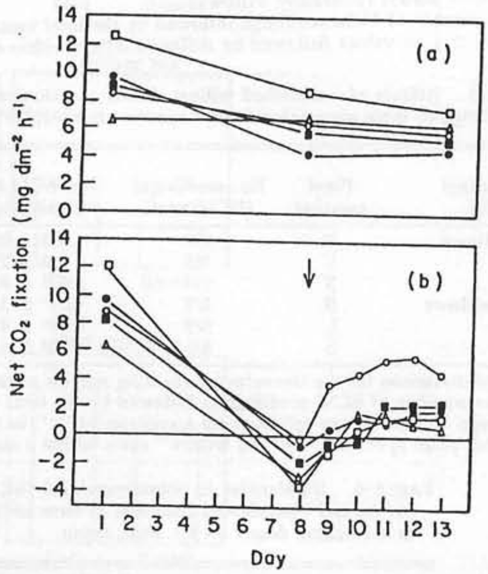
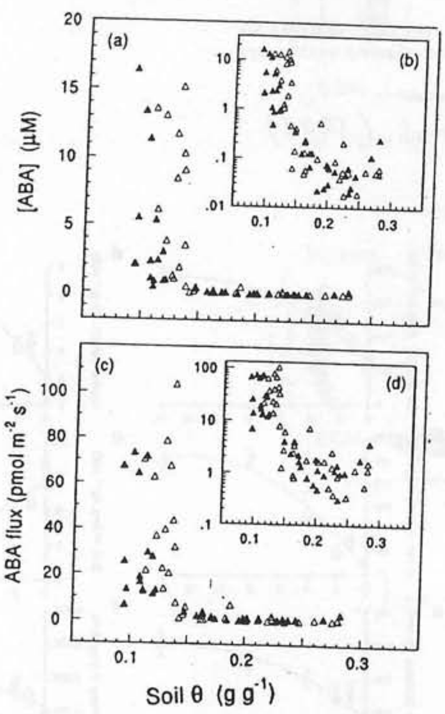


Fig. 2. Comparison of net CO_2 fixation by (a) non-stressed and (b) stressed Douglas-fir seedlings either non-mycorrhizal or inoculated with one of four ectomycorrhizal fungi. Arrow indicates time of re-watering for stressed seedlings. ○, *Rhizopogon vinicolor*; ■, *Laccaria laccata*; △, native fungus; □, *Pisolithus tinctorius*; ●, non-mycorrhizal.



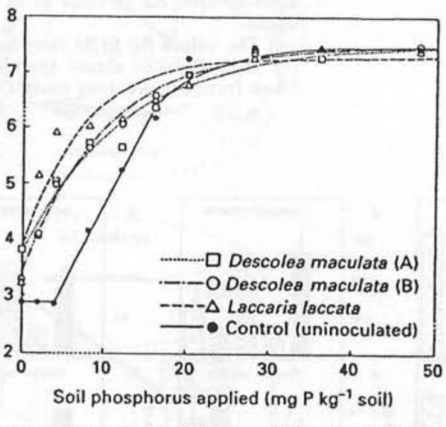


Figure 4. Dry weight of karri seedlings in relation to soil phosphorus application and mycorrhizal inoculum. Mitscherlich equation fitted to response data. For control data, $d = 5·96$ mg P kg^{-1} soil. Proportion of variance accounted for by response equation: *Descolea maculata* (A) 95·9%; *Descolea maculata* (B) 97·9%; *Laccaria laccata* 86·5%; Control 94·8%. ANOVA significant interaction ($P < 0·05$).

Boucher et al. (1990)

Duan et al. (1996)

Nara & Hogetsu 2004

TABLE 1. Effects of established willow (*Salix reinii*) shrubs on ectomycorrhizal (ECM) formation and the performance of transplanted *S. reinii* seedlings in a volcanic desert on Mt. Fuji, Japan.

Transplant sites†	No. seedlings‡ (ECM/total)	No. ECM root tips/ seedling§	Shoot dry mass§ (mg/seedling)	Shoot N amount§ (μg/seedling)	Shoot P amount§ (μg/seedling)
Bare ground	0/14	$0.0^{a} \pm 0.0$	$0.8^{a} \pm 0.1$	$10.8^{a} \pm 1.0$	$4.6^{a} \pm 0.4$
No-willow patch	1/17	$0.2^{a} \pm 0.2$	$0.8^{a} \pm 0.1$	$11.0^{a} \pm 1.2$	$4.5^{a} \pm 0.3$
Unhealthy willow	10/16	$9.3^{b} \pm 2.5$	$1.1^{a} \pm 0.2$	$20.4^{b} \pm 3.7$	$4.7^{a} \pm 0.4$
Healthy willow	17/17	$25.5^{c} \pm 2.9$	$2.2^{b} \pm 0.3$	$27.7^{b} \pm 1.6$	$6.4^{b} \pm 0.5$

† Seedlings were transplanted into four habitat types: bare ground, the periphery of vegetation patches lacking willow shrubs (no-willow patch), the periphery of vegetation patches containing normally growing middle-sized (2–10 m^2 canopy coverage) willow shrubs (healthy willow), and the periphery of vegetation patches containing apparently unhealthy middle-sized willow shrubs (unhealthy willow).
‡ The number of ECM seedlings followed by the total number of sampled (surviving) seedlings.
§ Mean ± 1 SE values followed by different letters within a column differ statistically (Tukey's hsd test, $P < 0.05$).

TABLE 3. Effects of established willow shrubs on ectomycorrhizal (ECM) formation and the performance of transplanted seedlings of three successional plant species co-transplanted into a volcanic desert on Mt. Fuji, Japan.

Transplant sites	Plant species†	No. seedlings‡ (ECM/total)	No. ECM root tips/seedling§	Shoot dry mass§ (mg/seedling)	Shoot N amount§ (μg/seedling)	Shoot P amount§ (μg/seedling)
No willows	B	0/8	0.0 ± 0.0	1.4 ± 0.2	15.3 ± 3.4	3.4 ± 0.5
	L	1/9	2.0 ± 2.0	29.5 ± 3.2	231 ± 17	14.4 ± 3.6
	S	0/7	0.0 ± 0.0	0.8 ± 0.1	11.7 ± 1.2	4.2 ± 0.4
With willows	B	8/9	$12.1^{a} \pm 3.8$	1.3 ± 0.2	13.0 ± 1.0	2.4 ± 0.7
	L	9/9	$21.9^{a} \pm 4.7$	27.9 ± 1.4	225 ± 9	20.2 ± 4.9
	S	6/6	$14.0^{a} \pm 5.4$	$1.9^{a} \pm 0.4$	$22.4^{a} \pm 4.8$	5.7 ± 1.0

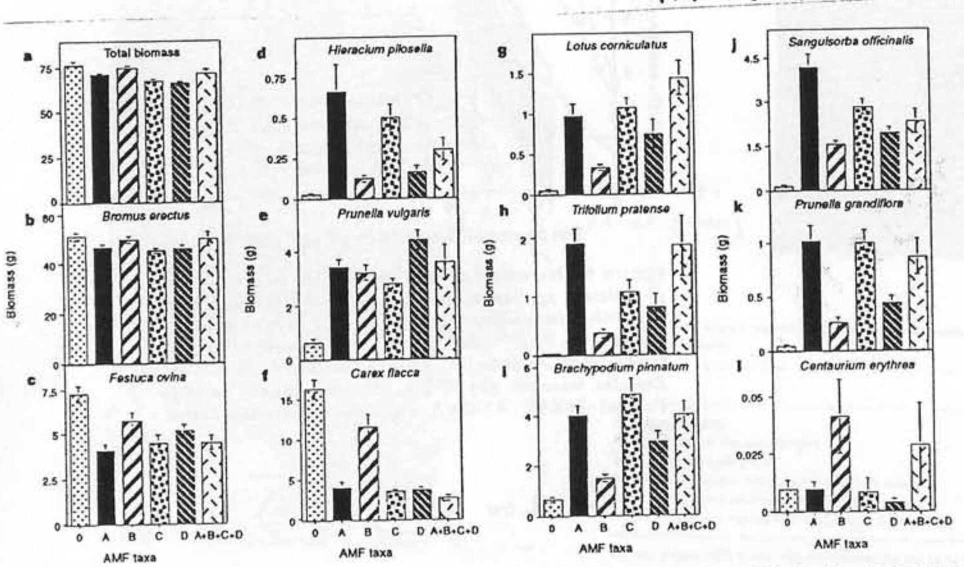
† Abbreviations for the transplanted seedling species are as follows: B, *Betula ermanii*; L, *Larix kaempferi*; S, *Salix reinii*.
‡ The number of ECM seedlings is followed by the total number of sampled (surviving) seedlings.
§ Mean ± 1 SE values followed by a superscript "a" in the "with willow" rows differs significantly from the value for the same plant species in the "no willow" rows within a column (t test, $P < 0.05$).

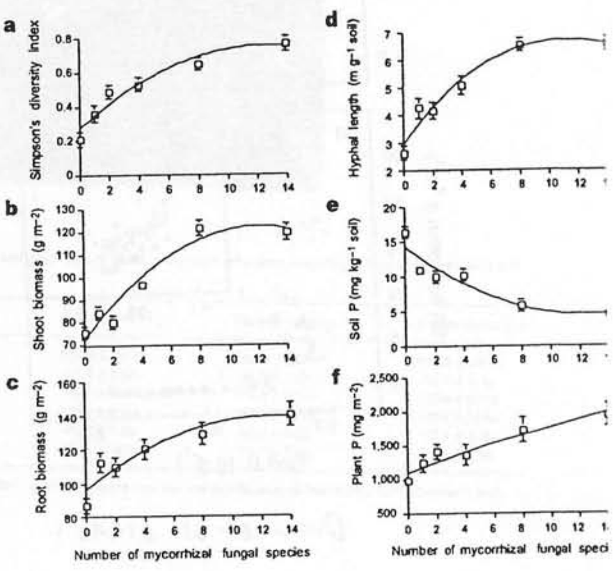
TABLE 4. Similarities in ectomycorrhizal (ECM) communities between established willow shrubs and transplanted seedlings of three successional plant species during early succession in a volcanic desert on Mt. Fuji, Japan.

Plant species	Relative abundance of ECM fungi (%)† Il	Ud	Ll	Th	Sb	Hm	Others	Total ECM root tips‡
Betula ermanii	43.8	42.5	8.2	2.7	2.7	0.0	0.0	109
Larix kaempferi	51.3	12.7	0.0	0.0	21.8	13.2	1.0	197
Salix reinii	66.9	9.5	10.5	1.2	11.9	0.0	0.0	84
Large willow shrubs§	3.0	16.9	3.1	0.4	7.3	0.2	69.1	1491

† Abbreviations for ECM fungi are as follows: Il, *Inocybe lacera*; Ud, UN-D1 (defined in Nara et al. 2003*b*); Ll, *Laccaria laccata*; Th, Thelephoraceae spp.; Sb, *Scleroderma bovista*; Hm, *Hebeloma mesophaeum*. Each value is the percentage of ectomycorrhizae formed by a fungal taxon out of all the ectomycorrhizae within a plant species.
‡ Values are the total number of ECM root tips of all transplanted seedlings of individual plant species. All of these ECM root tips were examined and used to calculate relative abundance.
§ The values for ECM relative abundance and total number of ECM root tips examined for the large *S. reinii* shrubs (periphery locations) that seedlings were transplanted next to are taken from our previous study (Nara et al. 2003*b*).

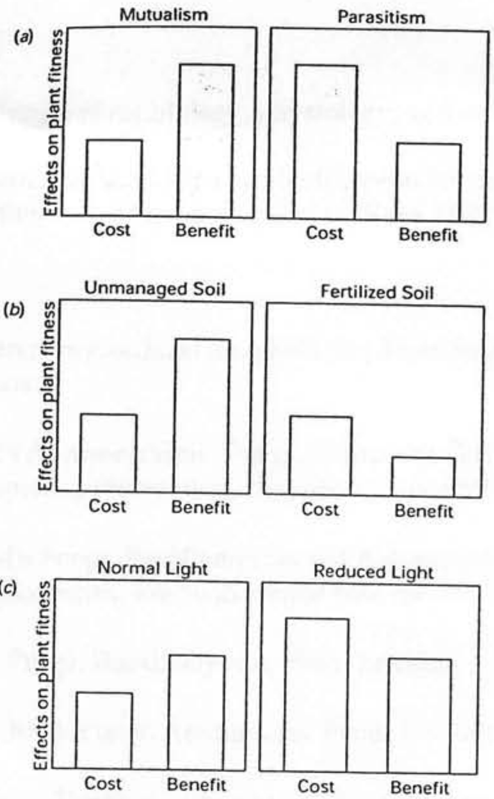
Van der Heijden et al. (1998)

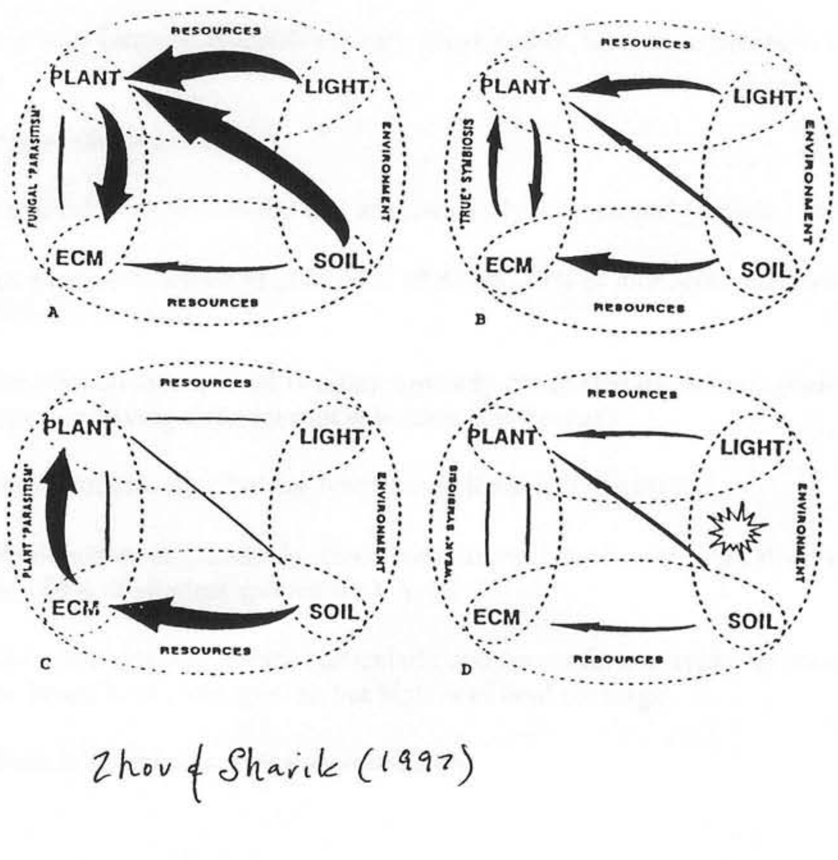




igure 1 Above-ground biomass of individual plant species and total above-round plant biomass (mean ± s.e.m.) in microcosms simulating calcareous rasslands, in which the composition of the AMF community was manipulated experiment 1). Microcosms contained no AMF (0); one of four different AMF (*Glomus* sp.; BEG 21) or AMF D (*Glomus* sp.; BEG 19); or all four AMF taxa (AMF A+B+C+D). The biomass of most individual plant species (c–k) and the total plant biomass (a) differed significantly among the six treatments (ANOVA[28], $P \leq 0.001$). The biomass of *Bromus erectus* (b) and of *Centaurium erythrea* (l) did not differ significantly among the treatments

Johnson (1997)





Zhou & Sharik (1997)