Effect of Mycorrhizal Inoculation on Growth, Nutrition and Gas Exchange of Ectomycorrhizal (EM) and Arbuscular Mycorrhizal (AM) Tropical Tree Seedlings of a Tropical Rainforest in Cameroon

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Ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) species are considered to have different basic properties concerning their ecophysiology, growth and nutrition. These properties could influence substantially the competitive advantages of the species in different habitats. In this study, photosynthetic gas exchange, growth parameters and nutrient concentrations of EM legume tree seedlings (*Tetraberlinia moreliana*, *Microberlinia bisulcata*) and AM (*Oubanguia alata*) seedlings from a dystrophic sandy lowland tropical rainforest in Korup National Park, Cameroon, were compared. Plants were grown in a greenhouse at different light intensities with (MYK) and without (COM) mycorrhizal inoculation. With MYK treatment, all species showed higher specific leaf area (SLA). EM species had lower shoot/root - ratios. No effect could be seen in AM. Leaf concentrations of N and K were higher in AM. P- concentrations were higher in all species with MYK. Only *T. moreliana* (EM) produced more biomass and leaf area with MYK at high light level, where patterns of photosynthetic parameters were similar for EM species (lower Pn_{max} and I_S with MYK) and different from *O. alata* (higher Pn_{max} and I_S with MYK). EM species had higher I_S and I_K and lower ϕ than *O. alata*. The effects of different levels of mycorrhizal colonization (increasing with light) on photosynthesis and the intensity of EM and AM symbiosis are discussed.

Keywords: arbuscular mycorrhiza, ectomycorrhiza, ecophysiology, tree seedlings, tropical rainforest

Introduction

The EM legume tree species *Tetraberlinia moreliana* and *Microberlinia bisulcata* (both Caesalpiniaceae) are large emergents which naturally grow in localized clumps of EM trees on extremely dry and dystrophic sandy soils in lowland tropical rainforest at Korup National Park, Cameroon (Newbery et al.,1988, Newbery, 1996). The abundant AM understorey/canopy species *Oubanguia alata* (Scytopetalaceae) is widely distributed in the Park and grows mainly on moister, more eutrophic soils of adjacent sites (Newbery et al.,1988, Newbery, 1996).

Ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) species are considered to have different basic properties concerning their ecophysiology, growth and nutrition. These properties could influence substantially the competitive advantages of the species in different habitats (Janos, 1985, Read, 1991). In this study, photosynthetic gas exchange and drought resistance, growth parameters and nutrient concentrations of EM and AM tropical tree species were compared.

This work is aiming to get information on the autecology of Korup (SW Cameroon) EM tree species. These species could later be integrated into rehabilitation programmes for degraded

land, as they naturally grow on extremely dystrophic soils and thus seem to be suitable for reforestation of strongly devastated sites.

Material and Methods

Experimental Design

In a greenhouse experiment tree seedlings were grown on a substrate of poor sand (pH $_{KCl}$ 4,8) mixed with vapour- sterilized compost at a ratio of 4:1 under controlled climatic conditions at three different light intensities (100 %, 17 % and 3 % of greenhouse radiation which is equivalent to 50 % of outdoor radiation). Three months old seedlings were inoculated with (MYK) and without (COM) an inoculum mixture of rootlets and soil from the original site in Cameroon. For control (COM) we used vapour- sterilized inoculum.

Methods

Biomass parameter
Seedlings (54 plants per species and inoculation method, 18 per light level) were grown for 9 months in the greenhouse. After 3, 6 and 9 months one third of the plants (18 per species and inoculum level, 6 per light level) was harvested, leaf area and dry weight of leaves, stems and roots were measured. Total biomass (TM), leaf area (LA), shoot/root-ratio (S/R) and specific leaf area (SLA) were calculated.

Mycorrhizal infection rate (%)
One part of the removed fine roots was used for quantification of mycorrhizal infection. EM-quantification was done according to Hatch (1937) with a dissecting microscope. EM characteristics were easily recognisable and no staining was necessary for scoring. At least 500 tips were scored per sample. For AM- determination roots were cleared and stained using a phenol- free modification of Philips & Hayman's (1970) method.

Nutrient concentrations
A mixed sample of leaves of all harvested plants was taken from each experimental treatment, grinded fine and analysed for phosphorus, calcium, potassium and magnesium according to Schlichting & Blume (1966).

Gas Exchange Parameters
Photosynthetic rate and transpiration were examined as a function of light for each of the experimental plant groups using a fully automated gas exchange measuring device (Fa. Walz, Effeltrich, Germany). The working principal of this device is described by Lange & Schulze (1971) and the relevant evaluation methods are elaborated by Kriebitzsch (1992). Gas exchange rates were calculated according to Caemmerer and Farquhar (1981) and referred to simple leaf area. Photosynthetic light response curves of the tree species were recorded three times (6 replicates per light intensity) throughout the duration of the growth experiments. Each net photosynthetic (Pn) light response curve consists of values recorded on several successive days. Each Pn - value of the different light intensities was calculated as arithmetic mean of 10 - 20 values. Gas exchange parameters like maximum photosynthetic rate (Pn_{max}), light saturation point (I_S), transpiration rate (E), stomatal conductance (c) and water use efficiency (WUE). were derived from net photosynthesis - light curves.

Statistics
Calculation of statistical parameters was done using programmes like Excel (calculation of means) and SAS (Gogolok et al., 1992). Calculation of analysis of variance and subsequent tests for differences of the mean values, calculation of regression analyses were executed.

Results

Mycorrhizal Infection Rate
Mycorrhizal infection rate decreased with decreasing light from > 80 % at high light to < 5 % at shade. At partial shading the infection rate for *Microberlinia bisulcata* amounted to 80 %, for *Tetraberlinia moreliana* to 45 %. The roots of the EM- species were infected by just one predominant dark brown EM- fungus with extremely thick mantle typical for the tropics.

Growth Parameters (Fig. 1 – Fig. 4)
All species and growth parameters showed clear response to the different light intensities. Shoot/root- ratio (S/R) and specific leaf area (SLA) increased with shading (Fig. 3, Fig. 4). Total biomass (TM) and leaf area (LA) of *O. alata* (Oub96) increased with light (Fig. 1, Fig. 2), whereas EM- species showed less increase (TM) or even decrease (LA) from partial shade to full light. *M. bisulcata* (Mic96) was more sensitve to light than *Tetraberlinia moreliana* (Fig. 1, Fig. 2). *T. moreliana* (Tet96) was the only species which produced higher TM and LA with mycorrhizal infection (MYK) at high light compared with control COM (Fig. 1, Fig. 2). The EM- species showed a tendency for higher SLA with MYK (Fig. 4). They also lower S/R with MYK, most prominent for *Microberlinia bisulcata* (Fig. 3).
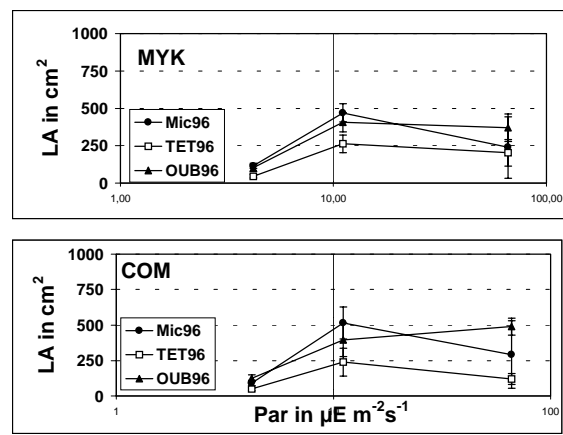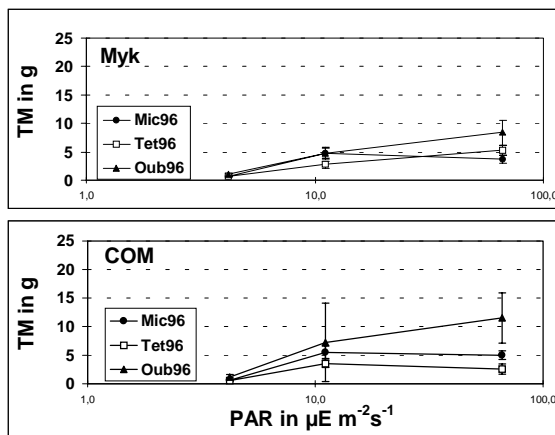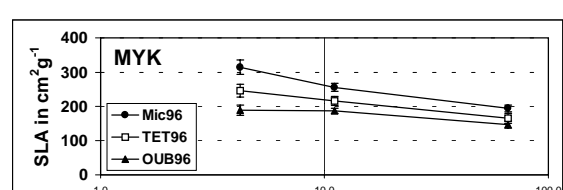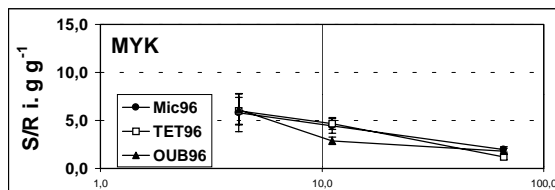

Fig. 1: Total biomass (TM) of the 3 species
with (MYK) and without (COM)
inoculation and 3%,17%,100% light

Fig. 2: Leaf area (LA) of the 3 species
with (MYK) and without (COM)
inoculation and 3%,17%,100% light

Fig. 3: Shoot/root-ratio (S/R) of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light

Fig.4: Specific leaf area (SLA) of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light
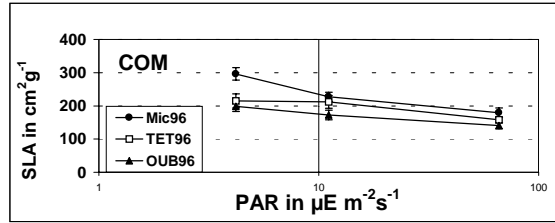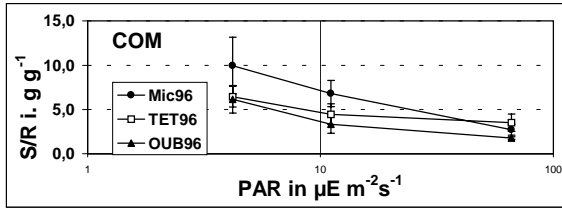
Nutrition: Leaf concentrations (Fig. 5 – Fig. 8)

P- concentration was higher with mycorrhiza for all species and light levels (Fig. 5). The K-concentration of *Oubanguia alata* (Oub96) was slightly higher with MYK treatment at the high light level and for *M. bisulcata* (Mic96) with partial shading (Fig. 6). The Ca-concentration increased with light especially in the COM treatment. It was reduced in the MYK treatment to a higher degree for the EM- species *Microberlinia bisulcata* than for the AM- species *Oubanguia alata* (full light only). The Mg- concentration of *Microberlinia bisulcata* was also reduced with mycorrhiza at high light, but less distinct than the Ca-concentration.

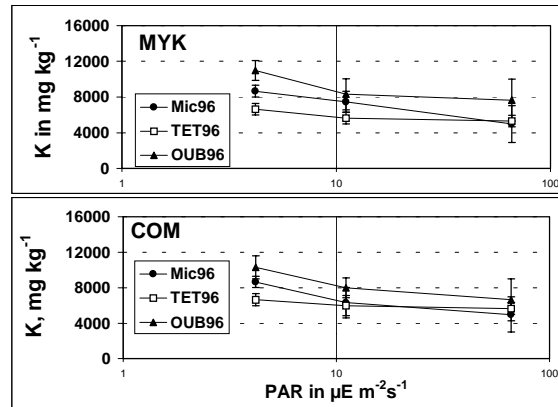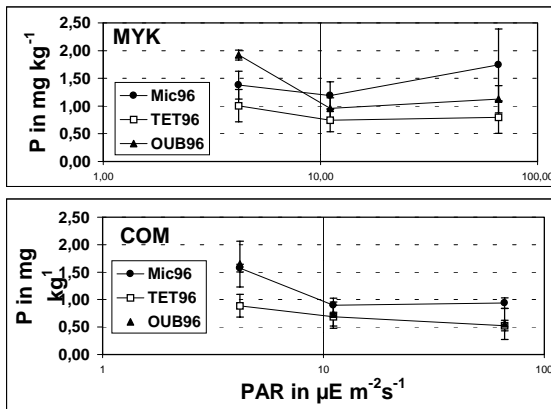Fig. 5: Leaf P- concentration of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light

Fig. 6: Leaf K- concentration of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light
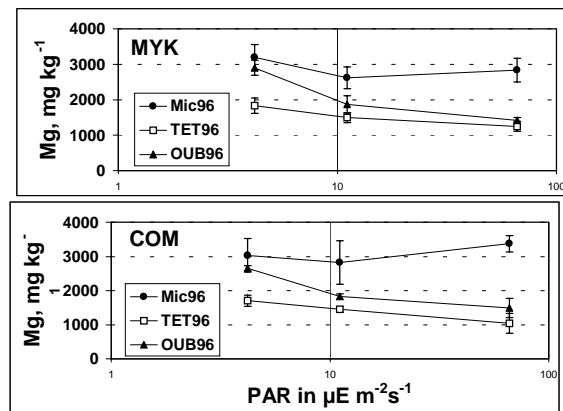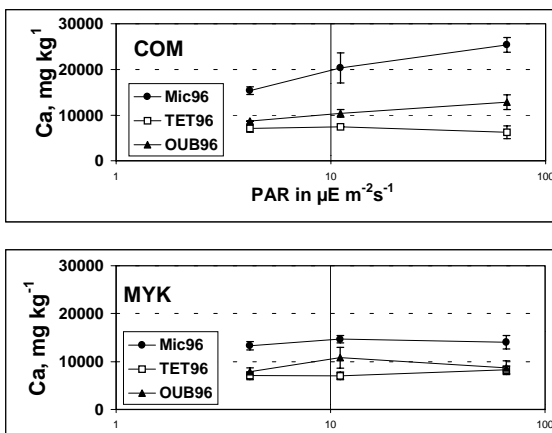

Fig. 7: Ca- concentration of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light

Fig. 8: Mg- concentration of the 3 species with (MYK) and without (COM) inoculation and 3%,17%,100% light

Gas exchange parameters
The low values of photosynthetic parameters indicate the general capability of these tropical tree seedlings for adaptation to very shady conditions. Shade plant character of *Oubanguia alata* and *Microberlinia bisulcata* was relatively higher compared to *Tetraberlinia moreliana*. *Microberlinia bisulcata* was best adapted to strong shading (Tab. 1).With high light and control treatment (COM) *T. moreliana* has significantly higher photosynthetic capacity (Pn $_{max}$) and light saturation point values (I$_S$) than *M. bisulcata* and the arbuscular mycorrhizal species *O. alata*. With MYK treatment and the same high light conditions this ranking becomes blurred and Pn $_{max}$ and I$_S$ of the EM- species are reduced in comparison to the COM treatment (Tab. 1, Tab. 3). Coincidentally with high light the MYK treatment provide decreased leaf dark respiration rates (R$_D$) for the EM- species which can perfectly be seen for *Microberlinia bisulcata*, but not for *Tetraberlinia moreliana* (Tab. 3). Pn $_{max}$ was significantly lower for *Tetraberlinia moreliana* at the high light level with MYK. At partial shading R$_D$ values of the EM- species are lower with MYK treatment; for *Tetraberlinia moreliana* even significantly (Tab. 3). No impact on Pn $_{max}$ or I$_S$ is distinct at this light level (Tab. 1, Tab. 3). No quantitative relation between mycorrhizal infection rates and leaf respiration rate (R$_D$) is existing for both light intensities (Tab. 3). By contrast to the above findings Pn $_{max}$ and I$_S$ of the AM- species *O. alata* tend to increase with mycorrhiza and almost no impact of MYK on R$_D$ is visible at high light (Tab. 1, Tab. 3).With MYK highest Pn $_{max}$ of *Oubanguia alata* was displaced from partial shading (COM treatment) to high light (MYK treatment) and I$_S$ increased tremendously at the high light level with MYK compared to the COM treatment (Tab. 2). By contrast maximum Pn $_{max}$ of the EM- species *Tetraberlinia moreliana* at high light within the COM treatment was displaced to slight shade with the MYK treatment (Tab. 2).

Transpiration rate (E) and stomatal conductance (c) were usually higher with MYK treatment (exception: *T. moreliana* at 17 %). E and c were significantly higher for *Oubanguia alata* (Tab. 3). Water use efficiency (WUE) of the EM- species *Microberlinia bisulcata* and *Tetraberlinia moreliana* was significantly lower with MYK treatment (Tab. 3). Evidently mycorrhiza causes – particularly ectomycorrhiza within the EM- species – a decreased photosynthetic capacity and at the same time increasing transpiration of the plants because of an improved water uptake by EM hyphae. In contrast with these findings the Pn $_{max}$ dry out experiments of the EM- species *Microberlinia bisulcata* and *Tetraberlinia moreliana* at slight shading show that drought resistance is higher for *Tetraberlinia moreliana* than for *Microberlinia bisulcata* in spite of higher infection rate of *Microberlinia bisulcata*.

Tab. 1: Species comparison of photosynthetic capacity (Pn $_{max}$) in µmol CO_2 m^{-2} s^{-1} and light saturation point (I$_S$) in µmol photons m^{-2} s^{-1} with (MYK) and without (COM) mycorrhizal inoculation for 3 light intensities (100 %, 17 %, 3 %). Different letters within a horizontal line are marked in bold type indicating statistically different values ($\alpha \geq 0,05$) within the 3 species *Microberlinia bisulcata* (MIC), *Tetraberlinia moreliana* (TET) and *Oubanguia alata* (OUB).

	Pn max						Is					
	MIC		*TET*		*OUB*		*MIC*		*TET*		*OUB*	
MYK												
100%	1,16	A	1,08	A	1,69	A	102	A	110	A	128	A
17%	2,08	A	2,28	A	1,26	A	**110**	**AB**	**156**	**A**	**69**	**B**
3%	**1,57**	**A**	0,69	B	0.95	B	99	A	114	A	84	A
COM												
100%	**2,18**	**AB**	**2,42**	**A**	**1,42**	**B**	**151**	**AB**	**167**	**A**	**87**	**B**
17%	2,04	A	1,74	A	1,90	A	140	A	155	A	**84**	**B**
3%	**1,38**	**A**	**0.95**	**B**	**1,27**	**AB**	113	A	99	A	91	A

Tab. 2: Light intensity comparison of photosynthetic capacity (Pn $_{max}$) in µmol CO_2 m^{-2} s^{-1} and light saturation point (I$_S$) in µmol photons m^{-2} s^{-1} with (MYK) and without (COM) mycorrhizal inoculation for, *M. bisulcata* (MIC), *T. moreliana* (TET) and *O. alata* (OUB). Different letters within a horizontal line are marked in bold type indicating statistically different values within the 3 light intensities ($\alpha \geq 0,05$).

	Pn max						Is					
	100%		17%		3%		100%		17%		3%	
MYK												
MIC	1,16	B	**2,08**	**A**	1,57	AB	102	A	110	A	99	A
TET	1,08	B	**2,28**	**A**	0,69	B	110	A	156	A	114	A
OUB	1,69	A	1,26	A	0,95	A	**128**	**A**	69	B	84	AB
COM												
MIC	**2,18**	**A**	**2,04**	**AB**	1,38	B	151	A	140	A	113	A
TET	**2,42**	**A**	1,74	A	0,95	B	**167**	**A**	155	AB	99	B
OUB	1,42	B	**1,90**	**A**	1,27	B	87	A	84	A	91	A

Tab. 3: Mycorrhizal inoculation effects comparison of photosynthetic capacity (Pn $_{max}$) and dark respiration (R$_D$) in µmol CO_2 m^{-2} s^{-1}, transpiration rate (E) in mmol H_2O m^{-2} s^{-1}, stomatal conductance (c) in µmol H_2O m^{-2} s^{-1} and water use efficiency (WUE) in µmol CO_2 mmol $^{-1}$ H_2O at high light (100 %) and partial shade (17 %) for *M. bisulcata* (MIC), *T. moreliana* (TET) and *O. alata* (OUB). Different letters within a horizontal line are marked in bold type indicating statistically different values within treatments MYK and COM ($\alpha \geq 0{,}05$, R$_D$: $\alpha \geq 0{,}1$).

|	Pn max			RD			E			c			WUE		
	MYK		COM	MYK		COM	MYK		COM	MYK		COM	MYK		COM
100%															
MIC	1,16	A	2,18 A	-0,332	A	-0,250 A	0,684	A	0,364 A	92,8	A	54,4 A	**1,19**	**B**	**5,86 A**
TET	**1,08**	**B**	**2,42 A**	-0,313	A	-0,338 A	0,602	A	0,804 A	82,2	A	97,3 A	**1,23**	**B**	**3,93 A**
OUB	1,69	A	1,42 A	-0,343	A	-0,320 A	**0,452**	**A**	**0,265 B**	**61,4**	**A**	**38,6 B**	3,18	A	4,86 A
17%															
MIC	2,08	A	2,04 A	-0,293	A	-0,248 A	0,700	A	0,236 A	-		-	**3,21**	**B**	**6,55 A**
TET	2,28	A	1,74 A	**-0,327**	**B**	**-0,295 AB**	0,652	A	0,326 A	59,6	A	36,7 A	3,60	A	4,14 A
OUB	1,26	A	1,90 A	-0,320	A	-0,300 A	**0,865**	**A**	**0,386 B**	**109,8**	**A**	**54,0 B**	1,89	A	4,97 A
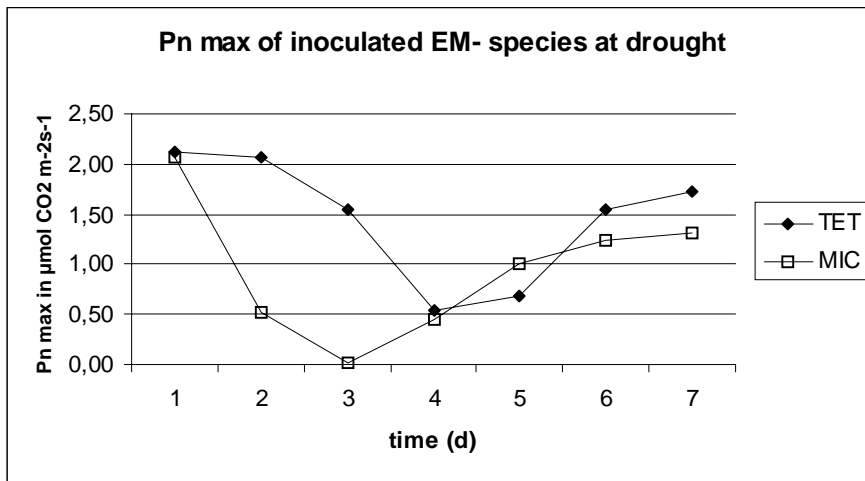
Fig. 9: Pn $_{max}$ dry out profile in µmol CO_2 m^{-2} s^{-1} of the EM- species *Microberlinia bisulcata* (MIC) and *Tetraberlinia moreliana* (TET) at partial shading (17 %).

Conclusions

All parameters assessed in our study show a great impact of radiation for seedling development. This confirm many similar experiments with tropical rainforest tree seedlings (Kriebitzsch et al., 1996 & 1997, Sanchez- Gallen & Alvarez- Sanchez, 1998). They seem to be well adapted to shade in their juvenile stage growing on the dark forest floor (Riddoch et al.,1991; Ducrey 1994). On the basis of Pn $_{max}$ and I$_S$ values *Tetraberlinia moreliana* seems to have an advantage at higher irradiance over the other two species *Tetraberlinia moreliana* and *Microberlinia bisulcata*. This corresponds very well to the biomass parameters.

The effects of both types of symbiosis seem to be dependent on infection rates which are increasing with light. Reid et al. (1983) found similar light reactions for the EM- species *Pinus taeda*.

High EM infection rates produce high carbon sinks to the roots (Colpaert et al., 1996). These C- sinks are caused by a higher fungal respiration rate , a colonization respiration for EM host roots and a greater proportion of active short roots (Reid et al., 1983, Rygiewicz & Andersen, 1994). Consequently the C- loss results in lower growth rate as shown by reduced leaf area (LA), total biomass (TM) and shoot/root- ratio (S/R) of the ectomycorrhizal (EM)- species *Microberlinia bisulcata* as well as of the AM- species *Oubanguia alata* in the MYK treatment in comparison to COM. LA and TM of *Tetraberlinia moreliana* is doubled with MYK treatment at high light and an infection rate of 80 % favouring an extremely positive benefit/cost- ratio of the EM- symbiosis. This species seems to be highly dependent on mycorrhiza. The EM plants of our experiment showed a decrease of Pn_{max} and I_S with MYK. We suggest that the decreased net assimilation rate is caused partly by the MYK induced increased light respiration rate of the leaves indicated by the remarkably higher dark respiration rate (R_D) of the MYK leaves (see Tab. 3). Increased respiration rates of mycorrhizal plants are not only associated with higher root, but also with enhanced shoot respiration rates (Reid et al., 1983, Rygiewicz & Andersen). In this context it is an interesting fact that R_D of *Tetraberlinia moreliana* at high light and MYK is not reduced and – in spite of lower Pn_{max} – growth is enhanced (see Fig. 1 and 2).
Our most recent experiments (unpublished) give evidence that lower N- concentrations and chlorophyll contents in the MYK treatment are further factors involved in the decrease of the net assimilation rate Pn_{max}.
AM- symbiosis seems to have positive effects at least on the gas exchange level increasing Pn_{max} and I_S of *Oubanguia alata* at high light. The displacement of Pn_{max} and I_S from slight shading in the control (COM) to high light with MYK is probably a direct consequence of the higher AM infection rate at high light conditions and shows how AM mycorrhiza could support invasion of high light sites discriminated without mycorrhiza. EM associations have a greater carbon cost (Janos, 1985). AM- symbiosis could be the less intensive type of mycorrhizal symbiosis with less carbon cost and better benefit/cost- ratio at high infection rates, but any conclusions about comparative mycorrhizal functioning cannot be drawn without studying EM and AM effects on the same host species.

Models of mycorrhizal symbiosis have been formulated recently to predict optimal infection rates for maximum plant growth as a function of net carbon gain and mineral nutrients provided cost-benefit (Kytöviita et al., 1998, Ruotsalainen et al., 1998).

The P- concentration in leaves is higher with MYK treatment (EM and AM) due to enhanced P- uptake (Reid et al., 1983, Cáceres & Cuenca, 1996, Moyersoen et al., 1998) alone in the case of *Tetraberlinia moreliana*. For *Microberlinia bisulcata* and *Oubanguia alata*, however, the improved P- concentration is partly resulting from P- accumulation as a consequence of reduced growth and biomass production. Hence, the differences between the P- concentrations in the leaves of plants from the MYK resp. COM treatment are particularly high for *M. bisulcata* and *O. alata* (Fig. 5). According to Moyersoen et al. (1998) EM are more effective than AM in increasing P uptake. This could be a possible explanation for the enhanced P- concentration of *Tetraberlinia moreliana* as well as increased growth in spite of high C- sink (see above) at the same time.

Nutrient supply (Ca, Mg, K) differs in EM- and AM- symbiosis: K- absorption and transport is enhanced by AM hyphae increasing K- concentration of *Oubanguia alata*. EM can reduce

Ca- and Mg fluxes strongly leading to Ca- shortage, disorder of optimum Ca/K- ratio for leaf production and therefore lower S/R, LA and TM.

EM hyphae and mantle favour better water storage and supply (Alexander, 1989) which could be responsible for the higher SLA values of EM- species (particularly of *M. bisulcata*, of *T. moreliana* just in full light) which in its turn is typical for moist sites. The improved water supply with the support of EM fungi enables particularly *M. bisulcata* to invade very dry soils. In contrast SLA of the AM- species *Oubanguia alata* is not at all influenced in our experiments. Parádi & Bratek (1998), however, found higher SLA also with AM infected plants, so this must be an effect not only typical for EM infection.

The enhanced transpiration and conductance values of all species emphasize the positive impact of MYK treatment (EM and AM) on plant water supply . Our results are confirmed by literature (e.g. Duddridge, 1980; Augé & Stodola, 1990, Morte et al. 1998). According to Morte et al. (1998) water relations are relatively more improved in water stressed conditions suggesting a competitive advantage of mycorrhizal symbiosis in dry habitats.

Drought resistance is strongly species dependent for both studied EM species. *Microberlinia bisulcata* is much more sensitive than *Tetraberlinia moreliana* in spite of a much higher infection rate of *Microberlinia bisulcata* (80 %, 45 % for *Tetraberlinia moreliana*) leading to expectations of MYK- induced higher resistance which is not confirmed.

Final Comment

According to our greenhouse results we assume that competitive advantages of the studied species in different habitats are rather assigned to basic properties like shade plant character, nutrient demands or reaction to drought rather than to the type of symbiosis they form. However, these basic properties are varied by the type of symbiosis they form. Thus, EM symbiosis could favour seedling survival rates on extremely dry habitats even at the cost of slower growth rates. At least AM symbiosis could increase Pn- capacity of shade plants to invade habitats of higher light intensities.

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