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Do mycorrhizas improve tropical tree seedling performance under water stress and low light conditions? A case study with *Dicorynia guianensis* (Caesalpiniaceae)

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Abstract: We tested the response of seedlings of *Dicorynia guianensis*, a major timber tree species of French Guiana, to mycorrhizal symbiosis and water limitation in a semi-controlled experiment under natural light conditions. Under well-watered conditions, mycorrhizal colonization resulted in an increase of net photosynthesis, growth and phosphorus uptake. When submitted to water stress, no growth reduction of mycorrhizal seedlings was observed. Mycorrhizal seedlings were more sensitive to drought than non-mycorrhizal ones in terms of carbon assimilation, but not with regard to stomatal closure. In contrast to previous studies on temperate tree seedlings, this result precludes a mycorrhizal effect on the hydraulic properties of this species. Furthermore, our results suggest that below a specific threshold of soil moisture, carbon assimilation of *D. guianensis* seedlings was decreased by the mycorrhizal symbiosis. This is probably related to the competition between the plant and its host fungus for carbon allocation under low light intensity, even though it did not seem to have a significant effect on mortality in our experiment.

Key Words: French Guiana, leaf gas exchange, mycorrhizal symbiosis, tropical forest, water limitation

INTRODUCTION

Arbuscular mycorrhizal fungi (AM, Order Glomales) colonize the roots of most vascular plants in all terrestrial ecosystems. This association is considered to be mutualistic even though the AM contribution to the functioning of the plants is not well understood. AM colonization is usually followed by growth stimulation generally thought to be due to improved plant nutrient uptake, particularly phosphorus (Koide *et al.* 2000, Smith & Read 1997). In turn, the plant provides carbon for growth and sporulation of the fungus (Harley & Smith 1983) and the level of benefit for the plant depends on the environmental conditions and on the fungal and tree species.

In tropical rain forests, AM association has been shown to be of great importance for phosphorus acquisition and growth of seedlings of several tropical tree species in acid and mineral-deficient soils (Béreau *et al.* 1997a, 2000; Janos 1980, Moyersoen *et al.* 1998). It can therefore be assumed that the symbiosis plays an important role in regeneration patterns in tropical rain forests although the AM dependency varies amongst tropical seedling life strategies (Gehring 2003, Zangaro *et al.* 2003).

The mechanisms involved in the physiological response of plants to colonization are still not well understood. A significant increase in net photosynthesis and decrease in stomatal conductance have been observed for mycorrhizal *Ziziphus mauritiania* plants (Mathur & Vyas 1995) as compared with non-mycorrhizal ones. The root hydraulic conductance of mycorrhizal *Piper* sp. and *Psychotria* sp. varied according to relative light demand of species and the light conditions during growth (Kyllo *et al.* 2003). Furthermore mycorrhizal plants may have a better ability to withstand drought compared with non-mycorrhizal ones (Safir *et al.* 1971), and mycorrhizal colonization seems to affect plant water relations (Fitter 1988, Koide 1993). The mechanisms by which plant water relations are modified by the mycorrhizal interactions are difficult to determine. Some authors suggest that improvement of plant water relations by

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mycorrhizal infection is only a secondary effect of enhanced phosphorus nutrition (Fitter 1988, Nelsen & Safir 1982) whilst others underline the influence of modifications of root hydraulic conductivity (Newman & Davies 1988), leaf gas exchange (Davies *et al.* 1993), osmotic adjustment (Augé *et al.* 1986), extraradical hyphal development (Davies *et al.* 1992), phytohormone production (Duan *et al.* 1996) or soil aggregation by mycorrhizal fungi preserving hydraulic continuity as the soil dries (Augé 2001).

In the neotropical rain forest of French Guiana, where *Paris*-type endomycorrhizas are dominant (Béreau *et al.* 1997b), forest seedlings and trees are submitted to fluctuating levels of soil moisture resulting from seasonal variations in rainfall and evapotranspiration (Guehl 1984). Variation in soil moisture availability can generate severe stress for some tree species by inducing stomatal closure and reducing carbon assimilation rates, resulting in high mortality (Bonal & Guehl 2001, Bonal *et al.* 2000). Whether the association between AM fungi and young tropical rain forest seedlings improves seedling performance and growth under soil water stress conditions remains an open question.

We designed an experiment to examine how seedlings of *Dicorynia guianensis* Amshoff (Caesalpiniaceae), a common large tree species of the tropical rain forest of French Guiana, grow and respond to water stress, both when they are or not in association with mycorrhizal fungi. In this study, we addressed the following questions: (1) would mycorrhizas of *Dicorynia guianensis* seedlings be advantageous for the plants in terms of growth, phosphorus uptake and leaf gas exchange characteristics under the low light levels such as those found in the understorey of the tropical rain forest?; (2) would mycorrhizas enhance *D. guianensis* seedling performances when subjected to water limitation under the same light conditions?

METHODS

Plant material

This study was conducted in Kourou (5°2′N, 52°45′W), French Guiana, from March 2001 to February 2002. Seeds of *Dicorynia guianensis* were collected in the forest (Paracou site) from different trees at the end of the 1998 wet season and kept at room temperature. Ferrallitic forest soil (top soil: 10–15 cm deep) was collected on the same site and sieved through a 1-cm screen. Seeds and soil were disinfected according to the procedures described by Béreau *et al.* (2000). On the same site, superficial young roots of mature *D. guianensis* trees were collected; 50 ml of thoroughly washed roots blended in water (250 g l^{-1}) were put in a 3-cm-deep hole at the centre of each 1.3-litre cylindrical pot containing disinfected soil (M1 treatment). Control pots (M0 treatment) received the same quantity of steam-sterilized blended roots. Each pot in both treatments was planted with a pregerminated seed and also received 10 ml of a solution obtained from thoroughly mixed forest soil and water 1/1 (v/v), filtered on Whatmann paper (4–7 μm) retaining glomalean fungal spores, but not bacteria. A total of 234 pots was prepared (117 M0 and 117 M1). Each pot received 10 ml of Hewitt nutrient solution (Hewitt 1966) without phosphorus per week (from July 2001 to February 2002) and 20 mg of nitrogen from an ammonium nitrate solution every second week from July to August 2001.

All plants were placed in a tunnel where the light regime was obtained by using neutral nylon black nets and transparent PVC sheets to keep out rain. From March to July 2001, plants were grown with a light regime corresponding to 15% full sunlight. Pots were automatically drip-watered for 2 min every day with approximately 50 ml of water that kept soil water content at field capacity. Anthracnose fungi should be *Gloeosporium* sp. on leaves favoured by high atmospheric humidity levels was treated with Dithane M45 Quino (Rohn & Haas France SA).

In August 2001, when seedlings were well developed (about 10 cm high and had about eight leaflets), they were submitted to a 4-mo acclimatization period to low light (about 1.5% full sunlight in the photosynthetic active radiation wavelength, PAR, Table 1) simulating light conditions at 0.5 m high in a natural tropical rain forest (Yoda 1974). At that time, a subsample of roots was collected in order to check mycorrhizal colonization rate.

In November 2001, half of the M0 and M1 plants were submitted to a 3-mo water limitation experiment (SM0, SM1), while the remaining plants were maintained at field capacity (WM0, WM1). Soil moisture level in the pots was measured every 2 wk using a TDR Trime FM2 (Imko, Ettlingen, Germany) in order to correct daily water input to maintain well-watered plants at field capacity (about 0.25 $m^3\ m^{-3}$) and to impose moderately increasing water limitation on droughted plants. Plants encountered low soil water content (less than 0.12 $m^3\ m^{-3}$) for about 6 wk. The experiment ended on 26 February, when many stressed plants presented wilting leaves. At that time, growth parameters and endomycorrhizal colonization were determined for all seedlings.

Table 1. Environmental conditions in the shade-house during the drought experiment.

Parameters	Mean	Range
Air temperature (°C)	27.0	25.1–29.7
Vapour pressure deficit (MPa)	7.3	3.7–12.5
PAR (% full sunlight)	1.5	
Soil temperature (°C)	23.9	22.3–26.2

Gas exchange measurements

Leaf gas exchange parameters were measured on all living plants every 2–3 wk under non-limiting environmental conditions (PAR = 670 ± 20 µmol m^{-2} s^{-1}; vapour pressure deficit = 1.2 ± 0.4 kPa; air temperature = 30.0 ± 2.1 °C) using a portable photosynthesis system (IRGA, CIRAS1, PP-Systems, Hoddesdon, UK) operating in open mode and fitted with a Parkinson leaf cuvette. Equations of Von Caemmerer & Farquhar (1981) were used to calculate leaf-area-based net carbon assimilation (A), stomatal conductance for water vapour (g_s) and instantaneous water-use efficiency (WUE = A/g_s).

Sampling, plant performance and analyses

At the end of the experiment, the number of leaflets and the stem length of each seedling were noted and the total leaf area was measured using a portable area meter (Li3000, LiCOR Inc, Lincoln, NE, USA). The root system was separated from soil and water-washed; a random subsample of fine roots was cut into 1-cm pieces then cleared and stained (Kormanik & McGraw 1982) in order to quantify endomycorrhizal colonization and structures (mycelium, coils, vesicles, arbuscules) according to Béreau *et al.* (2000). Endomycorrhizal colonization was expressed as the per cent of microscope fields containing colonised roots (Béreau *et al.* 1997a). The different seedling compartments (leaves, stem, roots) were oven-dried separately at 80 °C for 48 h and weighed. Since the amount of root or leaf dry material for each plant was not enough for mineral analysis, roots and leaves were pooled for a given treatment. Nitrogen and phosphorus concentrations in leaves and roots were determined in the INRA analysis laboratory in Bordeaux (France) based on methods of Marco *et al.* (2002) and Olsen *et al.* (1954).

Statistical analyses

Using Statview 4.5 (Abacus Concepts Inc) a parametric test, factorial analysis of variance (ANOVA), was performed at harvest on colonization after transformation by arcsine square root of the per cent and plant growth parameters for the four groups (WM0, WM1, SM0 and SM1). The effect of mycorrhizal status on leaf gas exchange parameters during the experiment was tested using factorial ANOVA. ANOVAs were followed by Fisher's least significant difference tests ($P < 0.05$). Relationships between leaf gas exchange characteristics and total plant leaf area or soil water content were tested using linear regressions (Statview 4.5, Abacus Concepts Inc). An analysis of covariance (ANCOVA, Statistica 1997) was performed to test if the linear regressions between g_s or WUE and SWC were significantly different between SM0 and SM1 plants. After verifying for the different assumptions associated with an ANCOVA, this test compared the slope of the g_s or WUE vs. SWC relationships between M0 and M1 plants and whether the intercepts of these relationships were equal or not.

RESULTS

Mycorrhizal status

Mycorrhizal inoculation was not successful for all inoculated plants and contamination occurred in some uninoculated pots. All data from the non-mycorrhizal seedlings in the inoculated treatments (having received crushed fresh roots) and from the mycorrhizal seedlings of the uninoculated treatments were discarded from further analyses. Dead seedlings and those with wilted leaves were also discarded. This resulted in 5, 12, 12 and 9 seedlings in the SM0, WM0, SM1 and WM1 treatments, respectively, that is to say in total, 47% of the plant population before stress.

Mycorrhizal colonization and mycorrhizal structures

Before the water stress was imposed on the plants, average AM colonization in the mycorrhizal seedlings was 45.5% (range = 34–57%). At the end of the experiment, this colonization was still not different among the WM1 and SM1 plants (63.0 ± 9.6% and 53.0 ± 7.2%, respectively, $P = 0.68$). Regarding mycorrhizal structure, coils were dominant in all plants (between 41% and 45%). Drought-stressed plants presented slightly more mycelium than non-stressed ones (2.76% and 0.56%, respectively).

Mycorrhizal effect on growth, nitrogen and phosphorus uptake and leaf gas exchange

Under well-watered conditions, plant height, number of leaflets and root mass did not differ significantly between mycorrhizal (WM1) and non-mycorrhizal plants (WM0), whereas total plant leaf area (× 2.5) and total dry mass (× 2) were higher in mycorrhizal plants (Table 2). Stem and leaf weight differed significantly between the M0 and the M1 plants (data not shown). Leaf nitrogen concentration values were higher in WM0 than in WM1, whereas it was the opposite for the phosphorus values which were doubled in WM1 (Table 3). Roots represented 34.9 and 20.4% of the biomass allocation in WM0 and WM1, respectively (Figure 1). Leaves represented 34.3

Table 2. Mean ± SE of different growth parameters per *Dicorynia guianensis* seedling at harvest according to treatment; M0: control; M1: root inoculated treatment; S: Water Stressed; W: Non-Water Stressed; degree of Freedom = 3; within columns entries followed by the same letter are not significantly different (PLSD Fisher test, $P < 0.05$).

Plant groups by treatment	n	Height (cm)	Number of leaflets	Leaf area (cm^2)	Total dry mass (g)	Root dry mass (g)
WM0	12	14.1 ± 1.0 a	10.9 ± 1.6 ab	133.2 ± 27.4 c	1.02 ± 0.16 b	0.33 ± 0.04 a
WM1	9	14.7 ± 1.0 a	15.3 ± 2.5 a	340.1 ± 51.1 a	1.91 ± 0.27 a	0.41 ± 0.06 a
SM0	5	15.1 ± 0.6 a	7.0 ± 1.4 b	80.9 ± 12.6 c	1.01± 0.08 b	0.43 ± 0.05 a
SM1	12	14.7 ± 0.8 a	15.4 ± 1.9 a	285.7 ± 31.1 b	1.82 ± 0.19 a	0.38 ± 0.04 a
F-value		0.19	3.31	13.94	6.63	1.24
P-value		0.902	0.032	< 0.0001	< 0.001	0.309

Table 3. Nitrogen (N) and phosphorus (P) concentration of leaves of *Dicorynia guianensis* seedlings at 54 wk. M0: control; M1: root inoculated treatment; S: Water Stressed; W: Non-Water Stressed. Since the amount of root or leaf dry material for each plant was not enough for mineral analysis, roots and leaves were pooled for a given treatment.

Plant groups by treatment	N (‰)	P (‰)
WM0	36.8	0.36
WM1	27.1	0.67
SM0	47.6	0.44
SM1	26.9	0.57

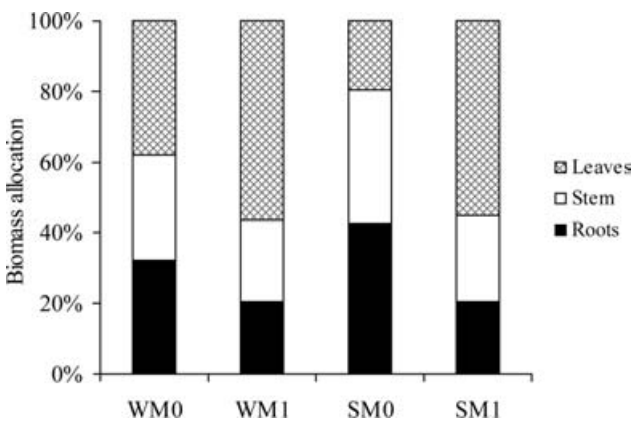

Figure 1. Biomass allocation of *Dicorynia guianensis* seedling at harvest according to treatment. M0: control; M1: root inoculated treatment; S: Water Stressed; W: Non-Water Stressed.

and 56.6% of the biomass allocation in WM0 and WM1, respectively (Figure 1).

Before the water limitation was imposed (end of acclimation phase), there was no significant difference in net carbon assimilation rate (A), stomatal conductance (g_s) or water use efficiency (WUE) between well-watered plants and plants that were subsequently to be drought-stressed, for mycorrhizal or non-mycorrhizal plants (Table 4). At the same time, however, when comparing mycorrhizal (WM1 and SM1) and non-mycorrhizal (WM0 and SM0) plants, mycorrhizal plants displayed higher A and WUE values, whereas g_s values were not statistically different (Table 4). There was a statistical positive linear relationship between net carbon assimilation rate (A) and total plant leaf area ($R^2 = 0.31$, $P = 0.001$; Figure 2).

Table 4. Mean ± SE of net carbon assimilation rate (A, μmol m^{-2} s^{-1}), stomatal conductance for water vapour (g_s, mmol m^{-2} s^{-1}) and instantaneous water use efficiency (WUE = A/g_s, μmol mol^{-1}) for the mycorrhizal or non-mycorrhizal plants before drought stress. M0: control; M1: root inoculated treatment; degree of Freedom = 1; within columns entries followed by the same letter are not significantly different (PLSD Fisher test, $P < 0.05$).

Mycorrhizal status	A (μmol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	WUE (μmol mol^{-1})
M0	1.86 ± 0.05 a	55.7 ± 3.1 a	39.4 ± 2.1 a
M1	2.14 ± 0.06 b	48.2 ± 2.8 a	50.0 ± 2.3 b
F-value	12.08	3.23	9.48
P-value	< 0.001	0.075	0.002

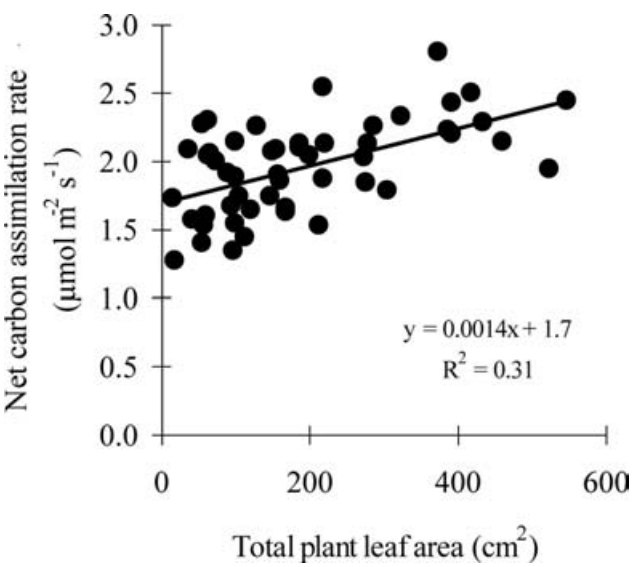

Figure 2. Relationship between net carbon assimilation rate (A, µmol m^{-2} s^{-1}) and total plant leaf area (cm^2) for well-watered mycorrhizal *Dicorynia guianensis* plants. Each dot corresponds to one plant.

Effect of water limitation on growth, nitrogen and phosphorus uptake, and leaf gas exchange

Under water-stress conditions, all growth parameters except plant height and root biomass were significantly higher in mycorrhizal plants as compared with non-mycorrhizal ones (Table 2). Biomass allocation did not differ significantly between WM1 and SM1 plants (Figure 1). Leaf and root nitrogen concentrations were higher in

non-mycorrhizal plants (Table 3), whereas phosphorus concentrations were higher in mycorrhizal plants (Table 3).

Leaf biomass allocation was much lower in SMO plants compared to SM1 ones (19.5 and 54.7%, respectively), while root biomass allocation in SMO plants was twice that of the SM1 plants (Figure 1).

Soil water content limitation resulted in a linear increase in WUE and a linear decrease in g_s for both SM0 and SM1 plants (Figure 3). In contrast, there was a logarithmic decrease in A with decreasing SWC for SM1 plants and no significant relationship between A and SWC was observed for SM0 plants (Figure 3). For g_s and WUE, there was no statistical difference in the slopes and the intercepts of the regression lines between SM0 and SM1 plants ($P > 0.10$).

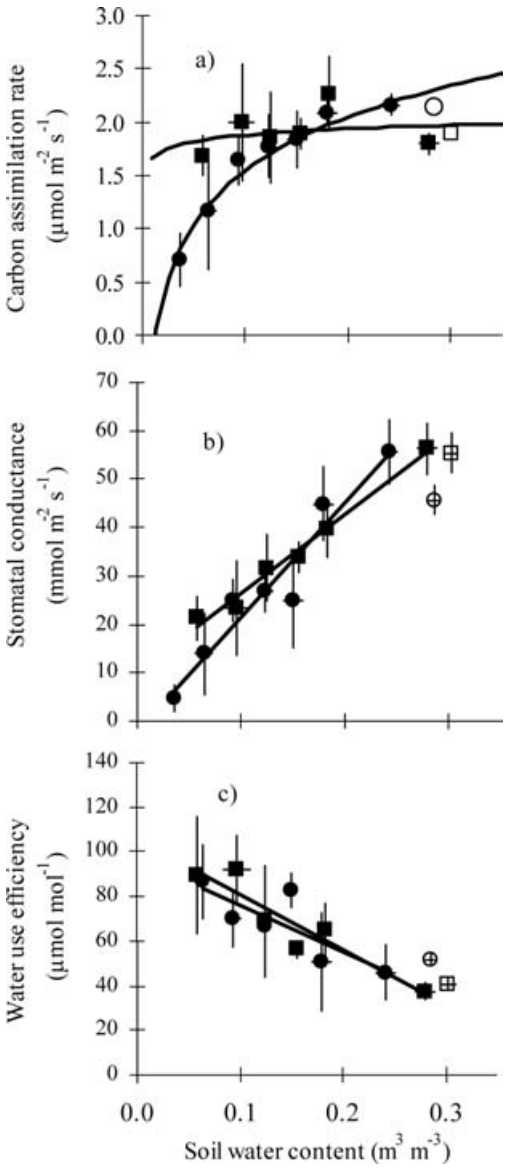

Figure 3. The relationship between (a) net carbon assimilation rate (A, µmol m^{-2} s^{-1}), (b) stomatal conductance (g_s, mmol m^{-2} s^{-1}), (c) water use efficiency (WUE = A/g_s, µmol mol^{-1}) and soil water content (SWC, m^3 m^{-3}) for mycorrhizal (SM1, ●) and non-mycorrhizal (SM0, ■) plants submitted to water stress. Averaged values for well-watered plants are also presented (○ for WM1 and □ for WM0). Plants were grouped according to classes of soil water content. Vertical bars are ± 1 SE (n = 2–15 plants per group). Data were fitted with linear (g_s and WUE) or logarithmic (A) regression (Statview 4.5). The differences in regression equations for g_s or WUE vs. SWC between mycorrhizal and non-mycorrhizal plants were tested using an ANCOVA (Statistica, 1997). For mycorrhizal plants (●), A = 0.72 ln (SWC) + 3.20 ($P = 0.005$), g_s = 180 SWC + 3.75 ($P < 0.01$), WUE = −243 SWC + 108 ($P = 0.017$). For non-mycorrhizal plants (■), the relationship between A and SWC was not significant ($P = 0.81$), g_s = 155 SWC + 10.8 ($P < 0.001$), WUE = −224 SWC + 103 ($P = 0.002$).

DISCUSSION

Well-watered conditions

The results obtained on mycorrhizal effects in well-watered conditions (plant biomass, total leaf area, phosphorus concentration) were in agreement with existing references on other tropical species (Janos 1980, Moyersoen *et al.* 1998, Smith & Read 1997) and previous results for this species (Béreau *et al.* 1997a, 2000).

One main objective of this study was to infer whether the colonization of *D. guianensis* roots by mycorrhizal fungi would influence leaf gas exchange characteristics. Under well-watered conditions, leaf carbon assimilation rate (A) increased when plants were mycorrhizal (Figure 3). The concomitant increase in growth characteristics and A for the mycorrhizal plants suggests that assimilation is stimulated by AM fungi and this association is beneficial for *D. guianensis* seedlings under very low light conditions such as those which young seedlings might encounter in the natural rain forest. The mechanisms explaining such interactions are not known, but it has already been shown that endomycorrhizas contribute to increased phosphorus nutrition for plants under limiting phosphorus availability (Nelsen & Safir 1982), which tends to increase plant photosynthetic capacity (Augé 2001, Koide 1993). Under well-watered conditions, our study did not emphasize the role of endomycorrhizas on *D. guianensis* hydraulic characteristics, as has been observed in other species (Kyllo *et al.* 2003).

Water limitation conditions

Water limitation did not result in a reduction of plant biomass production for mycorrhizal plants. Biomass allocation only varied slightly between SM1 and WM1, even though a decrease in total leaf area was observed for stressed plants. These differences were explained by the slight increase in specific leaf area of the stressed

plants (data not shown), as already observed in previous water limitation experiments (Huc *et al.* 1994). The lack of strong differences in biomass production between SM1 and WM1 could be related to the short duration (3 mo only) of the imposed water limitation experiment.

Under severe water limitation, a strong stomatal closure as well as an increase in WUE for mycorrhizal and non-mycorrhizal plants occurred (Figure 3), in agreement with previous observations in tropical rain forests (Bonal *et al.* 2000). However, in contrast with most previously published studies on endomycorrhizal fungi (Augé 2000), the observed decrease in stomatal conductance (g_s) was not modified by the presence of endomycorrhizas (Figure 3). This result again suggests the absence of a strong effect of endomycorrhizas on hydraulic properties of *D. guianensis* at the leaf/stomatal level.

In contrast with g_s, the presence of endomycorrhizas and the slightly improved carbon assimilation rate (A) under non-limiting water conditions, modified the response of plants to water limitation in terms of carbon assimilation rate. Mycorrhizal *D. guianensis* plants appeared to be more sensitive to soil water limitation in terms of carbon assimilation, compared with non-mycorrhizal plants. Indeed, A for SM1 plants started to decrease at soil water content close to $0.15\,m^3\ m^{-3}$ (Figure 3), whereas SM0 plants displayed rather stable A values (no statistical relationship with SWC) over the observed range of soil water content. These results suggest that the association between endomycorrhizal fungi and *D. guianensis* roots might be detrimental to the growth of the plant (reduced carbon assimilation) when light conditions are very low and soil water content strongly decreases such as during the dry season in French Guiana.

Despite an apparent discrepancy for the effect of endomycorrhizas on averaged A, g_s and WUE values, our results were consistent with the mathematical relationship between these variables ($WUE = A/g_s$). Indeed, when considering low SWC values (Figure 3), A and g_s averaged values for SM0 plants were higher than for SM1 plants and WUE for SM0 and SM1 plants was similar. However, the only significant difference between SM0 and SM1 plants for a given SWC appeared for A. This apparent discrepancy can be explained by the high variability in leaf gas exchange values among plants in the different treatments for a similar SWC (high standard error of the mean in Figure 3).

Results of this study on mycorrhizal *D. guianensis* were not in agreement with most previous studies on cultivated plants or trees and stress the complexity of the relationships between endomycorrhizas and plants in temperate and tropical regions (Gehring 2003, Zangaro *et al.* 2003). Nevertheless, it should be noted that all the literature available on this matter deals with *Arum*-type endomycorrhizas, while *D. guianensis*, as most of the rain-forest trees in French Guiana (Béreau *et al.* 1997b), have *Paris*-type, characterized by the dominance of hyphal coils instead of arbuscules as endocellular exchange structures. The mechanisms of nutrient and carbon transfer involved in these relationships are still unknown. The carbon cost for the plants induced by the association, although beneficial under non-limiting water conditions, seems to become detrimental under severe water limitation conditions because of the additional carbon requirements of the mycorrhizal fungi colonizing the roots (Wright *et al.* 1998). The influence of this mycorrhizal colonization observed under the semi-controlled environment here might be substantially modified in natural conditions. Indeed, the root system limited by the pots was unable to explore more soil volume, as indicated by the same root biomass in all the treatments, and to be colonized by more diverse AM fungus communities.

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