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Original article

Effects of endomycorrhizal development and light regimes on the growth of *Dicorynia guianensis* Amshoff seedlings

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Abstract – The influence of mycorrhizal infection rate and light environment on growth traits was examined for 50-week-old *Dicorynia guianensis* Amshoff tree seedlings. The seedlings were grown on two soil substrates (control and inoculated) in shade tunnels under three relative light levels (50%, 14% and 1% of full sunshine). For seedlings growing under 1% of full sunlight no significant differences between control and inoculated plants were observed in plant traits though a high rate of endomycorrhizal infection was recorded. In partial shaded sunlight, 14% and 50%, the rate of mycorrhizal infection was positively related to the growth performances of seedlings. The optimal growth was obtained under 14% of full sunlight, showing a greater efficiency of the mycorrhizas.

tropical rainforest / *Dicorynia guianensis* / seedlings / endomycorrhizas / light / experimental approach

Résumé – **Effet des mycorhizes et de la lumière sur la croissance des semis de *Dicorynia guianensis* Amshoff, une césalpiniacée de la forêt tropicale humide de Guyane française.** Des semis de *D. guianensis* ont été cultivés en pots sur un sol désinfecté, inoculé ou non avec du sol forestier, dans des serres tunnels sous trois régimes lumineux (1 %, 14 %, 50 % du plein découvert). Des paramètres de croissance des plants et la colonisation endomycorhizienne des racines ont été mesurés au bout de 50 semaines. Les semis soumis à 1% d'éclairement et croissant sur les deux types de sol ne présentaient aucune différence significative pour aucun des caractères mesurés, bien qu'un taux élevé de mycorhization aie été noté chez les plants sur sol inoculé. En éclairement partiel, 14 et 50 %, les performances de croissance des semis étaient positivement reliées au taux d'infection mycorhizienne. L'optimum de croissance était obtenu pour l'intensité lumineuse moyenne (14 %), montrant ainsi une meilleure efficacité des mycorhizes.

forêt tropicale humide / *Dicorynia guianensis* / semis / endomycorhizes / lumière / approche expérimentale

1. INTRODUCTION

Tropical forests often present a nutrient limitation related to acid soils, poor in mineral elements and organic matter. Thus, one of the major adaptations of plants to low availability of nutrients resources has been the help of the greater mobilizing capacity of their symbiotic mycorrhizal fungi. Benefits from mycorrhizas are recognised as improving the uptake of most low-mobility nutrients as phosphorus, copper, zinc or ammonium [27], but the fungus derives a substantial part of the plant photosynthates. Between 4% and 20% of net photosynthates

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are transferred to the fungus for its growth and maintenance, particularly under low light conditions [20, 42]. Mycorrhizal associations are the rule in most plant species and genera [34], and arbuscular endomycorrhizas are the most common symbiotic associations among woody plants in French Guiana [8, 9].

Tree growth and reproduction are closely related to aboveground environmental factors, particularly to small changes in light availability, associated with openings in the forest canopy [13]. Lower mortality rates under some degree of canopy opening than under intact forest canopy have also been underlined [3, 13, 15]. This pattern is most easily explained by more favourable carbon balances in light environments [19]. However, differences in light requirements among seedlings of different tropical tree species have already been demonstrated [4, 17] but little is still known about the autecological characteristics of these species [6, 18, 33]. It has been suggested that low light intensity limits root growth and reduces the root:shoot ratio because of a low supply of carbohydrates to the roots [29].

The effect of photon irradiance on the development on endomycorrhizal fungi has been studied as early as 1940 by Peyronel [37] who found in cereals a positive relationship between the two parameters. Since that time, many investigators have reported conflicting results [25, 36, 44]. Interactions between mycorrhizal efficacy and light are complex because light affects plant growth not only directly through photosynthesis, but also indirectly through its effects on other factors [12, 21].

Because many tropical tree species require shelter from direct sunlight to establish, this study is focused on the dependency of the growth of seedlings of *Dicorynia guianensis* (an important tree in French Guiana) to both endomycorrhizal infection rate and light intensity available during the establishment phase. The hypothesis which is tested experimentally is that the dependency or responsiveness of *D. guianensis* seedlings to arbuscular mycorrhizas depends on light intensity, i.e. to their environmental status on the forest floor. This is part of a cooperative programme on the determinism of the natural regeneration of the tropical rainforest.

2. MATERIALS AND METHODS

2.1. Site location, seed harvesting and plant material

This study was conducted in Kourou (52°45 W, 5.2° N) located on the coast of French Guiana**.**

Dicorynia guianensis Amshoff, an Amazon endemic forest tree species belonging to the Caesalpiniaceae, was chosen in this study because of its importance in the wood market (first commercial species) in French Guiana [16, 39] and also because of the capacity of its seedlings to develop in a large range of light intensity [7, 35, 38].

Seeds were extracted from pods collected on the forest floor at the experimental site of Paracou [5] at the end of the wet season (May-June 1996). The seeds were soaked in pure sulphuric acid for 10 min and rinsed 5 times with sterile distilled water in order to break down dormancy. They were then surface-sterilized with a 0.1% mercury chloride solution ($HgCl_2$) for 5 min and rinsed four times with sterile water. The seeds were then kept in aseptic conditions during the germination phase. The root emerged within one week, and the germinations were transplanted in black plastic pots under shade tunnels.

2.2. Soil substrate

A ferrallitic forest soil (top fifteen cm) was collected at the experimental site of Paracou and sieved through a 0.5 cm mesh (0.5 cm diameter) to remove coarse particles. It was mixed with 1/3 (v/v) white sand and steam-disinfected at 90 °C three times for two hours each with one-day intervals. The disinfected soil was kept and used two weeks later. Mycorrhizal inoculum was provided by fresh forest soil. The pots were filled according to the following protocol:

(i) Control (disinfected soil substrate with addition of 10 ml per pot of a microbial filtrate soil solution obtained from the thoroughly mixed forest soil and water, 1:1 v/v, filtered on Whatman paper, 4–7 μm, retaining mycorrhizal fungal spores but not bacteria).

(ii) Inoculated soil (disinfected soil substrate mixed with 30% v/v of the same non-disinfected soil mix).

Each pot was filled with 1.3 l of the required soil substrate and received one germinated seed. Prior to planting, pots were saturated using tap water. Thereafter, 50 ml of water was brought to each pot daily, using an automatic drip-irrigation system [9].

2.3. Light regimes and temperature variations in the shade tunnels

Three light regimes were imposed ranging from 1% of full sunlight (Low Light Intensity: LLI) to 14% (Medium Light Intensity: MLI) and 50% (High Light Intensity: HLI), simulating variation in light intensity from an intact canopy to a large gap. The light regimes were obtained by using waterproof transparent PVC sheets (intercepting all precipitations) overlapped by neutral

nylon black nets. For each sheltered tunnel, light measurements were made simultaneously outside and inside the tunnel using two quantum sensors (LiCor Instruments, Lincoln, Nebraska) during bright sunny days. The light regime was calculated as the mean ratio of the instantaneous photosynthetic photon flux densities (PPFD) measured over the daytime in the sheltered tunnel and outdoor in full sunlight.

The use of shelters leads to an alteration of the local climate. Among the climate parameters, only the temperature, read with a minima-maxima thermometer, received further attention, especially during the exceptional and heavy dry season encountered on September 1997 in French Guiana. The water deficit was very high and midday air temperature reached 50 °C during a few days under the less shaded tunnel (HLI) and the values of the soil temperature in the pots ranged from 42 to 47 °C. The soil temperature recorded under the two other tunnels (i.e. 1% and 14% of full sunlight) was in the range of 32 to 36 °C. This parameters were extreme compared to the normal air temperature (33 °C) and humidity (55%) for the season.

2.4. Experimental set-up

The potted plants were randomly distributed in a full-block design with six treatments (two soil substrates × three light regimes), four blocks and 10 plants within each block-treatment combination in order to minimize the spatial heterogeneity effects in light availability under the tunnel shelters. The pots were assigned to shade tunnels. The seedlings were grown for 50 weeks and harvested for measuring growth parameters and endomycorrhizal colonization.

2.5. Sampling and measurement

Dicorynia guianensis Amshoff has pinnate composite leaves. From November 1996 to October 1997, the leaflets of the seedlings were counted every 8–12 days and the height of their stem measured from the soil level to the apical meristem, in order to describe the kinetic of leaf production and shoot growth.

At the end of the experiment (350 days), the seedlings were harvested and the following operations were performed:

– the total leaf blade area of each seedling was measured using a LI-3000 area meter (LI-COR Inc, Lincoln, NE, USA). Leaves and stems were separately oven-dried at 80 °C for 72 hours and weighed. As endomycorrhizas had been shown to enhance root acquisition of phosphate (P) from poor tropical soils [26], the phosphorus concentration of sampled leaves (3 replicates from mixed leaves) of the seedlings involved in each treatment were determined. The analyses were performed in the INRA *Laboratoire central d'analyses des plantes* in Bordeaux (France).
– the root systems were separated from soil and water-washed. The abundance of mycorrhizal external mycelium surrounding the fine roots was assessed using a stereomicroscope. A random sub-sample of fine roots was cut into 1 cm pieces, cleared and stained for quantifying endomycorrhizal colonization [8, 9]. The remaining root systems were oven-dried at 80 °C for 72 h and weighted.

These data were then used to assess the number of leaflets of plants, height, leaf area and weight, total above and below-ground biomass, leaf area ratio, root:shoot ratio and endomycorrhizal infection.

2.6. Data analysis

Using Statview 4.5 from Abacus Concepts Inc., a fully factorial ANOVA analysis of the data at harvest was performed in order to detect any interactions between the 3 factors (light, mycorrhizal inoculation and blocks). Significant differences ($P < 0.05$) between individual treatments were detected using Fisher's pooled least significant difference.

The endomycorrhizal infection was expressed as a percent of colonised root length [9], and the results were transformed by arcsinus square root before being subjected to the analysis of variance.

3. RESULTS

The overall analysis of variance indicated that there was no significant block effect (*table I*) and that the treatment factor was statistically significant at the 0.05 probability level for all parameters. Regarding the total biomass, *table I* and *figure 1* showed interactions between light and mycorrhizas.

3.1. Mortality rate

At the beginning of the experiment (day 30), the seedling mortality was the same (less than 5%) in the partially shaded treatments (MLI and HLI) in both soils, while at 1% of full sunlight (LLI), the mortality was 17% for the control seedlings and 27% for the inoculated ones.

Table I. Full factorial Analysis of Variance for the total biomass per seedling at 50 weeks. Effects are considered as significant for $P < 0.05$; DF: degree of freedom; Myco: mycorrhizal treatment (control and inoculated soil).

	DF	Sum of squares	Mean square	F - ratio	*P*
Blocks	3	3.469	1.156	0.683	0.5634
Light	2	321.426	160.713	94.933	< 0.0001
Blocks × Light	6	16.595	2.766	1.634	0.1401
Myco	1	126.455	126.455	74.697	< 0.000
Blocks × Myco	3	8.461	2.820	1.666	0.1759
Light × Myco	2	60.022	30.011	17.727	< 0.000
Blocks × Light × Myco	6	12.741	2.124	1.254	0.2808
Residues	182	308.109	1.693		

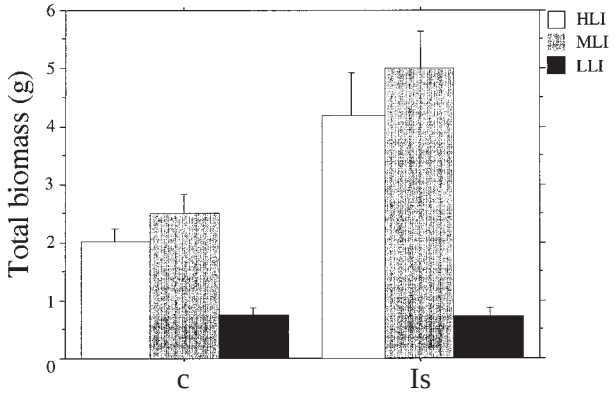

Figure 1. Interaction graph between light and mycorrhizas for the total biomass per seedling after 50 weeks. C: control treatment; Is: inoculated soil treatment; HLI: high light intensity; MLI: medium light intensity; LLI: low light intensity. Bars represent standard errors.

At the end of the experiment (350 days), the proportion of dead plants had increased only for the latter treatments (20 and 32%, respectively).

3.2. Growth kinetics

At 200 days, leaflet number was higher for seedlings grown under HLI than under MLI and LLI. Soil treatment (control or inoculated) had no effect on leaflet number and production when seedlings where grown under LLI. Therefore, leaflet production rate is more light-dependent than mycorrhiza-dependent. About 60 days later, a natural soil drought occurred in relation to extreme climatic conditions, leading to leaf fall only on seedlings growing under HLI. Leaflet production resumed at least 42 days earlier for seedlings grown in inoculated soil than for those grown in the control soil. At MLI, no leaf fall was observed in the inoculated treatment.

No difference in height growth rate under the three light intensities was noted at 200 days for the control (*figure 2*), while a faster growth was observed under MLI for the inoculated soil treatment (+35%). This difference was still marked and increasing at the end of the experiment.

3.3. Growth parameters and mycorrhizal colonization at the end of the experiment (350 days)

3.3.1. Leaflet number, height and leaf area per seedling (table II)

At the end of the experiment, the number of leaflets per seedling was the same in all treatments, except in the inoculated soil with medium or low light intensity where it was significantly higher (almost twofold). The leaf area was even more markedly affected, with values more

Table II. Number of leaflets, height and leaf area per seedling afatter 50 weeks. C: control**,** non-inoculated soil; Is: inoculated soil. HLI: high light intensity; MLI: medium light intensity; LLI: low light intensity. Values in a column followed by the same letter are not significantly different (Fisher pooled least significant difference, $P \leq 0.05$).

Treatments	Means and standard errors of the mean		
	Number of leaflets	Height (cm)	Leaf area (cm^2)
C - HLI	10.27 ± 0.74 ^{bc}	14.42 ± 0.33 ^{a}	92.17 ± 5.41 ^{a}
Is - HLI	17.92 ± 1.54 ^{a}	15.99 ± 0.46 ^{b}	215.42 ± 21.17 ^{b}
C - MLI	9.78 ± 0.60 ^{bc}	15.51 ± 0.43 ^{ab}	142.17 ± 9.89 ^{c}
Is - MLI	18.78 ± 1.07 ^{a}	20.34 ± 0.58 ^{c}	408.47 ± 27.40 ^{d}
C - LLI	10.66 ± 0.22 ^{bc}	16.14 ± 0.59 ^{b}	173.60 ± 12.34 ^{bc}
Is - LLI	10.44 ± 0.26 ^{bc}	16.61 ± 0.63 ^{b}	175.00 ± 15.23 ^{bc}

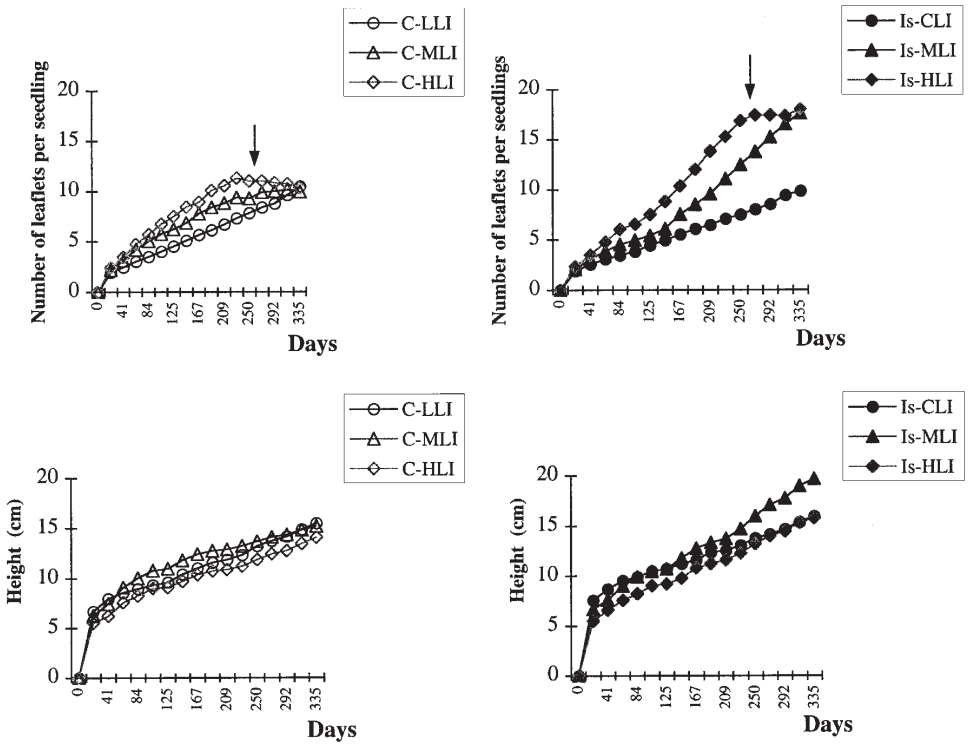

Figure 2. Number of leaflets and seedlings height against light intensity and time. C: control treatment; Is: inoculated soil treatment; LLI, MLI, HLI: respectively low, medium and high light intensity. Arrow: environmental drought.

than four times higher for the treatment with inoculated soil and medium light intensity than for the treatment with control soil and high light intensity.

Height was less affected, with treatments ranking as for leaf area.

The colour of the leaves differed according to the treatments: they were dark green in both LLI treatments, pale green at MLI and pale green with brown and yellow spots at HLI.

3.3.2. Total dry weight

Seedlings grown under medium light intensity on inoculated soil produced the highest amount of total dry matter. No significant difference of root dry weight between HLI and MLI on the inoculated soil substrate (*figure 3)* was noted, but the seedlings grown under the same light intensities on inoculated soil produced twice more root dry matter. There was no difference in root dry matter production (which was extremely low) between seedlings grown under low light intensity, whatever the soil treatment .

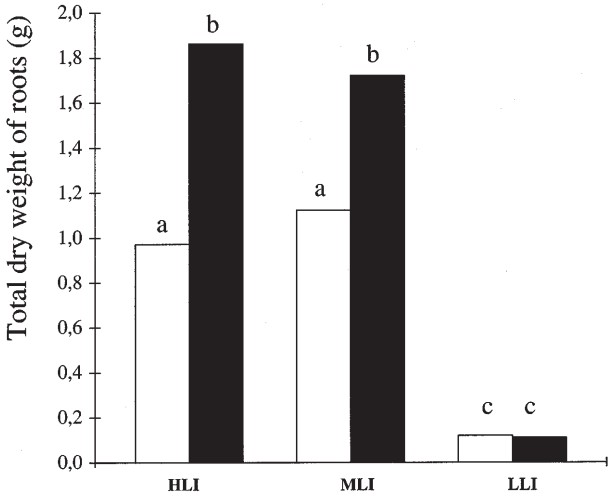

Figure 3. Total root dry weight per seedling after 50 weeks. White: control treatment; black: inoculated soil treatment. LLI, MLI, HLI: respectively low, medium and high light intensity. a, b, c: values with the same letter are not significantly different (Fisher pooled least significant difference, $P \leq 0.05$, one factor ANOVA).

3.3.3. Root:shoot ratio and leaf area ratio

Figure 4 shows that the root:shoot ratio was considerably reduced by shading, and to a lesser extent by mycorrhizal inoculation under medium light intensity.

The Leaf Area Ratio (LAR) of seedlings grown under LLI was much higher than in the two others light treatments (*figure 4*). The only significant (positive) effect of mycorrhizal inoculation on LAR was found for MLI.

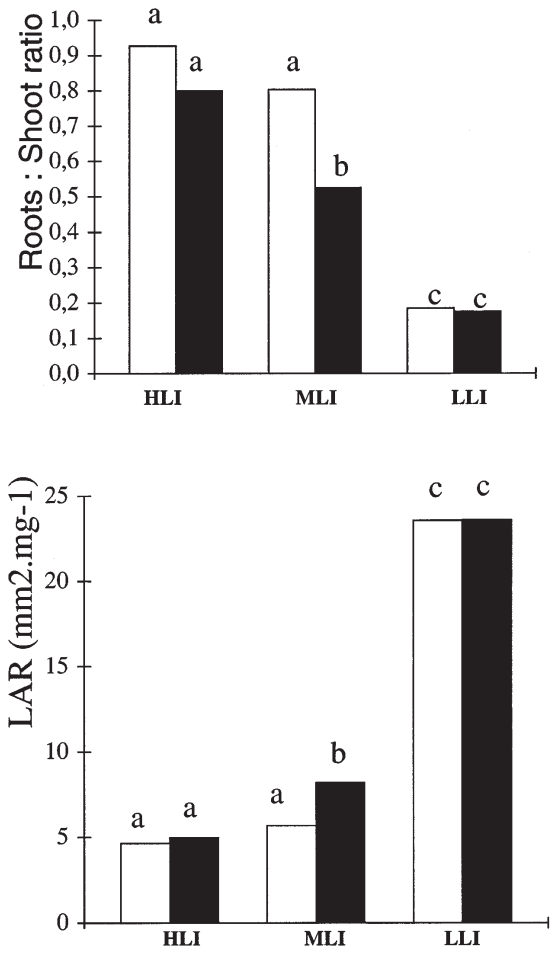

Figure 4. Root:Shoot ratio and leaf area ratio (LAR) per seedling after 50 weeks. White: control treatment; black: inoculated soil treatment; LAR: leaf area ratio; LLI, MLI, HLI: respectively low, medium and high light intensity; a, b, c: values with the same letter are not significantly different (Fisher pooled least significant difference, $P \leq 0.05$, one factor ANOVA).

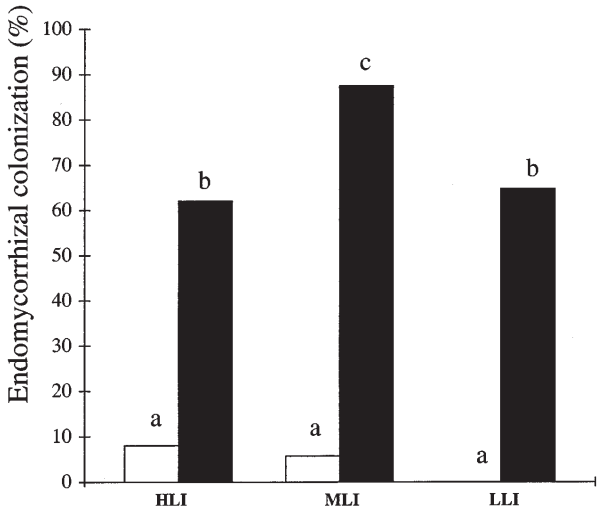

Figure 5. Endomycorrhizal colonization (%) per seedling after 50 weeks. White: control treatment; black: inoculated soil treatment. LLI, MLI, HLI: respectively low, medium and high light intensity; a, b, c: values with the same letter are not significantly different (Fisher pooled least significant difference, $P \leq 0.05$), one factor ANOVA).

3.3.4. Endomycorrhizal colonization

Figure 5 shows that the mycorrhizal colonization of the roots was very low in the non-inoculated controls (less than 10%) while it was 60% for extreme light intensity and significantly higher under medium intensity. Therefore, all significant effects due to the inoculation treatment can be attributed to the mycorrhizal symbiosis.

As previously observed with *D. guianensis* [8, 9], mycorrhizas were characterized by abundant intra-cellular hyphal coils. External mycelium was particularly abundant on the root surface in the low-intensity light treatment.

Table III. Phosphorus content of the leaves of *Dicorynia guianensis* seedlings at 50 weeks. C: control, non-inoculated soil; Is: inoculated soil. Values in a column followed by the same letter are not significantly different (Fisher pooled least significant difference ($P \leq 0.05$).

Light intensity (% of full sunlight)	Treatment	Ashes %	Phosphorus content ‰
1%	C	8.3	0.74 [b]
	Is	6.8	0.94 [c]
14%	C	8.1	0.38 [a]
	Is	6.1	0.60 [b]
50%	C	6.5	0.42 [a]
	Is	5.7	0.43 [a]

3.3.5. Leaf phosphorus contents

The leaf phosphorus content was about twice as high under LLI than under HLI (*table III*). The positive effect of mycorrhizal inoculation on P content was particularly marked under MLI, and to a lesser extent under LLI.

4. DISCUSSION

4.1. Symbiotic status and growth response of the seedlings to the treatments

It has been shown in a previous work with the same materials and under similar experimental conditions [9] that steam disinfection did not significantly modify the basic physico-chemical properties of the soil substrate (pH, total N, extractable P and exchangeable cations). Because 30% only of the forest soil mix used as inoculum were added to the steamed soil, we may consider that the substrates were not significantly different in the two treatments. Soil bacteria were re-introduced with the soil filtrate in the disinfected control, but no bacterial nodules appeared on seedling roots whatever the treatment, confirming the results of previous experiments [9] and field survey [8] which showed that *D. guianensis* was generally devoided of bacterial symbiotic nodules. The growth difference between the control (not or poorly mycorrhized because of accidental contamination) and the inoculated soil treatment (heavily mycorrhized as a consequence of the inoculation) can therefore be attributed to mycorrhizas.

Consistently with previous works with the same tree species in the same region, the endomycorrhizas found in the *D. guianensis* seedlings were typical of the *Paris* type according to Gallaud [22], in which arbuscules are replaced by intracellular hyphal coils as exchange sites (Smith and Read, [42]).

The seedlings behaved very differently depending on the light intensity they were submitted to. Under medium an high light intensity, they displayed thick leaves (low LAR), extensive mycorrhizal colonization (specially for MLI), strong growth response to the symbiosis and high root/shoot ratio (slightly reduced by mycorrhizas, however). In contrast, seedlings grown under low light intensity similar to that on the forest floor showed very thin leaves, no growth response to mycorrhizas in spite of the same colonization index as in the other light treatments, and a very low root-shoot ratio, unaffected by the mycorrhizal status. In addition, these seedlings grown in the shade displayed the highest proportion of external mycelium on their roots; together with the previous facts, this suggests that, under limiting photosynthetic conditions, priority is given to the fungus for photosynthate allocation.

4.2. Morphological adjustment to light intensity

The morphological adjustments observed under low light conditions reflect the priority for shoot growth over root growth (except for fungal growth which is enhanced), which is a common response of tree seedlings to shading [24, 28]. The capacity to tolerate shade involves adjustment of the photosynthetic apparatus and also the manner in which biomass is allocated [10, 30]. The effects of partial shading on growth and/or morphology were expected to differ between the mycorrhized and the non-mycorrhized seedlings. Morphological adjustments which might result in a shade-specific habit in older saplings [1] can be interpreted as a strategy to maximize the net rate of energy capture [23], allowing the plant to increase its photosynthetic capacity.

The root:shoot ratio is an important index which gives clues to the balance of growth between root and shoot. Low light availability generally reduces nutrient uptake by reducing root:shoot ratio [32], reflecting a different plant growth strategy. Under medium and high light intensity, non-mycorrhizal seedlings invested in roots, while the shoot biomass was favoured by the mycorrhizal ones .

Our results are consistent with many others found in the literature, which concern the benefits conferred by mycorrhizal colonization on the host plant [25, 26]: mycorrhizal infection stimulated the growth of *D. guianensis* seedlings, and the intensity of the stimulation was clearly affected by light intensity. The extra dry matter production was greatest under medium light intensity, which also led to largest leaf area. Under low light intensity, mycorrhiza were present but ineffective. Under our experimental conditions, about 14% of full sunlight seems to be the optimal light intensity for mycorrhizal efficiency of *D. guianensis* seedlings.

4.3. Phosphorus nutrition

The role of mycorrhizas in general, and more particularly of endomycorrhizas, in phosphorus acquisition by plants has been well documented for more than three decades [11, 14]. Except under high light intensity, we had an indirect evidence that mycorrhizal roots were more efficient in phosphorus uptake than non-colonized ones, because the former contained a higher P concentration in their tissues than the latter. This has also been found

by Marshner and Dell [31] on soil with low P mobility, which is also the case of the soil used in our experiment. However, these results are partially in contradiction with those of Smith and Gianinazzi-Pearson [41] who noted with *Allium cepa* L., at low irradiance, depressed growth and phosphorus content of mycorrhizal plants.

4.4. Water relations

During the dry period, endomycorrhizal colonization helped the seedlings to resist to drought stress and to recover rapidly as soon as better conditions were restored, as observed on maize by Subramanian et al. [43] and on wheat by Al-Karaki and Clark [2]. Mycorrhizas seemed to affect the water relations of the seedlings, but the experiment was not designed to elucidate the mechanisms involved which can be increase of stomatal conductance, reduction of the hydraulic resistance to water uptake in the roots, or indirect hyphal contribution in relation with nutrient uptake [42].

5. CONCLUSION

When ranking the importance of the two factors studied – light and mycorrhizas – for their effect on the growth of *D. guianensis* seedlings, light intensity clearly comes in the first place. Medium light intensity permits the best growth and survival, while low intensity leads to very poor growth an progressive die-back. This is consistent with the observations made in the forest with the same species, where seedlings develop vigorously in gaps while they merely survive in close stands.

The endomycorrhizal symbiosis enhances this contrast. In the shade, where the fungus competes with the plant for limited carbon resources, mycorrhizas do not improve growth and even tends to accelerates die-back, while in medium light – and to a lesser extent under high light – it very significantly improves growth and even water stress tolerance, in relation with enhanced phosphorus uptake.

According to our results, the endomycorrhizal symbiosis is decisive for the success of effective regeneration of *Dicorynia guianensis*, that is the ability of shaded seedling to respond rapidly to accidental canopy openings by vigorous growth and to compete with other plants for water and nutrients. But, on the other hand, the drawback of mycorrhizas for light-waiting shaded seedlings is a higher mortality rate in their early stage, when the fungus behaves more as a parasite because of the carbon cost of the symbiosis under C-limiting conditions. Therefore, in terms of competitive advantage an survival strategy at the population level, it seems that poor survival at early seedling stage is the price to pay for a few successful individuals in the long run and that endomycorrhizal symbiosis is a key component of the seedlings.

However, extrapolating these results to the real conditions in the forest must be done with precaution because the light spectrum might be different under nylon black nets or real leaf canopy. That is why we are now complementing this type of work by *in situ* experiments.

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REFERENCES

[1] Afm van H., Growth and morphology of pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) seedlings in relation to shading and drought, Ann. Sci. For. 54 (1997) 9–18.

[2] Al-Karaki G.N., Clark R.B., Growth, mineral acquisition and water use by mycorrhizal wheat grown under water stress, J. Plant Nutr. 21 (23) (1998) 263–276.

[3] Augspurger C.K., Light requirements of neotropical tree seedlings: a comparative study of growth and survival, J. Ecol. 72 (1984) 777–796.

[4] Barigah T.S., Huc R., Imbert P., Croissance et assimilation nette foliaire de jeunes plants de dix arbres de la forêt guyanaise, cultivés à cinq niveaux d'éclairement, Ann. Sci. For. 55 (1998) 681–706.

[5] Bariteau M., Geoffroy J., Sylviculture et régénération naturelle en forêt guyanaise, Rev. For. Fr. 16 (1989) 309–323.

[6] Bazzaz F.A., Pickett S.T.A., Physiological ecology of tropical succession: a comparative review, Ann. Rev. Ecol. Syst. 11 (1980) 287–310.

[7] Bena P., Essences forestières de Guyane, Bureau agricole et forestier guyanais, 1960.

[8] Bereau M., Gazel M., Garbaye J., Les symbioses mycorrhiziennes des arbres de la forêt tropicale humide de Guyane française, Can. J. Bot. 75 (1997) 711–716.

[9] Bereau M., Louisanna E., Garbaye J., Effects of endomycorrhizas and nematodes on the growth of seedlings of *Dicorynia guianensis* Amshoff, a tree species of the tropical rain forest in French Guyana, Ann. Sci. For. 54 (1997) 271–277.

[10] Björkman O., Responses to different quantum flux densities, in: Lange O.L., Nobel P.S., Omund C.B., Ziegler H. (Eds.), Encyclopedia of plant physiology, new series,

Physiological plant ecology I. Vol. 12A, Springer Verlag, Berlin, 1981, pp. 57–108.

[11] Bolan N.S., A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants, Plant soil 134 (1991) 189–207.

[12] Borges R.A., Chaney W.R., Solar irradiance and the development of endomycorrhizal green ash seedlings, Tree Physiol. 13 (1993) 227–238.

[13] Clark D.B., Clark D.A., Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree, Biotropica 19 (1987) 236–244.

[14] Clark R.B., Zeto S.K., Mineral acquisition by mycorrhizal maize grown on acid and alkaline soil, Soil Biol. Biochem. 28 (1966) 1495–1503.

[15] Denslow J.S., Schultz J.C., Vitousek P.M., Strain B.R., Growth responses of tropical shrubs to treefall gap environments, Ecology 71 (1990) 165–179.

[16] Detienne P., Fouquet D., Parant B., Les bois guyanais : Propriétés et utilisation, Bois et Forêts des Tropiques 219 (1990) 125–143.

[17] Ducrey M., Influence of shade on photosynthetic gas exchange of 7 tropical rainforest species from Guadeloupe (French West Indies), Ann. Sci. For. 51 (1994) 77–94.

[18] Fetcher N., Oberbauer S.F., Chazdon R.L., Physiological ecology of plants, in: Mc Dade L.A., Bawa K.S., Hespenheide H.A., Hartshorn G.S. (Eds.), La Selva. Ecology and natural history of a neotropical rain forest, University of Chicago Press, Chicago and London, 1994.

[19] Fetcher N., Strain B.R., Oberbauer S.F., Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees, Oecologia (Berlin) 58 (1983) 314–319.

[20] Fitter A.H., Costs and benefits of mycorrhizas: implications for functioning under natural conditions, Experientia 47 (1991) 350–362.

[21] Fitter A.H., Garbaye J., Interactions between mycorrhizal fungi and other soil organisms, Plant and Soil 159 (1994) 123–132.

[22] Gallaud I., Étude sur les mycorhizes endotrophes, Revue Générale de Botanique 17 (1905) 5–48; 66–83; 123–135; 223–239; 313–325; 425–433; 479–500.

[23] Givnish T.J., Adaptation to sun and shade: a whole plant perspective, Aust. J. Plant Physiol. 15 (1988) 63–92.

[24] Grime J.P., Plant strategies and vegetation processes, John Wiley and Sons, Chichester, UK, 1979.

[25] Hayman D.S., Plant growth responses to vesicular-arbuscular mycorrhiza, Rothamstead Report for 1972, 1974, Part I, p. 94.

[26] Janos D.P., Vesicular-arbuscular mycorrhizas affect lowland tropical rain forest growth, Ecology 61 (1980) 151–162.

[27] Johnson N.C., Graham J.H., Smith F.A., Functioning of mycorrhizal associations along the mutualism-parasitism continuum, New Phytol. 135 (1997) 575–585.

[28] Kozlowski T.T., Kramer P.J., Pallardy S.G., The Physiological Ecology of woody plants, Academic Press, San Diego, CA, 1991, 657 p.

[29] Kramer P.J., Boyer J.S., Water relations of plants and soils, Academic Press, San Diego, CA, 1995, 495 p.

[30] Loach K., Shade toleerance in trees seedlings II: growth analysis of plant raised under artificial shade, New phytol. 69 (1970) 273–286.

[31] Marschner H., Dell B., Nutrient uptake in mycorrhizal symbiosis, Plant soil 159 (1994) 89–102.

[32] Mooney H.A., Winner W.E., Partitioning response of plants to stress, in: Mooney H.A., Winner W.E., Pell E.J., Chu E. (Eds.), Response of plants to multiple stresses, Academic Press, Inc., London, 1991, 422 p.

[33] Mooney H.A., Bjorkman O., Hall A.E., Medina E., Tomlinson P.B., The study of the physiological ecology of tropical plants, Current status and needs, BioScience 30 (1980) 22–26.

[34] Newman E.I., Reddell P., The distribution of mycorrhizas among families of vascular plants, New Phytol. 106 (1987) 745–751.

[35] Oldeman R.A.A., Architecture de la forêt guyanaise, Mémoire ORSTOM, n° 73, 1974.

[36] Pearson J.N., Smith S.E., Smith F.A., Effect of photon irradiance on the development and activity of VA mycorrhizal infection in *Allium porum*, Mycol. Res. 95 (6) (1991) 741–746.

[37] Peyronel B., Prime osservazioni sui rapporti tra luce e simbiosi micorrizica, Lab. Chanousia Giard, Bot. Alpino Piccolo San Bernardo, 4, I, 1940.

[38] Sabatier D., Prevost M.F., Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane française, Bois et Forêts des Tropiques 219 (1990) 31–55.

[39] Schmitt L., Bariteau M., Gestion de l'écosystème forestier guyanais. Étude de la croissance et de la régénération naturelle. Dispositif de Paracou, Bois et Forêt des Tropiques 220 (1990) 3–24.

[40] Smith H., Sensing the light environment: the functions of the phytochrome family, in: Kendrick R.E., Kronenberg G.H.M. (Eds.), Photomorphogenesis in plants, Kluwer Academic Publishers, Netherlands, 1994, 2d edn., pp. 377–416.

[41] Smith S.E., Gianinazzi-Pearson V., Phosphate uptake and arbuscular activity in mycorrhizal *Allium cepa* L.: effects of photon irradiance and phosphate nutrition, Aust. J. Plant Physiol. 17 (1990) 117–188.

[42] Smith S.E., Read D.J., Mycorrhizal symbiosis (2d edn.), Academic Press, Harcourt Brace and Company Publishers, 1997.

[43] Subramanian K.S., Charest C., Dwyer L.M., Hamilton R.I., Effects of arbuscular mycorrhizae on leaf water potentiel, sugar content and P content during drought and recovery of maize, Can. J. Bot. 75 (1997) 1582–1591.

[44] Tester M., Smith S.E., Smith F.A., Walker N.A., Effect of photon irradiance on the growth of shoots and roots, on the rate of initiation of mycorrhizal infection and on the growth of infection units in *Trifolium subterraneum* L., New Phytol. 103 (1986) 375–390.