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ORIGINAL PAPER

N.A. Onguene · T.W. Kuyper

Importance of the ectomycorrhizal network for seedling survival and ectomycorrhiza formation in rain forests of south Cameroon

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Abstract An investigation was undertaken at two sites in south Cameroon to assess the importance of living roots of adult trees as sources of inoculum for survival, ectomycorrhizal colonisation and growth of seedlings of *Paraberlinia bifoliolata*. One-month-old seedlings of *Paraberlinia bifoliolata*, isolated from or in contact with roots of adult target trees, were transplanted in concentric circles 5, 10, 15, and 30 m away from the stem bases of four adult tree species (*Afzelia bipindensis*, *Brachystegia cynometroides*, *Paraberlinia bifoliolata* and *Tetraberlinia bifoliolata*). After 4 and 8 months, survival, ectomycorrhiza formation and seedling height were observed; plant biomass was determined after 8 months. After 4 months, there was no difference in seedling survival between seedlings in contact with roots of adult trees and isolated seedlings. The number of ectomycorrhizal seedlings was higher among seedlings in contact with adult trees than among isolated seedlings. After 8 months, both seedling survival and ectomycorrhiza formation were higher in seedlings in contact with roots than in isolated seedlings. Seedling survival and ectomycorrhiza formation were highest under *Brachystegia*. The fraction of surviving seedlings that had formed ectomycorrhizas was lowest under *Afzelia*. The fraction of surviving seedlings that were ectomycorrhizal declined monotonically towards the edge of the crown projection. Biomass of seedlings in contact with adult trees was significantly higher than that of isolated seedlings. This difference was consistent for all four tree species. The height of seedlings did not vary with the treatment.

N.A. Onguene
Tropenbos Cameroon Programme, P.O. Box 219, Kribi, Cameroon

T.W. Kuyper (✉)
Subdepartment of Soil Quality, Wageningen University,
P.O. Box 8005, 6700 EC Wageningen, The Netherlands
e-mail: thom.kuyper@bb.benp.wag-ur.nl
Tel.: +31-317-482352, Fax: +31-317-483766

Present address:
N.A. Onguene,
Institute of Agricultural Research for Development (IRAD),
P.O. Box 2123, Yaoundé, Cameroon

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Introduction

Regeneration and recovery of tropical rain forests depends on the survival and establishment rates of young plants. As almost all trees of the tropical rain forest form mycorrhizas, survival and establishment rates of seedlings depend on the rate with which they become mycorrhizal (Janos 1980, 1996). The amount and activity of mycorrhizal inoculum able to withstand disturbance will then affect recovery rates. An important component of mycorrhizal inoculum is the intact mycorrhizal network (Smith and Read 1997). In the presence of a mycorrhizal network, by which plants of the same or different species are interlinked, seedling establishment can be enhanced if seedlings become more rapidly colonised. Whether species can be integrated in an existing mycorrhizal network depends on the degree of compatibility between mycorrhizal fungus and mycorrhizal plant. If plants become connected to a mycelial network larger than they could maintain on their own, this could be highly beneficial (Newman 1988; Perry et al. 1992).

It has been suggested that rapid and early integration of seedlings into adult mycorrhizal root systems has potential benefits in terms of carbon transfer from donor- to receiver plants (Simard et al. 1997a). Carbon transfer to seedlings of subordinate plants could maintain species diversity (Grime et al. 1987) or enhance seedling survival under mother trees. Yasman (1995) suggested that such mother trees effectively function as nurse trees by enabling seedling maintenance under conditions below the light compensation point. However, the issue of carbon transport, in ecologically significant amounts, from donor- to receiver plants has remained highly controversial (Robinson and Fitter 1999).

The rain forest of south Cameroon consists predominantly of arbuscular mycorrhizal trees, but local patches dominated by ectomycorrhizal trees occur regularly

(Newbery et al. 1988, 1997, 2000; Onguene and Kuyper 2001). These patches probably arise because of the very low dispersal capacity of the ectomycorrhizal symbiosis, as the legume seeds do not possess a dormancy mechanism and the fungal propagules have no capacity to survive saprotrophically. Establishment of seedlings of ectomycorrhizal trees in such patches could be facilitated in the presence of the ectomycorrhizal network in which the seedlings become integrated.

Only few studies on the functioning of ectomycorrhizal networks have been carried out in tropical rain forest areas. In Malaysia, Alexander et al. (1992) observed that the dual mycorrhizal tree *Intsia palembanica* Miq. (Caesalpiniaceae) became more rapidly mycorrhizal when in direct contact with the roots of mature *Shorea leprosula* Miq. (Dipterocarpaceae) than when isolated from mature trees. They concluded that early infection of seedlings would be much enhanced if seedlings were in contact with living ectomycorrhizal roots, a point that should be recognised in sustainable forest management programmes. In Korup National Park, southwest Cameroon, Newbery et al. (2000) found that proximity to conspecific adult trees enhanced seedling survival in one ectomycorrhizal legume tree, but not in two other tree species.

The objectives of this present investigation were to assess the importance of living roots of adult trees as sources of inoculum for seedling survival and ectomycorrhiza formation in rain forests of south Cameroon. Growing seedlings in concentric circles at increasing distances from the stem base of conspecific and confamilial ectomycorrhizal adult trees allowed us to determine the distribution of ectomycorrhizal inoculum around the stem base and the optimal distance to trail logs without disturbing or destroying ectomycorrhizal mycelia. The use of four different tree species (one family, two tribus, four genera) provided information on the role of ectomycorrhizal specificity in maintaining these networks.

Materials and methods

Study site

Two field sites of the Tropenbos Cameroon Programme (TCP) research area were selected in Ebimimbang and Ebom, South Province, Cameroon. Ebimimbang (3°02′N; 10°28′E) is located about 80 km east of Kribi, in the southwest lowlands (80–200 m a.s.l.) of the TCP area. Soils are sandy clay loam (40–60% clay), pH(H_2O) 6.1 and poor in available phosphorus (0.01 µg P in H_2O ml^{-1} soil). Ebom (3°06′N; 10°44′E) is situated 34 km farther northeast, on a rolling landscape (350–500 m a.s.l.). Soils are clayey (60–80% clay), pH(H_2O) 4.7 and very poor in available phosphorus (0.005 µg P in H_2O ml^{-1} soil). Annual rainfall in the area varies between 1,500 and 2,000 mm, average monthly temperatures vary between 23°C and 27°C. Relative humidity is generally above 80%. At both sites, forests are under intense human influence, both shifting agriculture and selective logging (Van Gemerden and Hazeu 1999; Onguene and Kuyper 2001).

Field bioassays

At the Ebom site, one large specimen of *Afzelia bipindensis* Harms and one of *Brachystegia cynometroides* Harms, and at the Ebimimbang site, one large tree of *Paraberlinia bifoliolata* Pellegr. and one of *Tetraberlinia bifoliolata* (Harms) Hauman were selected on flat terrain. The generic names will be used in this report. All tree genera belong to the Caesalpiniaceae; *Brachystegia*, *Paraberlinia* and *Tetraberlinia* belong to the exclusively ectomycorrhizal tribe Amherstieae and the dual mycorrhizal tree *Afzelia* belongs to the predominantly arbuscular mycorrhizal tribe Detarieae (Alexander 1989). *Afzelia* was located in an early successional forest stand. The other adult trees were found in old successional forest stands. Light conditions under the various adult trees were not measured.

Around each test tree, four concentric circles were laid out at a distance of 5, 10, 15, and 30 m from the stem base. On each circle, 40 1-month-old seedlings of *Paraberlinia* were transplanted beneath each target adult tree, either isolated inside a PVC tube (15 cm in diameter and 45 cm long) or in contact with roots of selected adult trees. Isolated seedlings and those in contact with roots were planted about 50 cm apart. Seeds were collected under a seed-bearer tree in Ebimimbang and seedlings were raised in sterilised, washed sea-sand in a greenhouse in Kribi, Cameroon (2°57′N; 9°59′E). Before transplanting, all seedlings lacked ectomycorrhizal colonisation as determined with a hand lens (10×). Seedlings were transplanted in the period 26 November to 2 December 1998, which corresponds to the end of the long rainy season. Seedlings were watered twice a week from January to April 1999 and harvested on 7–9 April and 7–9 August 1999. At each harvest, the survival rate was determined by counting the number of living seedlings. Ten isolated seedlings and 10 others in contact with roots of adult trees were harvested. Pairs of seedlings (one in contact and one isolated) were randomly selected at the start of the experiment. In the field, height was measured from the stem collar to the point of insertion of the youngest fully expanded leaf. At the second harvest, shoot dry weight was determined after drying the shoots at 70°C for 72 h. The root system was separated from the shoots. As collecting fine roots of the seedlings was difficult in these clayey soils, it was not possible to determine the number of ectomycorrhizas per seedling. Root samples were washed free of soil debris and placed in a large glass dish in water. Five selected root tips were examined for the presence of ectomycorrhizal colonisation using a dissecting microscope (40×) and a microscope (100–400×) after mounting in water between a slide and a cover glass and squashing.

Statistics

Effects of treatment (seedlings in contact with or isolated from roots of adult trees), distance (5, 10, 15, 30 m), tree species (*Afzelia*, *Brachystegia*, *Paraberlinia*, *Tetraberlinia*) and site (Ebimimbang versus Ebom) were tested with the likelihood ratio test (*G* test in Sokal and Rohlf 1995), which is approximately distributed as chi square. It should be noted that the factor site was not independent of the factor tree species (different tree species at both sites).

Results

Four months after outplanting, the majority of seedlings (75%) had survived, independent of treatment and tree species. There was a significant effect of distance; the number of seedlings surviving at 30 m was by far the lowest. The number of seedlings with ectomycorrhizas was significantly affected by treatment (twice as many in-contact seedlings as isolated seedlings), distance (the number was highest at 15 m), and tree species (the number was highest under *Brachystegia* and lowest under *Afzelia*). Only 25% of surviving seedlings growing under *Afzelia* had formed ectomycorrhizas, compared with 85% under *Brachystegia* (Table 1).

Table 1 Effect of treatment, distance, tree species and site on number of seedlings of *Paraberlinia bifoliolata* surviving and forming ectomycorrhizas 4 months after transplantation

		Survival	Ectomycorrhiza
Treatment (*df* 1)	In contact	116	85
	Isolated	129	42
	G statistic	0.69	10.80
	P	n.s.	**
Distance (m) (*df* 3)	5	80	30
	10	60	20
	15	72	54
	30	33	23
	G statistic	22.72	20.64
	P	***	***
Tree (*df* 3)	*Afzelia*	60	15
	Brachystegia	70	60
	Paraberlinia	60	30
	Tetraberlinia	55	22
	G statistic	1.90	34.34
	P	n.s.	***
Site (*df* 1)	Ebimimbang	115	52
	Ebom	130	75
	G statistic	0.92	4.19
	P	n.s.	*

*0.01≤P≤0.05, **0.001≤P≤0.01, ***P≤0.001, n.s. not significant

Table 2 Effect of treatment, distance, tree species and site on number of seedlings of *Paraberlinia bifoliolata* surviving and forming ectomycorrhizas 8 months after transplantation

		Survival	Ectomycorrhiza
Treatment (*df* 1)	In contact	107	63
	Isolated	59	24
	G statistic	14.08	18.12
	P	***	***
Distance (m) (*df* 3)	5	35	35
	10	58	37
	15	29	10
	30	44	5
	G statistic	12.26	42.38
	P	**	***
Tree (*df* 3)	*Afzelia*	42	14
	Brachystegia	55	40
	Paraberlinia	44	19
	Tetraberlinia	25	14
	G statistic	11.93	18.93
	P	**	***
Site (*df* 1)	Ebimimbang	69	33
	Ebom	97	54
	G statistic	4.75	5.12
	P	*	*

*0.01≤P≤0.05, **0.001≤P≤0.01, ***P≤0.001, n.s. not significant

Eight months after outplanting, survival of in-contact plants was significantly higher than survival of isolated plants. Effects of distance (highest survival at 10 m and lowest at 15 m) and tree species (lowest survival under *Tetraberlinia* and highest survival under *Brachystegia*) were also significant. The effects of treatment, distance, and tree species on the number of seedlings that formed ectomycorrhiza were all significant. A larger number of seedlings in contact with adult trees had formed ectomycorrhizas than isolated seedlings. More seedlings had formed ectomycorrhizas at 5 and 10 m than at 15 and 30 m. The fraction of surviving seedlings with ectomycorrhiza declined strongly with distance from the adult tree, from 100% at 5 m to 11% at 30 m. Again, the number of seedlings that had formed ectomycorrhizas was highest under *Brachystegia* and lowest under *Afzelia*. The fraction of surviving seedlings with ectomycorrhiza was also dependent on the tree species, being again highest under *Brachystegia* (73%) and lowest under *Afzelia* (33%) (Table 2).

The mean dry weight of surviving seedlings in contact with roots of the adult plant was on average 35% higher than for isolated plants (1.87±0.70 versus 1.39±0.39 g; T=5.68; P<0.001). These differences were consistent for the four tree species. Surviving plants under *Paraberlinia* and *Tetraberlinia* had higher dry weights than those under *Brachystegia* and *Afzelia* (Table 3). Heights of surviving seedlings in contact with or isolated from roots of an adult plant were the same (22.3±3.8 versus 21.2±8.0 cm; T=1.20; P>0.2). Mean weight of seedlings growing in contact with adult trees was not significantly different between ectomycorrhizal and non-mycorrhizal plants (1.89±0.70 versus 1.85±0.71 g; T=0.29; P>0.5), but seedlings that had formed ectomycorrhizas were significantly larger (23.4±4.3 versus 20.7±2.2 cm; T=3.83; P<0.001).

Table 3 Shoot biomass (g) of surviving seedlings of *Paraberlinia bifoliolata* in contact with or isolated from the root system of different adult tree species after 8 months

	In contact	Isolated	Significance
Afzelia	1.59±0.36	1.16±0.25	*
Brachystegia	1.48±0.50	1.24±0.32	*
Paraberlinia	2.43±0.81	1.52±0.47	*
Tetraberlinia	2.19±0.57	1.78±0.08	*

*Significant difference (P≤0.05) according to a *t* test

Discussion

A higher number of seedlings in contact with roots of adult trees survived and formed ectomycorrhizas than isolated seedlings. This effect was greater after 8 months than after 4 months. Our data confirm the importance of the ectomycorrhizal network in a tropical rain forest for regeneration of ectomycorrhizal trees, as suggested by Alexander et al. (1992). They noted with *Intsia palembanica* that half of the plants isolated from the adult tree remained without ectomycorrhiza 6 months after outplanting. This is slightly lower than our result of 65%. They also observed delays in colonisation of seedlings isolated from roots of parent trees of 5–6 months.

Two other methods have been applied to study the importance of the ectomycorrhizal network. Newbery et al. (2000) outplanted ectomycorrhizal legume tree seedlings of three different species at sites with a high or low basal area of ectomycorrhizal trees. Seedlings of *Tetraberlinia bifoliolata* showed higher survival at sites with a higher basal area of ectomycorrhizal trees, whereas there was no difference in survival for *Tetraberlinia moreliana* Aubr. or *Microberlinia bisulcata* A. Chev. Biomass of seedlings of *T. moreliana* increased over time, whereas that of the other two species decreased. The authors found only limited support for the hypothesis that survival and growth of seedlings of ectomycorrhizal tree legumes is higher at sites with a higher basal area of ectomycorrhizal trees. However, three further ectomycorrhizal tree legumes (and one other ectomycorrhizal tree species) occurred at the sites reported as having a low basal area of ectomycorrhizal trees. Thus, the ectomycorrhizal inoculum may have been sufficiently high at all sites to mask the importance of the ectomycorrhizal network provided by the conspecific adult trees at the sites with a high basal area of ectomycorrhizal trees. Simard et al. (1997b) applied trenching in a temperate, mixed forest to study the importance of the ectomycorrhizal network. Here, the presence of an intact ectomycorrhizal network resulted in seedlings with higher photosynthetic rates than seedlings in the trenched treatment. Mycorrhizal diversity was also greater when seedlings were in contact with (untrenched treatment) instead of isolated from (trenched treatment) overstorey conspecific trees. However, trenching may affect soil water and nutrient availability and this could have a greater effect than isolation from overstorey trees.

Most ectomycorrhizas are located in the uppermost 5 cm of the soil. Thus, the length of the PVC tubes used (45 cm) made it unlikely that colonisation of isolated seedlings occurred after they emerged from the bottom of the tubes. Data from adult trees obtained by Moyersoen et al. (1998) suggest that over 80% of fine root biomass and ectomycorrhizal abundance is located in the upper 10 cm, while Newbery et al. (2000) noted that the ectomycorrhizas of the legume tree seedlings were all in the upper mineral layer. Colonisation by ectomycorrhizal fungi of seedlings isolated from adult trees is most likely due to fungal propagules already present in the soil or introduced through spore rain. Fleming (1983, 1984) and Simard et al. (1997b) showed that seedlings isolated from roots by trenching acquired mycorrhizal fungi different from those in contact with living roots. In the present study, the identity of the ectomycorrhizal morphotypes was not determined.

While in the investigations of Alexander et al. (1992) seedlings and adult trees belonged to different families, our experiment also allowed an independent evaluation of host tree specificity. Onguene (2000) showed that trees of *Afzelia* and of *Tetraberlinia* to some extent experienced different ectomycorrhizal inoculum potentials in the same soil. While ectomycorrhizal inoculum potential increased during forest succession, when seedlings of *Tetraberlinia* were used as bait plant, no consistent change in inoculum potential was observed with *Afzelia* seedlings. This difference could be related to their ecology; *Afzelia* easily establish as isolated trees in early successional sites and *Tetraberlinia* are almost completely dependent on the existence of clumps of ectomycorrhizal trees. These ecological differences suggest that both trees are colonised by (or respond differentially to) different ectomycorrhizal fungi. The data reported here are consistent with these observations, as the number of ectomycorrhizal seedlings (and the fraction of surviving seedlings with ectomycorrhiza) were lower for seedlings planted under *Afzelia* than under the three other genera.

Surprisingly, the number of ectomycorrhizal seedlings (and the fraction of surviving seedlings with ectomycorrhiza) was not highest under a conspecific tree (*Paraberlinia*) but under a different species (*Brachystegia*) that belongs to the same tribe Amherstieae. Differential survival could be due to differences in the light environment under the various trees. We did not measure light availabilities under the mature trees but consider this explanation unlikely, as seedlings planted under *Paraberlinia* were heavier than those planted under the other legume trees. Alternatively, lower survival of seedlings under a mature conspecific tree could be related to the Janzen-Connell model of tree spacing. According to this model, tree seedling survival is less under parent trees because of host-specific predation and parasitism, which results in a disproportionally high mortality under conspecifics (Janzen 1970; Connell 1971; Clark and Clark 1984). This model has an interesting implication for the importance of ectomycorrhizal networks in carbon transport between adult and juvenile plants. If the Janzen-Connell model applies, there is a higher chance that carbon flows to non-conspecific trees than to conspecific seedlings (or even seedlings that are direct progeny of the adult tree), i.e. there are better chances for cheaters (seedlings that take carbon in the seedling stage without donating carbon when adult).

A higher number of seedlings survived and formed mycorrhiza at Ebom than at Ebimimbang. As different species were used as adult trees at the two sites, it is possible that the site effect is related to the species present.

After 8 months, the fraction of tree seedlings that became ectomycorrhizal declined monotonically with distance from the stem base. Seedling survival, on the other hand, showed no such consistent pattern with distance from the stem base. It is possible that seedling survival depends both on the amount of ectomycorrhizal mycelium (being highest close to the tree) and on the intensity of competition (both root density and light conditions are apparently more favourable for survival at the edges of the crown projection). Seedling survival and ectomycorrhiza formation at 30 m may also have been affected by neighbouring trees. Other ectomycorrhizal tree species were recorded in the vicinity of the trees studied. A mature *Tetraberlinia* was noted in the vicinity of the adult tree of *Paraberlinia*, a mature *Uapaca* and a mature *Afzelia* near the adult *Tetraberlinia* and a mature *Berlinia* near the mature tree of *Brachystegia*. These surrounding trees may also have affected the colonisation of some seedlings at 30 m from the stem base.

Smits (1994) outplanted non-mycorrhizal seedlings of *Shorea assamica* Dyer at different distances from mature trees of various dipterocarps (both congeneric and of different genera). Survival was independent of distance to the stem base. Surprisingly, after 1 year none of these surviving plants possessed any ectomycorrhizas. Smits concluded that there is a high degree of ectomycorrhizal specificity for certain host trees as seeds of a conspecific tree became very rapidly ectomycorrhizal. Our results, like those of Alexander et al. (1992), do not support this observation. The question of host-tree selectivity has potentially large practical implications for sustainable management of ectomycorrhizal timber species. If host-tree selectivity is high, regeneration should be carried out under conspecific parent trees. In the case of *Afzelia*, which yields a highly priced timber, this question of specificity or selectivity needs future attention.

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