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Short communication

Ectomycorrhizal colonization and seedling growth of *Shorea* (Dipterocarpaceae) species in simulated shade environments of a Sri Lankan rain forest

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Abstract

The purpose of our study was to examine whether the degree of ectomycorrhizal (EM) colonization was associated with amount of shade for potted seedlings of five rain forest tree species. Seedlings were exposed to a range of shade treatments—from the open to that emulating the degree of shade beneath a deep-canopied forest. The experiment was carried out at the field station (580 m.a.s.l) of the Sinharaja World Heritage Site in southwestern Sri Lanka. We selected five species for the study: *Shorea affinis* (Thw.) Ashton, *S. congestiflora* (Thw.) Ashton, *S. cordifolia* (Thw.) Ashton, *S. gardneri* (Thw.) Ashton, and *S. zeylanica* (Thw.) Ashton, all members of a sympatric clade of endemic canopy trees in the family dipterocarpaceae. Results show that the percentage EM colonization was significantly different among shade treatments, for all five species ($p < 0.05$). However, EM root colonization was not significantly different among species. Highest percentages of EM colonization for all species, except for *S. congestiflora*, were in treatments providing full open conditions. However, seedling growth of all species were best under partial shade conditions ($p < 0.05$), intermediate between the deep shade of a forest understory and no shade of open environments. The non-linear relationship between seedling growth performance and EM colonization is discussed.

Keywords: Dipterocarps; Ectoycorrhizae; Light; Rain forest; Shade; *Shorea*; Sinharaja; Sri Lanka

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1. Introduction

The Dipterocarpaceae, of which *Shorea* is a member genus, is a tree family that dominates the canopies of rain forests in South and Southeast Asia. Dipterocarps show ectomycorrhizal associations

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(Singh, 1996; de Alwis and Abenayake, 1980; Becker, 1983; Smits, 1983; Alexander and Hogberg, 1986; Alexander et al., 1992; Louis, 1988). The mycorrhizal associations of *Shorea* appear to be obligately symbiotic (Smits, 1983, 1992). *Shorea* spp. (*S. leprosula* (Miq.)) may have as many as 23 mycorrhizal types of which individual seedlings can have as many as five at any one time (See and Alexander, 1996).

Some studies have investigated the effects of soil nutrition on the growth of *Shorea* spp. in relation to ectomycorrhizal colonization. The level of ectomycorrhizal colonization of *Shorea* spp. shows a closer correlation with growth and survival of unfertilized seedlings than those that were fertilized (Turner et al., 1993). This suggests that ectomycorrhizal (EM) associations may be of greater importance to seedlings growing in low nutrient conditions. However, the relative importance of shade on EM formation has not been quantitatively determined in dipterocarps that dominate the rain forests in tropical Asia.

Ectomycorrhizal fungi derive their carbon requirements from symbiotically associated plant hosts (Simard et al., 1997). The EM formation and function in tropical forest plant communities must therefore be influenced by light availability. Becker (1983) reported increased rates of mycorrhizal colonization with seedlings regenerating in openings of a forest canopy as compared to those in the understorey. The purpose of our study was to examine this phenomenon further under controlled shade conditions in artificial shelters. We tested whether the degree of ectomycorrhizal colonization of potted seedlings of five *Shorea* spp. was associated with the amount and quality of daily photosynthetic photon flux density (PFD). We also investigated the combined effects of ectomycorrhizal root colonization and PFD on the growth of these potted seedlings.

2. Methods

2.1. Site description

The experiment was carried out at the field station (580 m.a.s.l.) of the Sinharaja World Heritage Site in southwestern Sri Lanka (6° 22′N, 80° 22′E). The forest in this region has been classified as a *Mesua-Doona* community (de Rosayro, 1942) of the Mixed Dipterocarp Forest Type (Gunatilleke and Gunatilleke, 1981; Gunatilleke and Ashton, 1987). This forest region receives an annual rainfall of 5016 mm, with little seasonality, and annual minimum and maximum temperatures of 22 and 28 °C (Munidasa et al., 2002). The topography is steeply undulating with metamorphic rocks overlain with ultisols (USDA, 1975; Cooray, 1984; Panabokke, 1996).

2.2. Experimental design

We selected five plant species for the study: *Shorea affinis* (Thw.) Ashton, *S. congestiflora* (Thw.) Ashton, *S. cordifolia* (Thw.) Ashton, *S. gardneri* (Thw.) Ashton, and *S. zeylanica* (Thw.) Ashton. All are members of a sympatric clade of endemic species of Section *Doona*, *Shorea* (Ashton, 1977; Gunatilleke et al., 1998). *Shorea congestiflora* is a dominant canopy tree at lower elevations (50–300 m). *Shorea affinis* and *S. cordifolia* have wider elevational ranges from 50–700 m. While *S. zeylanica* has an altitudinal range of about 600–900 m *S. gardneri* is the dominant canopy species at elevations between 900 and 1600 m (Ashton, 1977).

Mature fruits were collected from all *Shorea* spp. during the 1989 mast fruiting year. Seeds from the different individuals of a species were pooled and planted in a shaded nursery bed for 1 month. Healthy and uniformly grown seedlings were transferred to pots containing forest topsoil taken from a single location in a valley. Only the upper mineral soil was collected and mixed with humus from the litter layer. Pots were black cylindrical polythene containers of diameter 15 cm and height 30 cm with a soil volume of 5 L. Soils were characterized as ultisols (USDA, 1975) and described along a catena by Gunatilleke et al. (1996). The soils in the pots had percentage concentration of 2.18% total N, and total concentration of mineral nutrients that included Mg 0.73 mg g^{-1}, K 0.63 mg g^{-1}, P 0.35 mg g^{-1}, and Ca 0.09 mg g^{-1} (see Gunatilleke et al. (1996) for details of soil analysis).

Seedlings of each species were grown in these pots for two years under well-watered conditions in five different shade treatments each in a separately constructed shelter (sensu Ashton, 1995). Treatments simulated a range of shade environments that had been previously measured at the ground surface of 32–45 m high rain forest (Ashton, 1992).

Shade treatments included (i) DS—deep shade (95% shade; R: FR ratio 0.46; 1.1 mols $m^{-2}d^{-1}$); (ii) LS—light shade (82% shade; R: FR ratio 0.97; 5.8 mols m^{-2} d^{-1}); (iii) SD—short duration direct light (2 h direct sunlight; R: FR ratio 1.27; 7.2 mols m^{-2} d^{-1}); (iv) LD—long duration direct light (6 h direct sunlight; R: FR ratio 1.27; 13.2 mols m^{-2} d^{-1}); and (v) FS—full sun (0% shade; R: FR ratio 1.27; 40 mols m^{-2} d^{-1}). For treatments (i.e. DS, LS) that simulated different shade qualities (red to far red ratio (R:FR)) and intensities (photosynthetic photon flux density (PFD) measured as mols m^{-2} d^{-1}), a ratio of paint pigment in a varnish base was sprayed on to clear plastic film covering a shelter (see Lee, 1985; Ashton and Berlyn, 1992; Ashton, 1995). The treatment (i.e. FS) with full sun conditions had a shelter that was covered in clear plastic film only. Treatments (i.e. SD, LD) that exposed seedlings to a specific duration of direct sunlight were created by erecting parallel slats that were vertically aligned north-south to each other. The duration was controlled by the width apart and the depth of the slats (for details see Ashton, 1995).

The pots were placed on a plastic lining to prevent any root contact from the pots with the ground of the shelter. Soil moisture was maintained as close to saturation as possible by regular watering. Any excess water from watering drained into the ground via the perforations made in the plastic container.

One hundred seedlings of each species were assigned to four equal groups within a single shade treatment. Because only one shelter was used for each shade treatment, limitations from pseudo-replication were reduced by the large number of seedlings used in each shade treatment and the extended period (two years) of the experiment (Hurlbert, 1984). Each main treatment (shade) therefore, included five subtreatments (species). A total of 2500 seedlings (100 seedlings × 5 species × 5 light treatments) were monitored over the duration of the experiment.

Shoot growth was determined by measurements of height to the tip of the leader at the time of transplanting into pots, and thereafter measuring at bi-monthly intervals for 2 years. After 2 years, twelve seedlings per species and treatment (three from each seedling group per shelter) were randomly selected for mycorrhizal examination. A power test and data from previous studies (Ashton, 1995; Gunatilleke et al., 1998) showed that a destructive sample of twelve seedings per treatment and species was adequate. Seedling root systems were removed carefully from the soil. When plant roots were removed from their pots for ectomycorrhizal counts at the end of the experiment, no evidence of pot-binding could be found. Furthermore, the periodic shoot growth measurements indicated that at the end of two years seedlings were still increasing in height logarithmically, suggesting no evidence of root confinement inside the pots. Roots were then washed and taken to the University of Peradeniya for analysis. The entire root system of a seedling was spread on trays and the total number of root tips and mycorrhizal short tips were counted with a hand lens to determine the ectomycorrhizal colonization. The colonization was confirmed to be ectomycorrhizal from gross morphology and microscopic observations of mantle and Hartig net development in microtome transverse sections of random root segments (Tennakoon, 1996; Agerer, 1986).

In this study mycorrhizae were not identified to different morphotypes. Other studies have shown that there may be differences in fungal species associations that were not measured in this study and that should be considered in a future investigation.

2.3. Data analysis

Analysis of variance (ANOVA) was performed to determine the linear response of EM formation and shoot growth to shade. Analyses were carried out with shade as a covariate, using the statistical analysis system (SAS) (Little et al., 1991). Inverse sine transformations (arcsine) were carried out as suggested by Steel and Torrie (1980) on the percentage ectomycorrhizal colonization data because they covered a wide range of values. As a result of seedling mortality under certain shade treatments, an unbalanced ANOVA using the GLM procedure of SAS was performed on the height data. All height data were log-transformed prior to analysis.

3. Results

The percentage EM colonization was significantly different among shade treatments for each species

Table 1
(a) Mean percentage of ectomycorrhizal root colonization; and (b) mean heights for five *Shorea* species grown for 2 years in different shade treatments

	DS	LS	SD	LD	FS
(a) Percent ectomycorrhizal colonization					
S. affinis	0.5d	9.9c	18.1b	17.2b	72.0a
S. congestiflora	11.6c	36.7ab	47.8a	26.1b	39.2a
S. cordifolia	16.6c	26.4b	19.2bc	38.7a	46.1a
S. gardneri	8.3c	19.9b	17.1b	28.7a	37.8a
S. zeylanica	28.2bc	32.3b	15.1c	49.3a	55.2a
(b) Height (cm)					
S. affinis	14.0d	22.5c	35.5b	94.6a	39.3b
S. congestiflora	8.3c	25.7a	27.5a	22.7ab	15.7b
S. cordifolia	12.6b	10.8b	24.3a	25.7a	24.7a
S. gardneri	17.5b	32.5a	23.0b	31.7a	19.0b
S. zeylanica	22.7c	31.0c	53.3b	82.3a	31.3c

DS—deep shade; LS—light shade; SD—short duration of direct light; LD—long duration of direct light; FS—full sun. Letters denote significant differences in performance among light treatments for each species at the $p < 0.05$ level, based on Tukey's honest significant difference test. Treatments followed by the same letter are not significantly different. Analyses were made on log-transformed data for heights and on inverse sine transformed data for ectomycorrhizal colonization.

($p < 0.05$; Table 1a). However, EM root colonization was not significantly different between any of the species examined. For *S. congestiflora,* percent EM colonization was highest in the full-sun (FS) and short duration of direct sunlight (SD). *S. cordifolia, S. gardneri* and *S. zeylanica* exhibited highest colonization of EM in the brightest treatments (LD, FS). However, EM colonization in *Shorea affinis* was the highest solely in the full sun (FS) (Table 1a).

Shorea spp. had varying *r*-squares for linear regressions predicting percent EM colonization from amount of shade (Fig. 1a). Greatest *r*-squares were for *S. affinis* ($r^2 = 0.98$), followed by *S. gardneri* ($r^2 = 0.82$), *S. cordifolia*($r^2 = 0.77$), *S. zeylanica* ($r^2 = 0.57$) and lastly for *S. congestiflora* ($r^2 = 0.13$).

Significant differences were evident in shoot growth of seedlings among the shade treatments ($p < 0.05$) and among species ($p < 0.01$; Table 1b). Seedling height growth of any given species was best under any treatment that provided partial shade (LS, SD, LD). Growth of *S. affinis* and *S. zeylanica* was highest in the LD treatment. *S. gardneri* had highest shoot growth in both LD and LS shade treatments. *S. congestiflora* had greatest shoot growth in a range of partial shade treatments (LS, SD, LD) (Table 1b). *Shorea cordifolia* showed best shoot growth in the broadest range of shade conditions including full-sun (FS). Shoot growth was lowest in the deep shade (DS) treatment for all species.

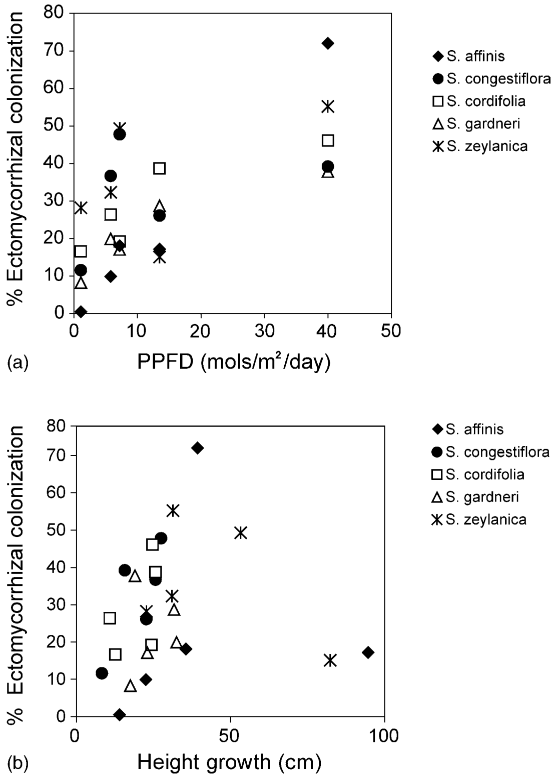

Fig. 1. Relationship between, (a) ectomycorrhizal (EM) root colonization and photosynthetic photon flux density (PPFD); and (b) EM root colonization and shoot growth, of five *Shorea* species raised in different shade qualities and quantities under simulated conditions.

The only significant linear regression (as depicted by the *r*-square) predicting height growth from percent EM colonization was shown by *S. congestiflora* ($r^2 = 0.60$) (Fig. 1b). All the other species showed very weak relationships predicting height growth from percent EM colonization (*S. affinis* $r^2 = 0.02$; *S. cordifolia* $r^2 = 0.17$; *S. gardneri* $r^2 = 0.02$*; S. zeylanica* $r^2 = 0.03$).

4. Discussion

Our findings support Becker's (1983) field observations that EM colonization is higher for seedlings growing in more exposed environments that receive greater amounts of PFD and higher light quality. In contrast to the findings of Smits (1992), our study showed that seedlings grown under full sun and regular watering enhanced root colonization, perhaps as a result of the fungal partners' ability to utilize the higher amount of photosynthate that the host seedlings could produce under brighter light conditions (Bücking and Heyser, 2001). These results also suggest that mycorrhizae could be a carbon drain on a seedling when grown under deep shade conditions and that host plants tend to dispense with mycorrhizae when growing in shade environments in which net carbon balance, rather than nutrients or moisture, limits growth and survival (Bücking and Heyser, 2001).

Previous studies have also demonstrated that for several other species of *Shorea* section *Doona*, best growth environments are those that provide partial shade (Ashton and Berlyn, 1992, Ashton, 1995). These species appear to adjust their photosynthetic induction periods favourably according to their successional status and the duration of exposure to light (Kuppers et al., 1996). Differences in height growth among species may be a reflection of habitat preferences; two of the species examined (*S. gardneri* and *S. zeylanica*) are lower-montane species and *S. congestiflora* is dominant at lower altitudes (Gunatilleke et al., 1998; Ashton et al., 1995; Ashton, 1977).

Our results also suggest that degree of colonization is not necessarily associated with height growth in the majority of the species examined. An exception was *S. congestiflora* where EM colonization appeared more directly associated with height growth. In this case fungal symbionts may stimulate seedling net photosynthesis and increase shoot growth (Colpaert et al., 1996). The use of soils from one single locality may also have had an effect on EM colonization particularly if host species come from different habitats than that locality. For example, fungal symbionts are known to form specific linkages to facilitate bi-directional transfer of photosynthates between trees, and even species in their natural habitats (Bücking and Heyser, 2001; Simard et al., 1997).

The high degree of EM colonization associated with seedlings growing in the brighter light treatments might be a reflection of a response of seedling exposure to greater environmental stress. For example, in full sun, seedlings are more susceptible to desiccation. We speculate that in open conditions, the greater availability of water made possible to the host seedlings by their symbiotic relationship with the fungus may facilitate higher survival as a trade-off to enhanced growth. Under partial shade in a forest canopy gap, seedlings might have a relatively lower level of this symbiotic activity during regeneration establishment than in the full sun. The presence of well established EM colonization in all root sections examined suggests that the symbionts may help maintain an enhanced sink strength of the host roots thereby increasing the host's survivorship (Ziegler, 1975). Other factors such as nutrient foraging ability of the associated fungal symbionts could also affect positive growth responses to colonization.

These five *Shorea* spp. seem to differ in their autecology as an adaptation to their habitat preferences in the Sri Lankan rain forests (Gunatilleke and Ashton, 1987; Ashton, 1995; Ashton et al., 1995; Gunatilleke et al., 1998, Ashton et al., 2001). We do not know the nature of the host fungal associations in natural communities that exist in this partially sympatric and ecologically heterogeneous clade of host species and how this may have affected our present experimental outcome. Further, there may have been differences between the fungal composition of the experimental soil and those of the hosts in their natural habitats. Future investigations on the EM fungal symbiont composition of this host tree genus on which a considerable amount of autecological (Ashton et al., 1995; Ashton and Berlyn, 1992; Gunatilleke et al., 1996, 1998) and phylogenetic information (Dayanandan et al., 1999; Tsumura et al., 1996) is available and their genetic and functional compatibilities may throw further light on symbiotic contribution to their niche partitioning potential.

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