

The significance of mycorrhizal diversity of trees in the tropical mountain forest of southern Ecuador

Abstract

Rootlets were sampled in the mountain rain forest of southern Ecuador from individual trees of 115 species in order to investigate the mycorrhizal state. The results show that the arbuscular mycorrhization predominates and is independent from the soil type supporting the high diversity of trees on mineral soil in the ravines as well as on the thick humus layer on the mountain ridge. The Melastomataceae *Graffenrieda emarginata* is associated with arbuscular mycorrhizas and additionally forms ectomycorrhizas regularly with an ascomycete closely related to the ericoid mycorrhizal fungus *Hymenoscyphus ericae*. The latter was shown to mobilize organically bound nutrients. *G. emarginata* is the most frequent tree on the mountain ridges where root formation is restricted to the pure organic soil layer. The ectomycorrhizal state is most probably improving nutrient uptake from the humus layer and thus supporting the competitiveness of this tree species. One *Guapira* sp. and one *Neea* sp. (Nyctaginaceae) form ectomycorrhizas with one theleporacean basidiomycete only. *Guapira* and this *Neea* species root in the mineral soil of the nutrient rich slopes and the ecological implication of the ectomycorrhiza is estimated to be low. Another *Neea* species forms typical ectomycorrhizas with several basidiomycetes and one ascomycete quite abundantly. This *Neea* occurs on the border of the primary forest, along old roadsides and the main river slopes demonstrating an improved stress resistance by regular ectomycorrhiza formation. Keywords: arbuscular mycorrhiza, ectomycorrhiza, humus, neotropics, *Hymenoscyphus*

Resumen

Raíces de 115 especies arbóreas del bosque montano lluvioso en el Sur de Ecuador fueron muestreadas en orden a investigar su estado de micorrización. Los resultados muestran el dominio de la micorrización arbuscular siendo independiente al tipo de suelo que soporta la alta diversidad de árboles en el suelo mineral en las quebradas, así como también en la gruesa capa de humus en la cima de las cordilleras. La Melastomataceae *Graffenrieda emarginata* es asociada con arbuscular micorrizas, y adicionalmente forma ectomicorrizas regularmente con un ascomycete estrechamente relacionado a el hongo ericoid micorrízico *Hymenoscyphus ericae*. Este último fue demostrado movilizar nutrientes orgánicamente unidos. *G. emarginata* es el árbol más frecuente en la cima de las montañas donde la formación de las raíces es restringida a la capa de suelo orgánico. El estado de micorrización probablemente fomenta la absorción de nutrientes desde de la capa de humus y así mejora la competencia de estas tres especies. Una *Guapira* sp. y una *Neea* sp. (Nyctaginaceae) forman ectomicorrizas solamente con un teleporaceo basidiomiceto. La implicación ecológica de la ectomicorriza en las raíces de *Guapira* sp. y *Neea* sp. en el suelo mineral en pendientes ricas en nutrientes es estimadamente baja. Otra especie de *Neea* forma típicas ectomicorrizas con varios basidiomicetos y un ascomiceto poco abundante. Esta *Neea* ocurre en el límite del bosque primario, a lo largo de las orillas de los caminos y en las principales riberas de los ríos demostrando un mejoramiento a la resistencia a estrés mediante la regular formación de ectomicorriza. Palabras clave: micorriza arbuscular, ectomicorriza, humus, neotropico, *Hymenoscyphus*

Introduction

The mycorrhizal state of trees largely influences their competitiveness and their integration or disintegration in the forest community. While symbiotic root-associations with glomeromycete fungi (arbuscular mycorrhiza) support a community of high diversity, symbiotic associations with basidio- or ascomycete fungi (ectomycorrhiza) promote monodominant forests (Kottke 2002 and literature therein). The arbuscular mycorrhiza is the most ancient type (about 400 MA; Taylor et al. 1995) and is associated with more than 80% of plant species (Smith & Read 1997). The arbuscular mycorrhiza was replaced several times in a restricted number of plant species by the ectomycorrhizal association, the ericoid or the orchid mycorrhiza, respectively. It was hypothesized that the change from

glomeration to asco- or basidiomycete associations was promoted by the seasonal climate connected to humus accumulation and minimization of water-soluble nutrients especially nitrogen (Read & Perez-Morena 1993). The predominance of ectomycorrhizal forests in the northern and of arbuscular mycorrhizal forests in the southern hemisphere could thus be partly explained (Read 1991). Our results show that the predominating arbuscular mycorrhization in the tropical mountain forest of southern Ecuador is independent of the amount of humus but is related to phosphate limitation. The investigations also point out that the replacement of arbuscular mycorrhiza by ectomycorrhiza developed gradually in the tropics starting with low ecological significance, then promoting few species in the primary forest, and ending up with the ectomycorrhiza predominance in some secondary forest species.

Materials and Methods

The study site is located on the eastern slope of the Cordillera El Consuelo in the Andes of southern Ecuador. The territory of about 1000 ha belongs to the Reserva Biológica San Francisco, a protected area bordering the north of Podocarpus Nationalpark, half way between Loja and Zamora, Loja-Chinchi province (3°58' S, 79°04' W). Fifteen permanent plots of 400 m² each were established between 1850 and 2600 m, along the mountain ridge and on the steep slopes of the ravine in the primary mountain rain forest, and most of the tree species were identified (Homeier et al. 2002). Fine roots were sampled from 115 tree species and the mycorrhizal state was analyzed by conventional methods (Haug and Pritsch 1992; Kottke et al. 2004). Arbuscular and ectomycorrhizal fungi were identified from DNA-sequences (Haug 2002).

Results and Discussion

Nearly all the 115 investigated tree species were found to form arbuscular mycorrhizas (Tab. 1, Kottke et al. 2004). The results substantiate the hypothesis that the highly diverse tropical forests harbor arbuscular mycorrhizas (Janos 1987). This mycorrhizal association may be considered as one important reason for the high diversity of the community because the rather unspecific and multigenomic symbiotic fungi promote diverse seedlings and adult plants (Smith & Read 1997, Kuhn et al. 2001; Kottke 2002). The investigations also showed that the arbuscular mycorrhizal state is not restricted to roots in the mineral soil as was hypothesized by Read (1993), but is the same well developed in the pure humus layers in the tropical mountain rain forest (Kottke et al. 2004). Phosphate limitation was observed in the humus layer and is mainly due to fact that phosphate is bound in organic form not available for plant roots (Wilcke et al. 2001, 2002 and personal communication). Arbuscular mycorrhizal fungi are well known to mobilize P from the organic fraction improving the P-nutrition of plants significantly (Smith & Read 1997). Arbuscular mycorrhizas are thus favorable for trees on this stand.

The Melastomataceae *Graffenrieda emarginata* is regularly found with arbuscular mycorrhizas, but additionally forms ectomycorrhizas with an ascomycete closely related to the ericoid mycorrhizal fungus *Hymenoscyphus ericae* (Haug et al. 2004). The fungus was shown to mobilize organically bound nutrients (Read & Perez-Morena 2003 and literature therein). *G. emarginata* is the most frequent tree on the mountain ridges where root formation is restricted to the pure organic soil layer. It appears obvious that the ectomycorrhizal state improves nutrient uptake from the humus layer and thus supports competitiveness of this tree species (Haug et al. 2004).

Three Nyctaginaceae were found to form ectomycorrhizas, two *Neea* species and one *Guapira* species. On *Guapira* and on one of the *Neea* species a variable percentage of rootlets displayed a special kind of ectomycorrhiza. The ectomycorrhiza development occurs only on the proximal part of the fine, but long rootlets. Only one fungal species, a Thelephoraceae forms the mycorrhizas (Haug et al. submitted). The *Guapira* and this *Neea* species root in the mineral soil of the nutrient rich slopes of the ravines and the ecological implication of the ectomycorrhiza is estimated to be low. Another *Neea* species forms typical ectomycorrhizas with all the absorptive rootlets. The bushy tree is associated with several basidiomycetes and one ascomycete (Haug et al. submitted). This *Neea* species occurs on the border of the primary mountain forest, along old roadsides and along the main river slopes in disturbed places where it forms a superficial, dense mat of ectomycorrhizal roots. The ectomycorrhizal state most probably improves drought resistance and competitiveness against *Pteridium arachnoideum*, *Chusquea* spp. and other grasses.

The investigation revealed that the mycorrhizal state of a tree poses a selective ecological pressure that cannot be ignored when species are selected for tree plantations and regeneration of tropical mountain forests. The mycorrhizal state also determines the root system development (Brundrett 2002). *Guapira* sp., as most of the other arbuscular mycorrhizal trees, has regularly branched, long fine roots with many root hairs that are only suppressed in the proximal part of roots that are transformed into ectomycorrhizas. *G. emarginata* displays an irregularly branched root system with rather short fine roots that have no root hairs (Haug et al. 2004). The ectomycorrhizal *Neea* species forms densely branched mats of short roots that are typical for ectomycorrhizal trees (Feil et al. 1988).

No other Melastomataceae was so far shown to form ectomycorrhizas with the ascomycete related to *H. ericae*. However, this fungal aggregate is spread world wide and associated with several ectomycorrhizal trees, ericaceous plants and hepatics occurring on acidic, humus-rich soils (Vrålstadt et al. 2000, 2001; Haug et al. 2004). Investigations are currently carried out to clarify if the fungal associate of *G. emarginata* is present in ericaceous plants and hepatics of the neotropical mountain forest. The latter could have served and still may serve as vectors for fungus distribution. The two Nyctaginaceae species *Guapira* sp. and *Neea* sp., positioned within a family that is mainly known from South America and contains mostly non-mycorrhizal plants (Brundrett 2002) have some ectomycorrhizal relatives in Peru (*Neea* sp.; Alexander and Högborg 1986), the Amazon forest near Manaus (*Neea* sp.; Singer 1979) and the Amazon valley in the south of Venezuela (*Neea obovata*, *N. robusta*, *Guapira sancarlosiana*; Moyersoen 1993). In the latter habitat all three species harbored arbuscular and ectomycorrhiza forming fungi and are large, dominating trees there. The ectomycorrhizal fungi connected to the trees in these habitats have not been identified, and it will be interesting to discover how close they are related to the Ecuadorian species. This knowledge could provide us with further information about the paleo-biogeography of the northern Andes, and may substantiate the hypothesis that lowland trees were more widely distributed in the Andes during the late Tertiary (van der Hammen & Cleef 1986; Taylor 1995). *Guapira* sp. and *Neea* sp. could be relicts from these times.

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Table 1 Investigated tree species of the mountain rain forest in southern Ecuador: All species form mycorrhizas, those in bold form ectomycorrhizas ECM, the others form arbuscular mycorrhizas.

Table 1. Arboles Investigados en tres bosques lluviosos en el sur de Ecuador: Todas las especies forman micorrizas, las que estan en negrita forman ectomicorrizas ECM, las otras forman micorrizas arbusculares.

Family	Species	Family	Species
Alzateaceae	<i>Alzatea verticillata</i>	Meliaceae	<i>Guarea cf. kunthiana</i>
Anacardiaceae	<i>Tapirira guianensis</i>		<i>Guarea pterorhachis</i>
	<i>Tapirira obtusa</i>	Mimosaceae	<i>Inga cf. acreana</i>

	<i>Camptosperma panamense</i>		<i>Inga striata</i>
Annonaceae	<i>Guatteria</i> cf. <i>recurvisepala</i>	Monimiaceae	<i>Siparuna aspera</i>
Aquifoliaceae	<i>Ilex</i> cf. <i>amboroica</i>	Moraceae	<i>Coussapoa villosa</i>
Araliaceae	<i>Dendropanax</i> sp.		<i>Ficus</i> cf. <i>subandina</i>
	<i>Schefflera</i> sp.		<i>Helicostylis towarensis</i>
Arecaceae	<i>Dictyocaryum lamarckianum</i>		<i>Morus insignis</i>
	<i>Euterpe catinga</i> <i>Euterpe precatoria</i>		<i>Naucleopsis glabra</i>
Asteraceae	<i>Critoniopsis floribunda</i>		<i>Pseudolmedia rigida</i>
	<i>Piptocoma discolor</i>	Myrsinaceae	<i>Myrsine coriacea</i>
Bignoniaceae	<i>Tabebuia chrysantha</i>		<i>Myrsine latifolia</i>
Cecropiaceae	<i>Cecropia gabrielis</i>	Myrtaceae	<i>Calyptanthus</i> sp.
Chloranthaceae	<i>Hedyosmum anisodorum</i>		<i>Eugenia</i> sp.
	<i>Hedyosmum goudotianum</i>		<i>Eugenia valvata</i>
	<i>Hedyosmum translucidum</i>		<i>Myrcia</i> sp.
Chrysobalanaceae	<i>Hirtella</i> cf. <i>pilosissima</i>		<i>Myrcianthes myrsinoides</i>
Clethraceae	<i>Clethra revoluta</i>	Nyctaginaceae	<i>Guapira</i> sp ECM <i>Neea</i> species (1) ECM <i>Neea</i> species (2) ECM
Clusiaceae	<i>Clusia</i> sp. (2 species)	Piperaceae	<i>Piper perareolatum</i>
	<i>Tovomita weddeliana</i>		<i>Piper</i> sp. (4 species indet.)
	<i>Vismia tomentosa</i>	Podocarpaceae	<i>Podocarpus oleifolius</i>
Cunoniaceae	<i>Weinmannia haenkeana</i>		<i>Podocarpus sprucei</i>
	<i>Weinmannia pinnata</i>		<i>Prumnopity montana</i>
	<i>Weinmannia pubescens</i>	Quiinaceae	<i>Quiina</i> sp.
	<i>Weinmannia spruceana</i>	Rosaceae	<i>Prunus opaca</i>

Cyrillaceae	<i>Purdiaea nutans</i>	Rubiaceae	<i>Dioicodendron dioicum</i>
Elaeocarpaceae	<i>Sloanea</i> sp.		<i>Elaeagea karstenii</i>
Euphorbiaceae	<i>Alchornea</i> cf. <i>grandis</i>		<i>Elaeagia pastoensis</i>
	<i>Alchornea pearcei</i>		<i>Faramea glandulosa</i> cf. <i>uniflora</i>
	<i>Alchornea</i> sp.		<i>Faramea uncinata</i>
	<i>Hyeronima asperifolia</i>		<i>Faramea</i> cf. <i>uniflora</i>
	<i>Hyeronima</i> cf. <i>duquei</i>		<i>Isertia laevis</i>
	<i>Hyeronima moritziana</i>		<i>Ladenbergia oblongifolia</i>
	<i>Hyeronima</i> cf. <i>oblonga</i>		<i>Macrocnemum</i> cf. <i>roseum</i>
Lauraceae	<i>Aniba</i> cf. <i>muca</i>		<i>Palicourea angustifolia</i>
	<i>Cinnamomum</i> sp.		<i>Palicourea andaluciana</i>
	<i>Nectandra</i> cf. <i>acutifolia</i>		<i>Palicourea canarina</i>
	<i>Nectandra crassiloba</i>		<i>Palicourea luteonivea</i>
	<i>Nectandra lineatifolia</i>		<i>Palicourea stenosepala</i>
	<i>Nectandra subbullata</i>		<i>Psychotria</i> sp.
	<i>Ocotea</i> cf. <i>aciphylla</i>		<i>Psychotria tinctoria</i>
	<i>Ocotea benthamiana</i>	Sabiaceae	<i>Meliosma</i> sp.
Magnoliaceae	<i>Talauma caricifragrans</i>	Sapindaceae	<i>Matayba</i> sp. nov.
Malpighiaceae	<i>Byrsonima</i> cf. <i>putamayensis</i>	Sapotaceae	<i>Micropholis guyanensis</i>
Melastomataceae	<i>Graffenrieda emarginata</i> ECM		<i>Pouteria austin-smithii</i>
	<i>Meriana drakei</i>	Solanaceae	<i>Cestrum schlechtendahlui</i>
	<i>Meriana hexamera</i>		<i>Solanum nutans</i>
	<i>Meriana rigida</i>	Symplocaceae	<i>Symplocos peruviana</i>
	<i>Meriana</i> sp. nov.	Tiliaceae	<i>Heliocarpus americanus</i>
	<i>Miconia</i> cf. <i>calophylla</i>	Theaceae	<i>Ternstroemia</i> cf. <i>jelskii</i>
	<i>Miconia crebribullata</i>		
	<i>Miconia jahnii</i>		

	<i>Miconia punctata</i>		
	<i>Miconia rigida</i> , <i>Miconia theaezans</i>		

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