



Root fungal associations in some non-orchidaceous vascular lithophytes

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ABSTRACT

Plant roots in natural ecosystems are colonized by a diverse group of fungi among which the most common and widespread are arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungi. Though AM and DSE fungal associations are well reported for terricolous plant species, they are rather poorly known for lithophytic plant species. In this study, we examined AM and DSE fungal association in 72 non-orchidaceous vascular plant species growing as lithophytes in Siruvani Hills, Western Ghats of Tamilnadu, India. Sixty-nine plant species had AM and 58 species had DSE fungal associations. To our knowledge, we report AM fungal association in 42 and DSE fungal association in 53 plant species for the first time. There were significant differences in total root length colonization and root length colonized by different AM and DSE fungal structures among plant species. In contrast, the differences in AM and DSE fungal colonization among plants in various life-forms and lifecycles were not significant. AM morphology reported for the first time in 56 plant species was dominated by intermediate type AM morphology. A significant negative relationship existed between total root length colonized by AM and DSE fungi. These results clearly suggest that AM and DSE fungal associations are widespread in lithophytes.

Keywords: arbuscular mycorrhizal fungi, dark septate endophyte fungi, life cycle, life-forms, microsclerotia

Introduction

Plants grow in a variety of habitats, including those which are not normally suitable for plant growth. One of the harshest habitats is the surfaces and crevices of rock where low moisture, nutrients and high temperatures limit plant's existence. Plants growing on rocks are termed lithophytes and these types of plants occur in different arid (Zwieniecki & Newton 1995; Bashan *et al.* 2002; Lopez *et al.* 2009) and non arid (Tozer *et al.* 2005; Gröger & Huber 2007; Muthuraja *et al.* 2014) ecosystems. Nevertheless, lithophytes also colonize rocks that are constantly misted by waterfalls or rocks dripping with water. Lithophytes

have certain biological peculiarities, including capturing moisture from rain, dew, melting snow or water trickling down the rocks, and acquire nutrients from rain water, litter, and feeding on insects or their own dead tissues (Alves & Kolbeck 1993; Gold & Bliss 1995; Tozer *et al.* 2005). These features enable lithophytes to occupy and thrive on the rock surfaces. Based on their existence and dependence on rock, lithophytes are classified as epilithic or epipetric and endolithic forms. Epilithic forms grow superficially on rock surfaces (e.g., orchids, ferns, algae, bryophytes), whereas endolithic forms grow embedded in rocks (e.g., algae, fungi). Further, plants growing exclusively on rocks are known as obligate lithophytes and those that growing

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on rocky as well as on other substrates are known as the facultative lithophytes.

Generally, success of plants growing on harsh environment depends on their ability to associate with microorganisms (Puente *et al.* 2004a; b; Bashan *et al.* 2007). Plants growing in different environments are colonized by arbuscular mycorrhizal (AM) fungi belonging to Glomeromycota, and it is one of the most widespread associations among land plants (Smith & Read 2008). The AM fungi aids plants in their uptake of water and nutrients, and impart tolerance against various stresses. This association enables plant's to survive and thrive under harsh environments that are not conducive for plant growth. Although the roots of several terricolous plant taxa have been examined for the presence of AM fungal association, their occurrence in lithophytic or saxicolous plant species is limited to certain plant groups. For example, the occurrence of AM fungal association has been examined in lithophytic mosses (Zhang & Guo 2007) and ferns (Lehnert *et al.* 2009; Kessler *et al.* 2010; Muthukumar & Prabha 2013; Muthuraja *et al.* 2014). The results of some of these studies suggest that non-mycorrhizal condition appears to be more prevalent in lithophytic than in terricolous taxa (Kessler *et al.* 2010).

A great diversity exists in inter- and intracellular distribution of AM fungal structures within plant roots. Based on the distribution of the fungal structures within plant roots, the AM colonization patterns have been termed as *Arum*-, *Paris*- and intermediate types. The intraradical fungal hyphae are linear and intercellular in *Arum*-type, and intracellular and coiled in *Paris*-type. In between these two extremes, there exists a diverse colonization patterns termed as intermediate types. Though AM colonization patterns in terricolous plant species are widely reported, it is rather scanty for lithophytic species (e.g., Muthukumar & Prabha 2013; Muthuraja *et al.* 2014).

A group of predominantly ascomycetous fungi belonging to the order Helotiales also colonizes plant roots either individually or along with AM fungi. These fungi termed as dark septate endophyte (DSE) fungi form dematiaceous, regularly septate hyphae with microsclerotia and/or moniliform cells in plant roots. Although these fungi have been recorded in roots of more than 1000 plant species growing in a range of habitats (Jumpponen & Trappe 1998; Mandyam & Jumpponen 2005; Muthukumar & Prabha 2013; Muthuraja *et al.* 2014; Kumar & Muthukumar 2014), their occurrences in many plant taxa and habitats are yet to be examined. Like mycorrhizal fungi, DSE fungi also associate with plants under extreme environmental conditions (Read & Haselwandter 1981; Newsham *et al.* 2009). The widespread occurrence of DSE fungi in stressed environments suggests that DSE fungi might act as surrogate mutualists in these environments (Bledsoe *et al.* 1990; Newsham 2011). In spite of their frequent occurrence in plant roots, the role of DSE fungi on plant growth, development and ecology is largely unknown. Limited studies exploring the role of DSE fungi on plant growth show that these fungi could enhance plant

performance when nutrients are available predominantly in organic forms (Newsham 2011). Like the incidence of AM, DSE fungal associations in lithophytes are also limited to certain plant groups. The occurrence of DSE fungal association in lithophytic fern and fern-allies has been reported recently from the Eastern and Western Ghats of southern India (Muthukumar *et al.* 2014; Muthuraja *et al.* 2014).

As lithophytic habitats are characterized by extreme environmental conditions and plants in stressed habitats depend more on association with endophytic microorganisms for their growth and survival, we hypothesized that the incidence of endophytic root fungal associations in lithophytes are high. To test this hypothesis, we examined the roots of non-orchidaceous lithophytes to assess the incidence and extent of AM and DSE fungal colonization. In addition, we assessed the influence of plant habit and life cycle on the occurrence of AM and DSE fungal associations. Finally, we also determined the existence of any possible relationship between the AM and DSE fungal variables as these fungal types occupy the same niche within plant roots.

Materials and methods

Sampling site and investigated plant species

Kovai Kuttralam (10°56'12.9"N 76°41'14.3"E), located 22 miles West of Coimbatore City in Siruvani Hills is a part of the Nilgiri Biosphere Reserve of Western Ghats, which is one of the biodiversity hotspots of the world (Balaji & Hariharan 2013). In addition to providing drinking water to the Coimbatore city, Siruvani Hills are also home to certain tribes like the Mudugars and Irulars. The vegetation at lower to higher altitudes ranges from southern dry mixed deciduous forest, southern moist mixed deciduous forest to tropical evergreen forest in hill tops (Balaji & Hariharan 2013). This region receives a rainfall varying from 750 to 2000 mm, mostly from the northeast monsoon during September to November, with a dry period from December to May. The minimum and maximum temperature range from 10 to 22 °C (average 16 °C) and 35 to 43 °C (average 39 °C) respectively (Balaji & Hariharan 2013). The 72 non-orchidaceous plant species in this study belong to 65 genera and 38 families (Tab. 1). Twelve of these were pteridophytes belonging to seven families. Fifty-five plant species were herbs, 14 were shrubs/under shrubs, and three were trees. Seventeen species were annuals, and 55 were perennials (Tab. 1). Plant nomenclature follows The Plant list (www.ipni.org).

Sample collection

All the root samples were taken between December 2009 and February 2010. Three plants were sampled for



Root fungal associations in some non-orchidaceous vascular lithophytes

Table 1. Life-form, life cycle, arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal status, AM morphology (in parenthesis) of non-orchidaceous lithophytes in Siruvani Hills of Western Ghats. In the last column, previous reports on the occurrence of AM and DSE fungal associations and AM morphological types (in parenthesis) are listed.

Family /Species	Life- form ^a	Life cycle ^b	Fungal Association ^c	Previous report ^d
Acanthaceae				
<i>Phaulopsis imbricata</i> (Forssk.) Sweet.	H	P	AM* (A)*,DSE*	---
<i>Justicia diffusa</i> Willd.	H	P	AM* (I4)*,DSE*	---
<i>Strobilanthes asperrimus</i> Nees.	S	P	AM* (I1)*,DSE*	---
Apocynaceae				
<i>Alstonia venenata</i> R.Br.	S	P	AM*(I4)*	---
Asclepidaceae				
<i>Caralluma umbellata</i> Haw.	H	P	AM(I2)*,DSE*	NM ¹⁸ , AM ²¹
Aspleniaceae				
<i>Asplenium zenkerianum</i> Kunze.	H	P	AM(I4)*,DSE*	AM ¹⁴
Asteraceae				
<i>Acmella paniculata</i> (Wall. ex DC.) R.K.Jansen	H	A	AM(A),DSE*	NM ²¹ , AM (I4) ⁹
<i>Ageratina adenophora</i> (Spreng.) R.M.King & H.Rob.	US	P	AM (A)*,DSE	AM ^{24,25,27,32} , DSE ^{24,30}
<i>Ageratum conyzoides</i> L.	H	A	AM(I4),DSE	AM ^{4,5,6,8,21,23,26} (A) ¹⁶ , (I4) ⁹ +DSE ⁹
<i>Blumea axillaris</i> (Lam.) DC.	H	A	AM* (I4)*,DSE*	---
<i>Blumea oxydonta</i> DC.	H	P	AM*(I4)*,DSE*	---
<i>Blumea virens</i> Wall. ex DC.	H	P	AM*(I4)*,DSE*	---
<i>Crassocephalum crepidioides</i> (Benth.) S. Moore	H	P	AM(I1),DSE*	AM (A) ¹⁶
<i>Vernonia cinerea</i> (L.) Less.	S	P	AM(I4)*,DSE*	AM ^{13,21}
Balsaminaceae				
<i>Impatiens parvifolia</i> Bedd.	H	A	AM*(I2)*,DSE*	---
Begoniaceae				
<i>Begonia malabarica</i> Lam.	S	P	AM (I4),DSE*	AM (P) ¹³
Chenopodiaceae				
<i>Anredera baselloides</i> (Kunth) Baill.	H	P	AM*(I1)*,DSE*	---
Commelinaceae				
<i>Cyanotis cristata</i> (L.) D.Don	H	P	AM(A)*,DSE*	AM ¹³
<i>Murdannia nudiflora</i> (L.) Brenan.	H	P	NM,DSE*	---
Convolvulaceae				
<i>Argyreia populifolia</i> Choisy.	CS	P	AM*(I4)*	---
<i>Merremia umbellata</i> (L.) Hallier f.	CH	P	AM*(A)*	---
Costaceae				
<i>Costus speciosus</i> (Koenig) Sm.	H	P	AM(I4)	AM (A) ^{16,28} , DSE ²⁸
Cyperaceae				
<i>Cyperus cyperinus</i> (Retz.) Valcken	H	A	AM(I1),DSE*	NM ¹⁶ , AM (I4) ^{9,15,17}
Eriocaulaceae				
<i>Eriocaulon robustum</i> Steud.	H	P	NM,DSE*	---
Euphorbiaceae				
<i>Acalypha fruticosa</i> Forssk.	US	A	AM(I4)*,DSE*	AM ^{13,21}
<i>Agrostistachys borneensis</i> Becc.	T	P	AM*(I4)*	---
<i>Phyllanthus tenellus</i> Roxb.	H	P	AM*(A)*,DSE*	---
<i>Phyllanthus urinaria</i> L.	H	A	AM(I1)	AM (A) ¹⁰
Fabaceae				
<i>Alysicarpus vaginalis</i> (L.) DC.	H	P	AM(I1),DSE	AM ¹⁰ , 21(P) ¹¹ , DSE ³⁰
<i>Chamaecrista pumila</i> (Lam.) K.Larsen	H	P	AM*(I4)*,DSE*	NM ²¹
<i>Hylodesmum repandum</i> (Vahl) H.Ohashi & R.R.Mill	S	P	AM* (I2)*,DSE*	---
<i>Smithia bigemina</i> Dalzell	H	A	AM*(I4)*	---
Gentianaceae				
<i>Canscora heteroclita</i> (L.) Gilg.	H	P	AM*(I4)*,DSE*	NM ²¹
Gesneriaceae				
<i>Henckelia incana</i> (Vahl) Spreng.	H	P	AM*(A)*,DSE*	---
Hemionietidaceae				
<i>Parahemionitis cordata</i> (Hook. & Grev.) Fraser-Jenk.	H	P	AM(I2)	AM ^{14,22} (I4) ¹² /DSE ¹²



Table 1. Cont.

Family /Species	Life- form ^a	Life cycle ^b	Fungal Association ^c	Previous report ^d
Lamiaceae				
<i>Anisochilus suffruticosus</i> Wight.	US	P	AM*(A)*,DSE*	---
<i>Plectranthus amboinicus</i> (Lour.) Spreng.	S	P	AM*(A)*,DSE*	---
<i>Pogostemon plectrantoides</i> Desf.	S	P	AM*(I1)*,DSE*	---
Lentibulariaceae				
<i>Utricularia uliginosa</i> Vahl	H	A	AM*(A)*,DSE*	NM ¹³
Liliaceae				
<i>Sansevieria zeylanica</i> (L.) Willd.	H	P	AM*(I1)*,DSE*	---
Lygodiaceae				
<i>Lygodium flexuosum</i> (L.) Sw.	H	P	AM*(I2)*	NM ⁷
Malvaceae				
<i>Hibiscus surattensis</i> L.	US	P	AM(I4)*,DSE*	AM ²¹
Melastomataceae				
<i>Osbeckia wynaadensis</i> C.B. Clarke	S	P	AM*(A)*,DSE*	---
Meliaceae				
<i>Melia azedarach</i> L.	T	P	AM(I1)*,DSE*	NM ¹³ , AM ¹⁶
Moraceae				
<i>Ficus microcarpa</i> L.f.	T	P	AM*(I4)*,DSE*	NM ²¹
Nephrolepidaceae				
<i>Nephrolepis cordifolia</i> (L.) C. Presl	H	A	AM(P)*,DSE	AM ^{1,12,14,22} , DSE ¹²
Oxalidaceae				
<i>Biophytum sensitivum</i> (L.) DC.	H	A	AM*(I4)*,DSE*	NM ²¹
Poaceae				
<i>Dimeria kanjirapallilana</i> K.C.Jacob.	H	P	AM*(I4)*,DSE*	---
<i>Eragrostis atrovirens</i> (Desf.) Trin.ex Steud.	H	P	AM*(I4)*,DSE*	---
<i>Garnotia tenella</i> (Arn. ex Miq.) Janowski	H	A	AM*(I4)*,DSE*	---
<i>Oplismenus burmanni</i> (Retz.) P.Beauv.	H	A	AM(I4)*	AM ²¹
<i>Oplismenus compositus</i> (L.) P. Beauv.	H	P	AM(I4),DSE*	AM (P) ¹³
<i>Pogonatherum crinitum</i> (Thunb.) Kunth	H	P	AM(I4),DSE*	AM ²⁹ (P) ¹³
<i>Setaria verticillata</i> (L.) P. Beauv.	H	A	AM(I4)*	AM ^{2,3} , DSE ²⁰
Polypodiaceae				
<i>Drynaria quercifolia</i> (L.) J. Sm.	H	P	NM	NM ¹⁴ , AM ²² (P/I) ¹⁹ (I4) ¹² , DSE ¹⁹
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	H	P	AM*(I4)*	---
Portulacaceae				
<i>Portulaca tuberosa</i> Roxb.	H	P	AM*(A)*,DSE*	---
Pteridaceae				
<i>Adiantum caudatum</i> L.	H	P	AM(I2)*,DSE*	AM ^{14,32}
<i>Adiantum lunulatum</i> Burm. f.	H	P	AM(I2),DSE	AM ^{7,14} , (I4) + DSE ¹²
<i>Cheilanthes swartzii</i> Webb & Berthel.	H	P	AM(I2)	AM ^{14,22} (I4) ¹²
Rubiaceae				
<i>Mitracarpus villosus</i> (Sw.) DC.	H	A	AM*(I4)*,DSE*	---
<i>Oldenlandia herbacea</i> (L.) Roxb.	H	P	AM*(I4)*,DSE*	---
Scrophulariaceae				
<i>Mecardonia procumbens</i> (Mill.) Small	H	A	AM*(A)*,DSE*	---
<i>Striga asiatica</i> (L.) Kuntze	H	A	AM*(A)*,DSE*	NM ^{13,21}
Selaginellaceae				
<i>Selaginella repanda</i> (Desv. ex Poir.) Spring	H	P	AM*(I2)*,DSE*	---
<i>Selaginella vaginata</i> Spring	H	P	AM*(I4)*,DSE*	---
Thelypteridaceae				
<i>Cyclosorus interruptus</i> (Willd.) H.Itô	H	P	AM(I2)*,DSE*	AM ¹⁴
<i>Macrothelypteris torresiana</i> (Gaudich.) Ching	H	P	AM(I2)*,DSE*	AM ^{14,31}
Urticaceae				
<i>Elatostema acuminatum</i> (Poir.) Brongn.	US	P	AM*(I4)*,DSE*	---
<i>Elatostema lineolatum</i> Wight.	H	P	AM*(I1)*, DSE*	---
<i>Girardinia diversifolia</i> (Link) Friis	H	P	AM*(I4)*,DSE*	---



Table 1. Cont.

Family /Species	Life-form ^a	Life cycle ^b	Fungal Association ^c	Previous report ^d
Urticaceae				
<i>Pouzolzia zeylanica</i> (L.) Benn.	H	P	AM*(I4)*,DSE*	NM ^{13,21}

^a CH, Climbing herb; CS, Climbing shrub, H, Herb; S, Shrub; US, Under shrub; T, Tree

^b A, Annual; P, Perennial

^{c,d} NM, Non-mycorrhizal; AM morphological types: A, *Arum*, P, Paris; I1, intermediate-1; I2, intermediate-2; I4, intermediate-4

^d Previous reports: ¹Gemma *et al.* (1992), ²Harley & Harley (1987a), ³Harley & Harley (1987b), ⁴Hazarika *et al.* (2009), ⁵Hazarika *et al.* (2010), ⁶Hemavani & Thippeswamy (2013), ⁷Khade & Rodrigues (2002), ⁸Kulkarni *et al.* (1997), ⁹Kumar & Muthukumar (2014), ¹⁰Li *et al.* (2004), ¹¹Louis (1990), ¹²Muthukumar & Prabha (2013), ¹³Muthukumar & Udaiyan (2000a), ¹⁴Muthukumar & Udaiyan (2000b), ¹⁵Muthukumar *et al.* (1996), ¹⁶Muthukumar *et al.* (2003), ¹⁷Muthukumar *et al.* (2004), ¹⁸Muthukumar *et al.* (2006), ¹⁹Muthuraja *et al.* (2014), ²⁰Peyronel (1924), ²¹Ragupathy & Mahadevan (1993), ²²Raja *et al.* (1995), ²³Santos *et al.* (2013), ²⁴Songachan & Kayang (2011), ²⁵Sun *et al.* (2013), ²⁶Tahira *et al.* (2012), ²⁷Thapa *et al.* (2015), ²⁸Uma *et al.* (2010), ²⁹Wang & Jiang (2015), ³⁰Zhang *et al.* (2011), ³¹Zhao (2000), ³²Zhao *et al.* (2006)

*New records

each plant species resulting in a total sample size of 216. The roots were scooped off the rock surfaces, and the debris and mosses attached to roots were removed. The roots were then gently washed in water and fixed in FAA (formalin-acetic acid-alcohol, 5ml:5ml:90ml) and transported to the laboratory for processing. As most of the roots were not associated with soil, or identifiable spores were absent in the substrates attached to the roots, we did not enumerate AM fungal spore numbers or diversity.

Preparation of roots for AM and DSE fungal assessment

Fixed roots were washed free of FAA, cut into 1-cm fragments, cleared in 10 % KOH (Phillips & Hayman 1970), acidified with 5 N HCl and stained with trypan blue (0.5% in lacto glycerol) overnight. Roots that remained dark after clearing were bleached in alkaline H₂O₂ prior to acidification. The percentage of root length colonized by AM and DSE fungal structures and total root length colonized were estimated according to a magnified intersection method (McGonigle *et al.* 1990). Briefly, five intersections between the microscopic eyepiece crosshair and roots were recorded in 10 1-cm long root bits for each plant at ×400 in an Olympus BX5 trinocular microscope. The presence of AM and DSE fungal structures was noted at each intersections were recorded. The percentage of root length colonized by AM and DSE fungal structures and total root length colonized were estimated as the proportion of root length containing different fungal structures (McGonigle *et al.* 1990).

The AM-morphology was classified as *Arum*-, *Paris*- and intermediate types based on whether the fungal hyphae were present, mainly as hyphae running through intercellular spaces or within cells as coils, respectively following descriptions of Dickson (2004). The intermediate subtypes categorized by Dickson (2004) are: linear hyphae are inter- and intracellular with the former possessing *Arum*-

type arbuscules (intermediate type–1, I1); intracellular linear hyphae bearing *Arum*-type arbuscules (intermediate type–2, I2); intracellular linear hyphae bearing arbuscules and intercellular linear hyphae (intermediate type–3, I3); hyphal/ arbusculate coils along with intercellular linear hyphae (intermediate type–4, I4). We checked the previous reports on AM and DSE fungal associations and AM colonization patterns, and the results are presented in Tab. 1.

Statistical analysis

Analysis of variance (ANOVA) was used to assess the significance of variation for fungal variables among plant species. Similarly, ANOVA and *t*-test was used to test the influence of plant life-forms and lifecycle patterns on the fungal variables. Regression analysis was used to assess the relationship between AM and DSE fungal variables. Percentage data on AM and DSE fungal root colonization was arcsine transformed prior to analysis. All statistical analysis was performed using SPSS for Windows (Version 9).

Results

Occurrence of AM and DSE fungal colonization

In present investigation, the roots of 69 of the 72 plant species examined were AM and roots only three plant species (*Murdannia nudiflora*, Commelinaceae; *Eriocaulon robustum*, Eriocaulaceae; *Drynaria quercifolia*, Polypodiaceae), lacked AM fungal structures (Tab. 1). AM fungal colonization was characterized by the formation of a swollen appressorium on the root surface. The fungal hyphae originating from the appressorium spread inter and/or intracellularly as linear hyphae or hyphal coils to form various types of AM morphologies in the root cortex (Fig. 1A-K). Arbuscules were found on inter or intracellular linear hyphae or hyphal coils



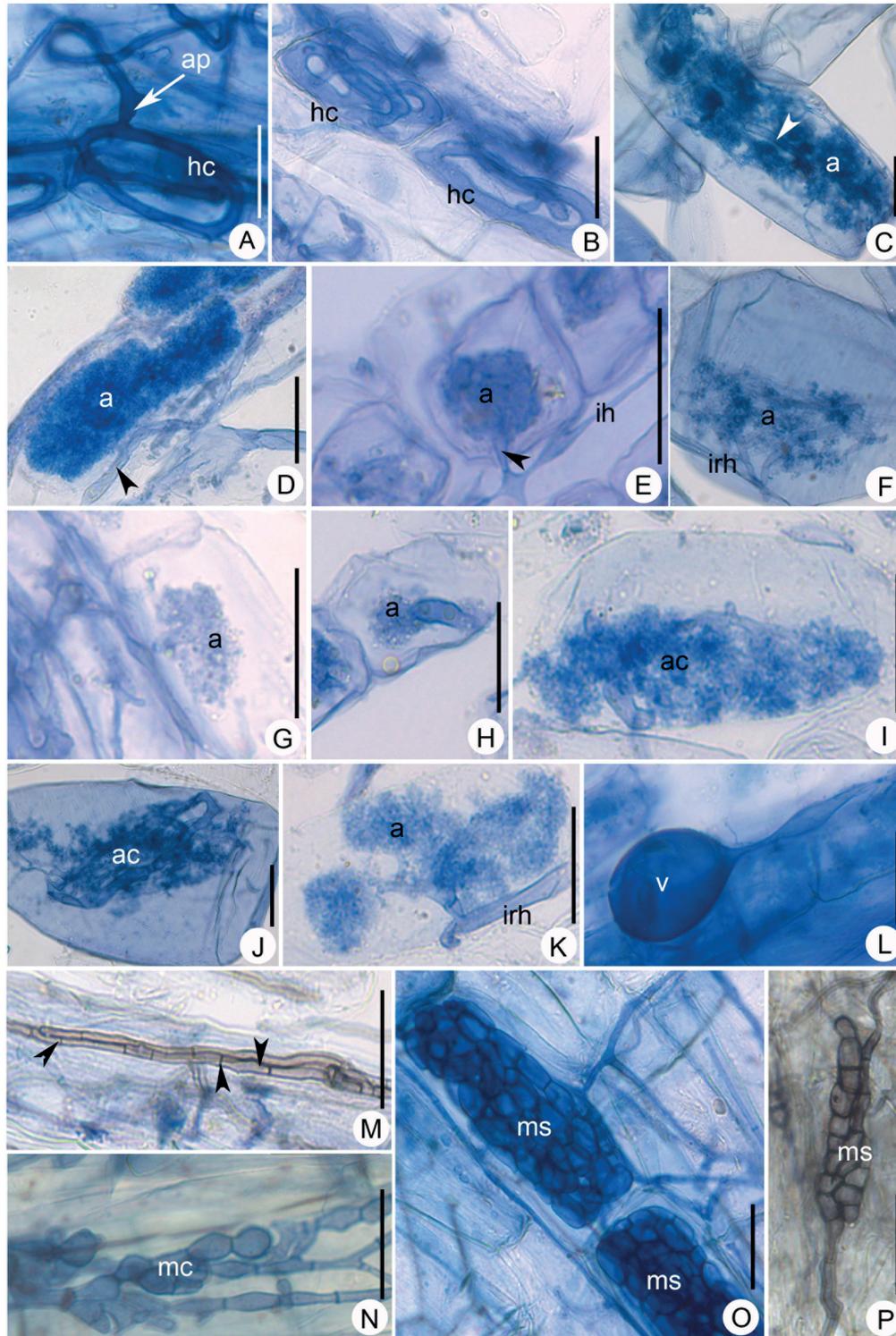


Figure 1. Arbuscular mycorrhizal (AM) (A-L) and dark septate endophyte (DSE) (M-P) fungi in the roots of lithophytic plant species of Siruvani Hills. (A) Appressorium (ap) and hyphal coil (hc) in the epidermal cell of *Anredera baselloides*, (B) Hyphal coils (hc) in cortical cells of *Justicia diffusa*, (C) Intracellular hyphae (white arrow head) and arbuscule (a) in *Caralluma umbellata*, (D) Intracellular hyphae (black arrow head) and arbuscule (a) in *Hylodesmum repandum*, (E) intercellular hyphae (ih), arbuscular trunk (black arrow head) and arbuscule (a) in *Striga asiatica*, (F) intracellular hyphae (irh) and arbuscule (a) in *Lygodium flexuosum*, (G-H) Arbuscule (a) in *Anisochilus suffruticosus* and *Utricularia uliginosa*, (I-J) Arbusculate coils (ac) in *Biophytum sensitivum* and *Nephrolepis cordifolia*, (K) Intracellular hyphae (irh) and arbuscule (a) in *Strobilanthes asperrimus*, (L) intercellular vesicle (v) in *Acmeilla paniculata*, (M) melanized septate hyphae (black arrow heads) in *Eriocaulon robustum*, (N) moniliform cells (mc) in *Eragrostis atrovirens*, (O-P) microsclerotia (ms) in *Phaulopsis imbricata* and *Ageratina adenophora*. Scale bars = 30µm



(Fig. 1C-K). Vesicles were either inter and/or intracellular (Fig. 1L). Vesicles were absent in 13 plant species.

The majority of the plant species investigated (81%) had DSE fungal colonization characterized by regularly septate hyaline/melanized hyphae bearing moniliform cells or microsclerotia (Fig. 1M-P). Of these, co-occurrence of DSE association along with AM was evident in 97% of these plant species. DSE fungal structures were absent in roots of *Alstonia venenata* (Apocynaceae), *Argyreia populifolia*, *Merremia umbellata* (Convolvulaceae), *Costus speciosus* (Costaceae), *Agrostistachys borneensis*, *Phyllanthus urinaria* (Euphorbiaceae), *Smithia bigemina* (Fabaceae), *Parahemionitis cordata* (Hemionietidaceae), *Lygodium flexuosum* (Lygodiaceae), *Oplismenus burmanni*, *Setaria verticillata* (Poaceae), *Drynaria quercifolia*, *Pleopeltis macrocarpa* (Polypodiaceae), *Cheilanthes swartzii* (Pteridaceae). Roots of two of the three nonmycorrhizal plant species (*Murdannia nudiflora*, *Eriocaulon robustum*) were colonized by DSE fungi (Tab. 1).

Extent of AM fungal colonization

The extent of AM fungal colonization and AM fungal structures varied significantly within plant species. The percentage root length with total colonization (%RLTC) varied significantly among plant species ($F_{71,144} = 2.23$; $P < 0.01$) and ranged from 17.45% (*Phaulopsis imbricata*, Acanthaceae) to 70.99% (*Costus speciosus*, Costaceae)

(Tab. 2). The percentage root length with hyphae (%RLH) ranged from 2.70 % in *Cheilanthes swartzii* (Pteridaceae) to 28.96% in *Pleopeltis macrocarpa* (Polypodiaceae). The %RLH significantly varied among plant species ($F_{71,144} = 9.51$; $P < 0.01$). The percentage of root length with vesicles (%RLV) varied significantly among plant species ($F_{71,144} = 5.60$; $P < 0.01$), and ranged from 1.93% in *Crassocephalum crepidioides* (Asteraceae) to 15.80% in *Chamaecrista pumila* (Fabaceae).

The percentage of root length with arbuscules (%RLA), $F_{71,144} = 44.49$ and arbusculate coils (%RLAC, $F_{71,144} = 29.30$; $P < 0.01$) also significantly ($P < 0.01$) varied with plant species. The %RLA ranged from 7.82% in *Phaulopsis imbricata* (Acanthaceae) to 57.40% in *Merremia umbellata* (Convolvulaceae), and %RLAC ranged from 8.02% in *Oplismenus compositus* (Poaceae) to 36.34% in *Nephrolepis cordifolia* (Nephrolepidaceae). The percentage of root length with hyphal coils (%RLHC) ranged from 2.22% (*Nephrolepis cordifolia*) to 30.37% (*Blumea axillaris*, Asteraceae) and significantly varied among plant species ($F_{71,144} = 8.57$; $P < 0.01$) (Tab. 2).

The average percentage of root length with different AM fungal structures (except %RLA) and %RLTC was maximum in trees and minimum in herbs (Fig. 2A). Among plants of different lifecycles, average %RLH, %RLA, %RLV was higher in annuals than in perennials (Fig. 2B). Contrarily, perennials had a higher %RLH, %RLAC and %RLTC than annuals. However, the differences between plant life-forms and life cycles were not significant.

Table 2. Extent of arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal colonization in non-orchidaceous lithophytes in Siruvani Hills of Western Ghats.

Family	AM colonization (%) ^a						DSE colonization (%) ^b			
	RLH	RLHC	RLA	RLAC	RLV	RLTC	RLDH	RLMO	RLMI	RLDTC
<i>Species</i>										
Acanthaceae										
<i>Phaulopsis imbricata</i>	9.63 ± 0.55 ^c	---	7.82 ± 0.56	---	---	17.45 ± 1.10	23.50 ± 1.07 ^a	6.04 ± 1.24	6.04 ± 1.24	35.57 ± 3.51
<i>Justicia diffusa</i>	24.27 ± 3.94	7.71 ± 0.70	---	15.20 ± 6.19	4.12 ± 0.52	51.30 ± 5.35	14.17 ± 0.81	---	---	14.17 ± 0.81
<i>Strobilanthes asperrimus</i>	15.08 ± 1.46	---	32.89 ± 0.44	---	4.60 ± 0.64	52.57 ± 0.95	10.52 ± 0.62	9.85 ± 1.93	---	20.37 ± 1.64
Apocynaceae										
<i>Alstonia venenata</i>	18.37 ± 2.69	7.98 ± 1.64	---	23.93 ± 1.92	3.06 ± 0.61	53.34 ± 2.61	4.90 ± 0.60	4.89 ± 1.60	---	9.79 ± 2.17
Asclepidaceae										
<i>Caralluma umbellata</i>	7.08 ± 0.40	---	31.00 ± 4.00	---	3.10 ± 0.58	41.18 ± 3.70	7.65 ± 2.38	10.17 ± 2.54	1.96 ± 0.00	18.47 ± 5.41
Aspleniaceae										
<i>Asplenium zenkerianum</i>	20.65 ± 3.48	---	---	31.65 ± 2.86	9.68 ± 3.47	61.99 ± 4.42	10.39 ± 0.73	---	---	10.39 ± 0.73
Asteraceae										
<i>Acmeilla paniculata</i>	13.23 ± 2.37	---	13.87 ± 2.79	---	10.88 ± 1.75	37.97 ± 2.68	15.35 ± 1.37	12.36 ± 1.25	1.97 ± 0.48	29.69 ± 1.42
<i>Ageratina adenophora</i>	10.79 ± 0.47	---	9.91 ± 0.72	---	---	20.70 ± 0.72	6.61 ± 0.86	3.86 ± 1.11	1.58 ± 0.00	10.47 ± 1.91
<i>Ageratum conyzoides</i>	22.97 ± 3.84	7.44 ± 1.73	---	11.37 ± 1.68	6.11 ± 2.80	47.89 ± 4.09	12.38 ± 2.38	6.76 ± 0.91	2.23 ± 0.50	21.37 ± 3.20
<i>Blumea axillaris</i>	11.10 ± 3.39	30.37 ± 4.76	---	14.20 ± 0.98	3.58 ± 1.10	59.25 ± 3.03	11.11 ± 4.52	13.16 ± 3.63	---	24.27 ± 2.13
<i>Blumea oxydonta</i>	19.41 ± 2.18	9.80 ± 2.30	---	14.82 ± 5.34	6.86 ± 0.15	50.89 ± 7.54	15.37 ± 3.36	---	---	15.37 ± 3.36
<i>Blumea virens</i>	7.70 ± 1.14	15.36 ± 2.12	---	30.04 ± 4.79	---	53.10 ± 5.58	6.43 ± 2.80	9.01 ± 4.49	---	15.46 ± 7.49
<i>Crassocephalum crepidioides</i>	25.13 ± 4.18	---	17.35 ± 3.14	---	1.93 ± 0.03	44.41 ± 2.61	6.43 ± 0.55	0.63 ± 0.63	2.90 ± 0.83	8.99 ± 1.62
<i>Vernonia cinerea</i>	22.52 ± 3.09	5.95 ± 1.07	---	18.47 ± 1.59	5.11 ± 2.30	52.05 ± 1.60	9.77 ± 1.08	9.12 ± 2.79	---	18.90 ± 3.45
Balsaminaceae										
<i>Impatiens parvifolia</i>	18.41 ± 1.68	---	16.98 ± 0.74	---	---	35.39 ± 2.17	9.10 ± 1.96	8.79 ± 1.69	---	17.89 ± 2.79
Begoniaceae										
<i>Begonia malabarica</i>	20.74 ± 3.10	13.56 ± 3.93	---	16.23 ± 0.57	5.17 ± 0.59	55.70 ± 4.88	12.38 ± 1.89	5.87 ± 1.20	3.17 ± 0.60	18.91 ± 3.71
Chenopodiaceae										
<i>Anredera baselloides</i>	5.37 ± 1.09	---	15.72 ± 0.91	---	9.81 ± 3.33	30.90 ± 2.96	13.74 ± 5.64	4.16 ± 2.31	---	17.90 ± 7.88



Table 2. Cont.

Family	AM colonization (%) ^a						DSE colonization (%) ^b				
Commelinaceae											
<i>Cyanotis cristata</i>	16.30 ± 1.21	---	13.87 ± 2.79	---	5.05 ± 1.09	35.22 ± 4.12	14.33 ± 2.32	5.62 ± 1.58	1.69 ± 0.00	20.51 ± 4.15	
<i>Murdannia nudiflora</i>	---	---	---	---	---	---	23.75 ± 2.69	3.27 ± 1.04	---	27.02 ± 2.98	
Convolvulaceae											
<i>Argyrea populifolia</i>	18.74 ± 0.93	13.80 ± 1.03	---	23.70 ± 1.09	4.80 ± 2.28	61.03 ± 1.05	---	---	---	---	
<i>Merremia umbellata</i>	4.94 ± 3.09	---	57.40 ± 5.35	---	---	62.34 ± 6.17	---	---	---	---	
Costaceae											
<i>Costus speciosus</i>	19.88 ± 2.49	11.93 ± 0.13	---	28.35 ± 2.68	10.84 ± 2.57	70.99 ± 2.02	---	---	---	---	
Cyperaceae											
<i>Cyperus cyperinus</i>	9.92 ± 0.73	---	33.49 ± 2.89	---	3.45 ± 0.99	46.87 ± 3.59	13.31 ± 2.17	3.46 ± 1.00	---	16.78 ± 2.60	
Eriocaulaceae											
<i>Eriocaulon robustum</i>	---	---	---	---	---	---	24.90 ± 1.60	1.92 ± 0.00	---	25.54 ± 2.23	
Euphorbiaceae											
<i>Acalypha fruticosa</i>	22.49 ± 2.03	11.54 ± 1.33	---	18.68 ± 2.93	5.46 ± 1.04	58.17 ± 0.54	8.50 ± 0.69	---	---	8.50 ± 0.69	
<i>Agrostistachys borneensis</i>	28.86 ± 1.23	14.48 ± 0.14	---	13.23 ± 2.32	9.64 ± 0.57	66.21 ± 4.39	---	---	---	---	
<i>Phyllanthus tenellus</i>	3.81 ± 0.81	---	21.46 ± 2.47	---	6.10 ± 1.59	31.37 ± 4.46	13.75 ± 3.29	4.25 ± 1.79	---	18.00 ± 2.46	
<i>Phyllanthus urinaria</i>	18.15 ± 0.70	---	21.42 ± 0.93	---	10.10 ± 1.52	49.67 ± 1.14	---	---	---	---	
Gentianaceae											
<i>Canscora heteroclita</i>	23.83 ± 2.35	17.13 ± 2.37	---	19.75 ± 0.62	3.66 ± 1.07	64.36 ± 5.32	6.04 ± 2.34	1.82 ± 0.03	---	7.25 ± 2.68	
Gesneriaceae											
<i>Henckelia incana</i>	6.28 ± 1.56	---	23.67 ± 4.58	---	9.83 ± 4.24	39.77 ± 7.52	13.75 ± 2.42	6.08 ± 0.86	---	19.82 ± 2.84	
Fabaceae											
<i>Alysicarpus vaginalis</i>	17.19 ± 1.87	---	17.40 ± 2.10	---	12.43 ± 0.40	47.01 ± 1.82	11.94 ± 2.29	3.99 ± 1.79	---	15.93 ± 4.08	
<i>Chamaecrista pumila</i>	24.94 ± 1.46	6.23 ± 1.06	---	15.93 ± 1.52	15.80 ± 1.59	62.91 ± 2.50	7.43 ± 0.83	2.85 ± 0.61	3.63 ± 0.00	11.50 ± 2.47	
<i>Hylodesmum repandum</i>	9.57 ± 0.42	---	28.28 ± 2.27	---	8.48 ± 2.59	46.32 ± 2.51	20.93 ± 3.16	8.49 ± 2.02	---	29.42 ± 5.18	
<i>Smithia bigemina</i>	19.04 ± 3.01	11.59 ± 3.16	---	28.48 ± 0.52	10.57 ± 2.98	69.67 ± 3.29	---	---	---	---	
Hemionietidaceae											
<i>Parahemionitis cordata</i>	23.69 ± 1.75	---	28.27 ± 4.57	---	---	51.96 ± 3.70	---	---	---	---	
Lamiaceae											
<i>Anisochilus suffruticosus</i>	15.12 ± 1.14	---	19.76 ± 0.73	---	5.71 ± 1.56	40.59 ± 2.08	10.17 ± 1.66	7.78 ± 3.20	---	17.95 ± 4.77	
<i>Plectranthus amboinicus</i>	6.17 ± 1.86	---	14.89 ± 4.22	---	6.15 ± 1.55	27.21 ± 2.94	19.39 ± 1.67	4.91 ± 2.43	1.66 ± 0.03	25.96 ± 4.07	
<i>Pogostemon plectrantoides</i>	17.15 ± 1.13	---	22.49 ± 1.82	---	3.49 ± 0.93	43.13 ± 1.17	9.04 ± 0.57	6.75 ± 1.65	3.44 ± 0.00	19.23 ± 2.22	
Lentibulariaceae											
<i>Utricularia uliginosa</i>	11.30 ± 0.53	---	20.49 ± 3.28	---	---	31.78 ± 2.99	10.79 ± 1.34	10.77 ± 0.56	1.69 ± 0.00	21.56 ± 1.74	
Liliaceae											
<i>Sansevieria zeylanica</i>	13.51 ± 1.12	---	27.34 ± 1.91	---	5.78 ± 1.22	46.63 ± 0.96	10.87 ± 1.44	1.96 ± 0.00	---	12.18 ± 1.91	
Lygodiaceae											
<i>Lygodium flexuosum</i>	6.59 ± 0.94	---	48.67 ± 4.74	---	7.55 ± 3.04	62.81 ± 1.93	---	---	---	---	
Malvaceae											
<i>Hibiscus surattensis</i>	13.95 ± 2.79	24.83 ± 5.62	---	21.35 ± 4.65	5.34 ± 2.80	65.47 ± 8.28	16.71 ± 4.37	---	---	16.71 ± 4.37	
Melastomataceae											
<i>Osbeckia wynaadensis</i>	3.96 ± 0.68	---	25.90 ± 5.30	---	8.67 ± 3.86	38.53 ± 2.91	9.97 ± 2.60	2.62 ± 0.47	---	12.59 ± 2.39	
Meliaceae											
<i>Melia azedarach</i>	15.48 ± 1.00	---	19.92 ± 2.17	---	---	35.40 ± 1.23	6.72 ± 0.62	3.05 ± 0.82	---	10.30 ± 0.46	
Moraceae											
<i>Ficus microcarpa</i>	13.04 ± 0.98	6.73 ± 2.05	---	19.30 ± 1.78	6.84 ± 0.68	45.90 ± 1.16	10.66 ± 1.91	---	---	10.66 ± 1.91	
Nephrolepidaceae											
<i>Nephrolepis cordifolia</i>	---	2.22 ± 0.53	---	36.34 ± 0.97	7.71 ± 0.44	46.27 ± 0.45	3.35 ± 0.11	2.81 ± 0.60	---	6.16 ± 0.69	
Oxalidaceae											
<i>Biophytum sensitivum</i>	13.02 ± 2.20	4.61 ± 0.70	---	22.85 ± 1.59	---	40.48 ± 2.40	9.16 ± 2.37	5.22 ± 1.70	1.96 ± 0.00	15.03 ± 1.31	
Poaceae											
<i>Dimeria kanjirapalliana</i>	19.09 ± 4.04	9.21 ± 1.88	---	17.56 ± 3.31	10.09 ± 1.33	55.95 ± 1.52	11.22 ± 2.00	7.41 ± 1.83	---	18.64 ± 1.57	
<i>Eragrostis atrovirens</i>	9.26 ± 2.35	7.64 ± 1.69	---	32.81 ± 1.80	---	49.71 ± 2.13	12.22 ± 1.57	13.49 ± 1.70	---	26.28 ± 1.84	
<i>Garnotia tenella</i>	15.06 ± 2.96	5.15 ± 1.11	---	33.80 ± 3.79	9.02 ± 1.04	63.02 ± 4.56	13.75 ± 3.28	4.51 ± 0.52	2.26 ± 0.59	20.52 ± 4.39	
<i>Oplismenus burmanni</i>	6.57 ± 0.63	10.52 ± 1.72	---	16.45 ± 3.48	---	33.55 ± 1.15	---	---	---	---	
<i>Oplismenus compositus</i>	21.51 ± 5.14	6.79 ± 0.62	---	8.02 ± 0.62	4.96 ± 1.65	41.28 ± 5.18	20.37 ± 3.71	1.85 ± 0.02	3.71 ± 1.10	25.93 ± 4.71	
<i>Pogonatherum crinitum</i>	20.24 ± 5.23	12.80 ± 1.89	---	12.10 ± 1.26	6.37 ± 0.67	51.51 ± 3.27	21.59 ± 2.49	8.32 ± 1.39	---	29.91 ± 3.88	
<i>Setaria verticillata</i>	14.34 ± 0.81	10.80 ± 2.10	---	23.95 ± 3.52	---	49.09 ± 5.08	---	---	---	---	
Polypodiaceae											
<i>Drynaria quercifolia</i>	---	---	---	---	---	---	---	---	---	---	
<i>Pleopeltis macrocarpa</i>	28.96 ± 3.49	7.62 ± 1.35	---	16.45 ± 3.48	7.04 ± 2.03	60.08 ± 2.63	---	---	---	---	



Table 2. Cont.

Family	AM colonization (%) ^a					DSE colonization (%) ^b				
Portulacaceae										
<i>Portulaca tuberosa</i>	7.88 ± 0.22	---	16.90 ± 1.12	---	6.03 ± 0.43	30.82 ± 1.33	19.15 ± 0.77	3.06 ± 0.67	---	22.21 ± 0.11
Pteridaceae										
<i>Adiantum caudatum</i>	17.54 ± 1.39	---	31.60 ± 4.05	---	2.08 ± 0.45	51.22 ± 1.89	15.05 ± 3.83	3.67 ± 1.03	4.91 ± 0.00	23.03 ± 4.86
<i>Adiantum lumulatum</i>	25.28 ± 3.16	---	31.47 ± 5.01	---	4.76 ± 0.50	61.51 ± 3.47	10.29 ± 2.57	---	---	10.29 ± 2.57
<i>Cheilanthes swartzii</i>	2.70 ± 0.66	---	34.33 ± 3.25	---	8.93 ± 0.30	45.96 ± 3.24	---	---	---	---
Rubiaceae										
<i>Mitracarpus villosus</i>	16.61 ± 2.90	12.10 ± 0.95	---	28.28 ± 2.17	5.38 ± 0.84	62.38 ± 0.72	6.81 ± 1.60	1.15 ± 1.15	---	7.96 ± 1.41
<i>Oldenlandia herbacea</i>	17.11 ± 1.54	10.51 ± 2.63	---	12.33 ± 5.19	5.04 ± 0.18	44.98 ± 1.92	18.64 ± 3.37	5.62 ± 0.71	---	24.26 ± 3.64
Scrophulariaceae										
<i>Mecardonia procumbens</i>	21.20 ± 1.08	---	39.63 ± 4.31	---	5.94 ± 0.65	66.76 ± 5.16	4.84 ± 1.66	3.65 ± 1.19	---	8.49 ± 2.85
<i>Striga asiatica</i>	6.81 ± 0.71	---	17.25 ± 1.38	---	8.13 ± 1.90	32.19 ± 1.96	14.93 ± 2.53	2.45 ± 0.56	---	18.12 ± 5.66
Selaginellaceae										
<i>Selaginella repanda</i>	18.51 ± 3.81	---	28.96 ± 6.63	---	7.40 ± 0.53	54.87 ± 3.35	8.46 ± 1.40	6.67 ± 3.88	2.99 ± 0.88	15.13 ± 2.75
<i>Selaginella vaginata</i>	21.78 ± 1.61	12.76 ± 1.79	---	17.22 ± 3.28	4.37 ± 2.10	56.12 ± 2.70	9.99 ± 2.71	2.16 ± 0.61	---	12.14 ± 2.39
Thelypteridaceae										
<i>Cyclosorus interruptus</i>	17.51 ± 3.44	---	27.29 ± 2.96	---	9.37 ± 2.09	54.48 ± 5.09	6.34 ± 0.84	---	---	6.34 ± 0.84
<i>Macrothelypteris torresiana</i>	14.49 ± 1.33	---	33.65 ± 4.76	---	3.88 ± 1.08	52.02 ± 2.71	3.90 ± 0.55	5.55 ± 1.06	---	9.45 ± 1.39
Urticaceae										
<i>Elatostema acuminatum</i>	17.48 ± 1.38	8.09 ± 1.42	---	14.21 ± 0.56	8.11 ± 1.69	47.89 ± 3.14	15.94 ± 2.31	3.88 ± 1.16	2.00 ± 0.01	21.82 ± 3.47
<i>Elatostema lineolatum</i>	15.43 ± 0.53	---	9.30 ± 1.23	---	6.73 ± 1.54	31.46 ± 0.63	17.28 ± 1.58	6.80 ± 0.69	---	24.08 ± 1.14
<i>Girardinia diversifolia</i>	6.88 ± 1.81	6.16 ± 0.51	---	33.43 ± 1.94	---	46.47 ± 3.24	7.51 ± 2.35	7.31 ± 5.44	1.89 ± 0.06	16.07 ± 4.25
<i>Pouzolzia zeylanica</i>	28.91 ± 5.47	7.56 ± 0.70	---	17.69 ± 1.16	7.55 ± 1.15	61.70 ± 4.69	11.21 ± 1.60	3.78 ± 0.61	---	14.99 ± 1.04

^a RLH, RLHC, RLA, RLAC, RLV, RLTC, root length with hyphae, hyphal coils, arbuscules, arbusculate coils, vesicles, and total colonization respectively

^b RLDH, RLMO, RLMI, RLDTTC, root length with dark septate fungal hyphae, moniliform cells, microsclerotia and total colonization respectively

^c Mean ± S.E.

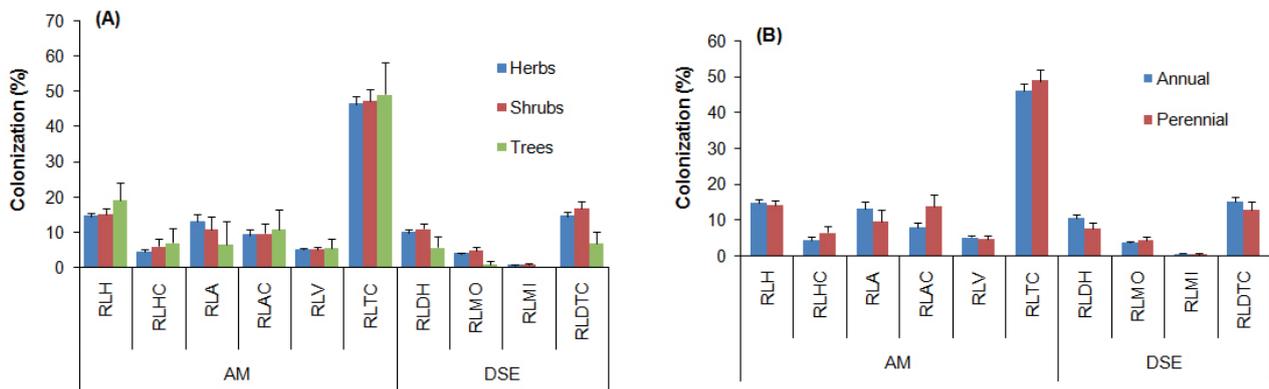


Figure 2. Average arbuscular mycorrhizal (AM) and dark septate endophyte (DSE) fungal colonization in lithophytes of various life-forms (A) and life cycles (B). RLH, RLHC, RLA, RLAC, RLV, RLTC, root length with hyphae, hyphal coils, arbuscules, arbusculate coils, vesicles, and total colonization respectively. RLDH, RLMO, RLMI, RLDTTC, root length with dark septate fungal hyphae, moniliform cells, microsclerotia and total colonization respectively. Error bars indicate ± 1 SE.

AM morphological types

Intermediate type AM morphology was dominant among the various life-forms and lifecycles. Typical *Paris*-type AM was present only in the fern *Nephrolepis cordifolia*. Typical *Arum*-type AM was observed in 14 species and among the intermediate types; I1 was present in 10 species, I2 in 11 species and I4 in 33 species.

Among the various plant life-forms examined, 79% of the herbs, 71% of the under shrubs/shrubs and 100% of the

trees had intermediate type AM (Fig. 3A). *Arum*-type AM was present in <30% of the herbs and shrubs. Like plants in different life-forms, plants with different lifecycles were also dominated by intermediate type AM with 71% of the annuals and 76% of the perennials possessing it (Fig. 3B).

Extent of DSE fungal colonization

The percentage root length with DSE fungal colonization (%RLDTTC) ranged from 6.16% (*Nephrolepis cordifolia*) to



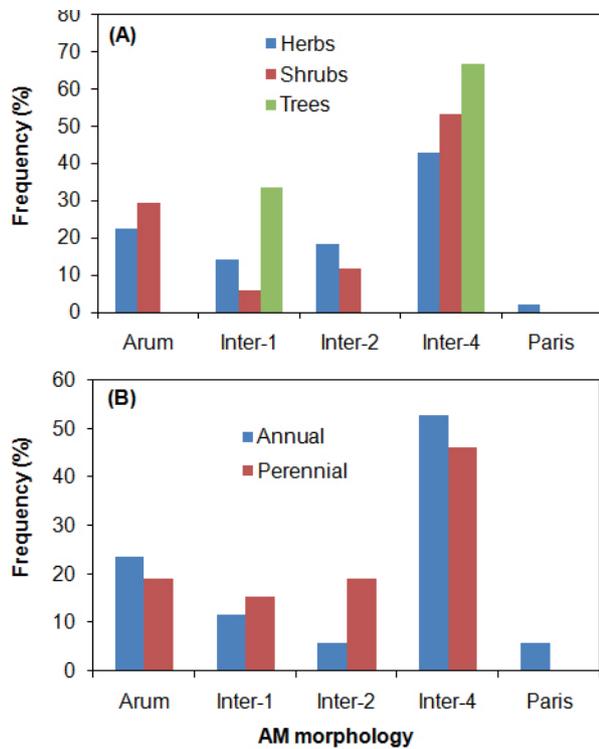


Figure 3. Frequency of arbuscular mycorrhizal (AM) morphology in lithophytes of various life-forms (A) and life cycle (B) patterns. Arum, Inter-1, Inter-2, Inter-4 and Paris represents *Arum*-type, intermediate type 1, intermediate type 2, intermediate type 4 and *Paris*-type respectively.

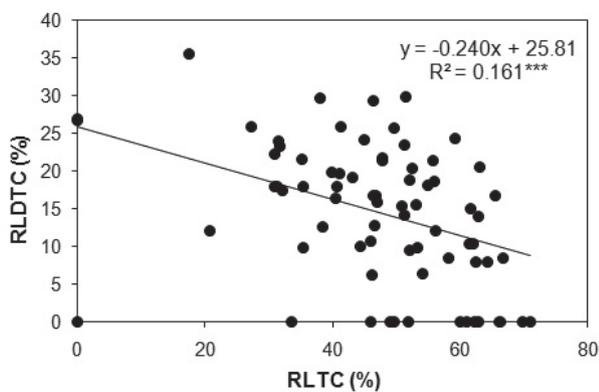


Figure 4. Relationship between total root lengths colonized by arbuscular mycorrhizal (RLTC) and dark septate endophytic (RLDTC) fungi in lithophytes. ***Significant at $P < 0.001$.

35.57% (*Phaulopsis imbricata*, Acanthaceae). Root length with dark septate fungal hyphae (%RLDH) ranged from 3.35% (*Nephrolepis cordifolia*) to 24.90% (*Eriocaulon robustum*, Eriocaulaceae) and root length with moniliform cells (%RLMO) ranged from 0.63% (*Crassocephalum cerpidioides*, Asteraceae) to 13.49% (*Eragrostis atrovirens*, Poaceae) and microsclerotia (%RLMI) ranged from 1.58% (*Ageratina adenophora*, Asteraceae) to 6.04% (*Phaulopsis*

imbricata, Acanthaceae) (Tab. 2). DSE fungal structures like hyphae ($F_{71,144} = 8.11$; $P < 0.01$), moniliform cells ($F_{71,144} = 5.75$; $P < 0.01$), microsclerotia ($F_{71,144} = 3.58$; $P < 0.01$) and total colonization ($F_{71,144} = 4.75$; $P < 0.01$) varied significantly among species. Average %RLDTC and average percentage root length with different DSE fungal structures were higher for shrubs than for trees and herbs (Fig. 2A). Likewise, average %RLDH, %RLMI and %RLDTC were higher for annuals and average %RLMO were higher for perennials (Fig. 2B). The %RLDTC was significantly and negatively related to %RLTC (Fig. 4)

Discussion

Incidence of AM fungal colonization in lithophytes

In this study, the lithophytic plant community consisted of species belonging to different plant groups and families. These results agree with the studies where lithophytic plant communities have been reported to contain a diverse plant assemblage (Gröger & Huber 2007; Jayanthi *et al.* 2011). Ninety-six percent of the non-orchidaceous lithophytes examined in the present study was colonized by AM fungi and to our knowledge, AM symbiosis is reported for the first time in 42 plant species. High prevalence of AM fungal association in lithophytes in this study is in accordance with other studies where such an observation has been reported (Muthukumar & Udaiyan 2000b; Zhang & Guo 2007; Muthukumar *et al.* 2014; Muthuraja *et al.* 2014). Plants growing on rocks or shallow substrates employ several adaptations, including reduction or absence of root hairs and increasing the root diameter to maximize returns from limited carbon investments (Zwieniecki & Newton 1995; Poot *et al.* 2012). This might have contributed to the high incidence of AM in lithophytes examined in the present study as coarse roots tend to increase the mycorrhizal dependency of plants (Fitter & Moyersoen 1996).

The mycorrhizal status of some plant species appears to be significantly influenced by the nature of the substrate they grow. For example, *Drynaria quercifolia* reported mycorrhizal when growing on soil was nonmycorrhizal in the present study (Muthukumar *et al.* 2014; Muthuraja *et al.* 2014). This fern has been reported to be both mycorrhizal and nonmycorrhizal when growing as an epiphyte (Muthukumar & Udaiyan 2000b; Muthukumar & Prabha 2013). Like *D. quercifolia*, *E. robustum* examined was nonmycorrhizal. Species of *Eriocaulon* were reported to be both nonmycorrhizal (Ragupathy & Mahadevan 1993; Muthukumar & Udaiyan 2000a; Kumar & Muthukumar 2014) and mycorrhizal (Khan & Belik 1995; Brundrett *et al.* 1995; Rodrigues & Bukhari 1995; Ragupathy *et al.* 1990; Harikumar 2001). Species in *Eriocaulon* have adaptations to cope with an extreme shortage of soil nutrients like N and P. In addition, plants of *Eriocaulon* are evergreen, and

any nutrient investment in leaves is amortized over an extended period, which considerably reduces its reliance on soil resources and subsequently on AM association (Keddy 2010). Like other species of the genus, *M. nudiflora* was nonmycorrhizal in the present study (Logan *et al.* 1989; Brundrett *et al.* 1995; Tester *et al.* 1987; Silva *et al.* 2001; Muthukumar & Udaiyan 2000a). However, non-functional mycorrhiza (lacking arbuscules) has been reported in *Murdannia semiteres* by Radhika & Rodrigues (2007).

In contrast to earlier observations, *Striga asiatica*, the obligate root hemiparasite associated with grasses was colonized by both AM and DSE fungi (Ragupathy & Mahadevan 1993; Muthukumar & Udaiyan 2000a; Gworgwor & Weber 2003). Nevertheless, atypical AM characterized by the presence of only hyphae and vesicles were reported in *Striga gesnerioides* parasitizing *Lepidagathis hamiltoniana* from the high-altitude region of Maharashtra, India (Kamble & Agre 2013). Similarly, species like *Chamaecrista pumila*, *Canscora heteroclita*, *Utricularia uliginosa*, *Lygodium flexuosum*, *Ficus microcarpa*, *Biophytum sensitivum*, and *Pouzolzia zeylanica* previously reported to be nonmycorrhizal had AM fungal structures in the present study (Ragupathy & Mahadevan 1993; Muthukumar & Udaiyan 2000a; Khade & Rodrigues 2002). This clearly emphasizes the need for more rigorous examination of plants from different habitats to resolve the true mycorrhizal status of a plant species (Wang & Qiu 2006; Brundrett 2009). Habitat conditions like the availability of adequate AM fungal propagules or conditions necessary for the AM formation along with host factors contribute to the varied mycorrhizal status of a plant species (Smith & Read 2008). Variations are likely to occur for facultatively mycorrhizal plant species that occupy diverse habitats (Brundrett 2009). Though the mycorrhizal status of sedges could be influenced by habitat conditions (Muthukumar *et al.* 2004), *Cyperus cyperinus* examined in the present study was mycorrhizal. This corresponds with the findings of Muthukumar *et al.* (1996) who also found AM in this sedge growing on soil. Results of recent experimental studies do indicate that sedges could benefit from AM association like other plant species (Lagrange *et al.* 2011; 2013).

Carnivorous plants inhabit nutrient-poor habitats and have highly specialized nutrient-capture strategies. These plants acquire substantial proportion of their nutrients by digesting their prey, and some have long and dense root hairs (Brundrett 2009; Ellison & Adamec 2011). Subsequently, carnivorous plants have become partially or fully independent of mycorrhizal associations (Brundrett 2009). However, the roots of *Utricularia uliginosa* examined in the present study had both AM and DSE fungal structures. This is in accordance with studies where mycorrhizal structures have been reported in the roots of carnivorous plants (Fuchs & Haselwandter 2004; Harikumar 2013). Although, the endophytic fungal associations have been reported in carnivorous plants, the nature and function

of the associations have yet to be ascertained.

It is interesting to note that in spite of absence of spores in their substrate, more than 48% of lithophytes had >50% of their roots colonized by AM fungi. This emphasizes the importance of propagules other than spores in initiating colonization under lithophytic conditions. The relevance of the extra radical mycelia and mycorrhizal roots as a propagule source in mycorrhization has already been well recognized (Schalamuk & Cabello 2010).

AM morphology

We found the intermediate type AM to be common among lithophytes and even in different life-forms and lifecycles than typical *Arum*- and *Paris*-types. This is similar to some recent studies where intermediate type AM was found to be common among plant species examined. To our knowledge, we report AM morphology for the first time in 56 plant species. This complements Dickson *et al.* (2007) observation that even in plant species for which mycorrhizal status is available, AM morphologies is not known. Further, we also found AM morphologies different from those already reported in 12 plant species. This corroborates studies where different AM morphologies have been reported for the same plant species (see Dickson *et al.* 2007 and references therein). For example, *Ageratum conyzoides* possessing intermediate AM morphology in the present study is also capable of both *Arum*- and intermediate type morphologies (Muthukumar *et al.* 2003; Kumar & Muthukumar 2014). Research had established that AM colonization patterns in plant roots are an interaction between plant root structure and the fungal partners. Although not examined in the present study, root structure, especially those of the cortical region tend to exhibit modifications in plants growing on rocks (Zwieniecki & Newton 1995). This could have contributed to the variation in AM morphology in certain plant species from those already reported. Brundrett & Kendrick (1990) indicated that the presence or absence of intercellular air spaces in the root cortical region to be an important determinant of AM morphology. Later studies elaborated this view and speculated the influence of factors like light, moisture and temperature of the substrates on AM patterns in roots as these factors can influence root growth (Yamato & Iwasaki 2002; Yamato 2004; Becerra *et al.* 2007). However, detailed studies exploring root anatomy of lithophytic plant species, especially the intercellular spaces in roots could reveal their contribution to AM morphology. In addition to these, Cavagnaro *et al.* (2001) and Smith *et al.* (2004) have shown that AM fungal species colonizing roots could also influence AM fungal colonization patterns.

Incidence of DSE fungal colonization in lithophytes

Occurrence of DSE fungal association has been reported in a wide range of terricolous plant species belonging to



diverse plant families (Mandyam & Jumpponen 2015). Nevertheless, reports on the occurrence of DSE fungal association in non-terricolous plant species are limited. We found DSE fungal association in 82% of the plant species examined, which included *Eriocaulon robustum* and *M. nudiflora* the two of the three nonmycorrhizal species. The presence of DSE fungal association in lithophytes that lacked AM association resembles the observations of Lugo *et al.* (2009) in South American bromeliads where all the epiphytic nonmycorrhizal plants were invariably colonized by DSE fungi. Roots of *Costus speciosus* (Costaceae), *Parahemionitis cordata* and *Drynaria quercifolia* reported possessing DSE fungal association in earlier studies lacked DSE fungal structures in the present study (Uma *et al.* 2010; Muthukumar & Prabha 2013; Muthuraja *et al.* 2014). To our knowledge, we report DSE fungal presence in 53 plant species for the first time. This clearly suggests the lack of information on the occurrence of DSE fungal occurrence in many habitats, especially in tropical regions (Jumpponen & Trappe 1998). Based on their observations, Lugo *et al.* (2009) hypothesized that DSE fungi could enable plants to survive extreme arid conditions prevailing in non-terricolous habitats by enhancing the drought tolerance mechanisms and nutrient capture.

Influence of plant habit and lifecycle on the occurrence of AM and DSE fungal associations

In the present study, we did not find any significant difference in the extent of colonization for plants in different life-forms and lifecycles. This contrasts the observations of Muthukumar & Udaiyan (2000a) where terricolous shrubs and trees growing in the Western Ghats region of southern India had higher colonization levels than herbs. Nevertheless, the average %RLTC of <50% in annuals and perennials accords with the observations of Muthukumar & Udaiyan (2000a) where a higher proportion of annuals and perennials examined had colonization levels between 25% and 50%. These clearly indicate that AM fungi are equally important for plant species with different life-forms and lifecycle strategies even under lithophytic conditions. Like AM fungal association, the extent of DSE fungal colonization also failed to exhibit significant variations among plants of different life-forms and lifecycle strategies. Nevertheless, the results of the present study suggest that lithophytes are more dependent on AM than DSE fungi. This is evidenced by the existence of a significantly higher average %RLTC than %RLDTC ($t_{71} = 13.095$; $P < 0.001$) in general as well as among different life-forms and lifecycles. For example, the %RLTC in herbs, shrubs and trees was respectively 3.21, 2.82 and 7.30 folds higher than %RLDTC. Similarly, the %RLTC of annuals and perennials was 3.04 and 3.80 folds respectively higher than %RLDTC. This may be due to more conducive conditions for AM formation and functioning

and is consistent with the trend observed for terricolous species (Lugo *et al.* 2009; Muthukumar & Prabha 2013).

Relationship between AM and DSE fungi

Co-occurrence of AM and DSE fungi were found in roots of 79% plant species examined. This is similar to studies where a high proportion of dual colonization of AM and DSE fungi in roots of plant species examined have been reported (Massenssini *et al.* 2014; Majewska *et al.* 2015). Our observation of a negative correlation between %RLTC and %RLDTC is in agreement with studies where an inverse relationship between these fungal variables has been reported (Muthukumar *et al.* 2006; Mandyam & Jumpponen 2008; Muthukumar & Tamilselvi 2010). While an interaction between AM and DSE fungal type is expected as they share the same niche within the root system, the nature of the relation between these two fungal types has received far less attention. It is generally believed that DSE fungi could aid plant growth and survival under circumstances where conditions are not conducive for AM functioning. For example, Barrow (2003) suggested that DSE fungi could enhance plant's performance in very dry soils of arid ecosystems. Similarly, DSE fungal colonization of the dominant grass *Bouteloua gracilis* from semi-arid grasslands of Mexico was four times higher than AM colonization (Medina-Roldán *et al.* 2008). The extent of root colonization by fungal endophytes depends on the carbon allocation by the host plant as well as the host, fungal and soil factors (Medina-Roldán *et al.* 2008; Smith & Read 2008). Recent research on the control of plant-fungal mutualism indicates that the symbionts offering the best benefits in terms of nutrients or carbon are rewarded, and the control is bidirectional (Kiers *et al.* 2011; Hart *et al.* 2013). Therefore, differential allocation of carbon to these fungal types by host plants may reason for the inverse relation between these fungal variables in the present study.

Conclusion

Overall, the results of the present study indicate that AM and DSE fungal associations are widespread among plants growing on rocks like those of saxicolous plant species. This is the first report of AM and DSE fungal associations for several plant species. We speculate that the dual association of AM and DSE fungi in lithophytes could improve plant adaptability and survival under rapidly changing conditions of rock surfaces as shown for some harsh habitats. Despite their common occurrence, the roles of these fungal associations on plant adaptations to grow and survive on rock surfaces are not known unlike the role of bacteria (Puente *et al.* 2004a; b). Experimental studies are, therefore, necessary to ascertain the role of AM and DSE fungal associations on growth and nutrition of plants growing on rock surfaces.



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