Agroforest Syst (2018) 92:485–498
https://doi.org/10.1007/s10457-017-0146-x

Arbuscular mycorrhiza effects on *Faidherbia albida* (Del.) A. Chev. growth under varying soil water and phosphorus levels in Northern Ethiopia

Mengsteab Hailemariam · Emiru Birhane · Girmay Gebresamuel · Abraha Gebrekiros · Yohannes Desta · Alazar Alemayehu · Hintsa Muruts · Tesfay Araya · Lindsey Norgrove

Received: 14 November 2015 / Accepted: 22 October 2017 / Published online: 30 October 2017

Abstract Tree seedling establishment, survival and growth in dryland areas is greatly impacted by water, land use effects and soil nutrient availability. Arbuscular mycorrhizal fungi (AMF) can have a substantial effect on water and nutrient uptake by seedlings and are affected by nutrient application, water availability and inoculum source. In this study, we examined the effect of AMF inoculation, phosphorus application levels, soil water status, and inoculum source on the growth of *Faidherbia albida* seedlings. Two greenhouse experiments were conducted on *F. albida* seedlings: to compare (a) ±AMF inoculation, at three levels of volumetric soil water content (field capacity (FC), 60% of FC and 20% of FC), and three AMF inoculum sources (derived from cultivated land, grazing land and area exclosure); (b) ±AMF inoculation, at four levels of phosphorus application (0, 25, 50 and 100 mg kg^{-1}) and three AMF inoculum sources. Inoculation with AMF, higher soil water and higher P application significantly increased the growth of seedlings ($P < 0.05$). *F. albida* seedlings responded positively to increased water levels. The highest growth and AMF colonization of seedlings was recorded under the lowest water stress with AMF inoculum from area exclosure followed by grazing land inoculum source. The lowest growth was recorded under the highest water stress and cultivated land inoculum source. Plant growth and biomass were positively correlated with increased soil P application, however, AMF colonization decreased with increasing P application. Applying P and inoculating *F. albida* seedlings with indigenous AMF under low

M. Hailemariam (✉) · E. Birhane · G. Gebresamuel · A. Gebrekiros · Y. Desta · H. Muruts
Department of Land Resources Management and Environmental Protection, Mekelle University, P.O. Box 231, Mekelle, Ethiopia
e-mail: mengsteabh@gmail.com; mengsteab.hailemariam@mu.edu.et

T. Araya
Department of Agronomy, University of Fort Hare, PO Box 1314, Alice 5700, South Africa

L. Norgrove
School of Agricultural, Forest and Food Sciences, Bern University of Applied Sciences, Länggasse 85, 3052 Zollikofen, Switzerland

E. Birhane
Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway

A. Alemayehu
Addis Ababa Science and Technology University, P.O. Box: 16417, Addis Ababa, Ethiopia

water stress enables optimum plant growth improvement in dryland farming systems.

Keywords Arbuscular mycorrhizal fungi · Water status · Inoculum source · Growth performance · Phosphorus application levels · *Faidherbia albida*

Introduction

Due to the rising cost of fertilizer, there is growing interest worldwide in increasing plant biomass production using few external inputs (Siddiqui and Pichtel 2008). Numerous biological, chemical and physical factors influence soil quality. Rhizosphere microbial communities directly affect soil fertility by carrying out essential processes that contribute to nutrient cycling, soil structural maintenance and ecosystem productivity (Cardoso and Kuyper 2006; Smith and Read 2008). Among the most influential soil microbiota are the arbuscular mycorrhizal fungi (AMF) which establish symbiosis with plant roots (Cardoso and Kuyper 2006; Smith and Read 2008; Varma and Kharkwal 2009). Mycorrhizal associations are integral functioning parts of terrestrial ecosystems (Barea et al. 2011; Haselwandter and Bowen 1996; Pellegrino et al. 2015), and are widely recognized as providing a direct physical link between soil and plant roots (Smith and Read 2008). AMF form an association with plants that enhances plant growth (Alho et al. 2015; Birhane et al. 2012; Cardoso and Kuyper 2006; Smith and Read 2008) and increases resilience in nutrient-deficient, drought-prone environments (Bucher 2007; Birhane et al. 2012). The beneficial effects of AMF on plant nutrient uptake, tolerance to drought, soil pH extremes and heavy metals, root pathogen suppression, and vegetation establishment in disturbed areas have been well documented (Barea et al. 2011; Cameron et al. 2013; García and Mendoza 2007; Marschner 1998; Smith and Read 2008; Veresoglou et al. 2012). Plant mycorrhizal associations are also of significant importance for the P supply as the fungal hyphae extend into the soil and allow roots to explore a larger soil volume (Jayachandran and Shetty 2003; Joseph and Martin 2010; Smith and Read 2008).

Tropical drylands have lost much of their forest cover due to agricultural expansion, fuelwood and charcoal production, home construction and livestock grazing (Bishaw 2001; Jama and Zeila 2005). Establishment and growth of trees in dryland areas is slow due to hostile environmental conditions such as low rainfall, high temperature and overall poor land management. Hence, the presence of AMF during re-vegetation of a tree species enhances the long-term stability by contributing to nutrient cycling processes and environmental adaptability (Haselwandter and Bowen 1996; Jasper et al. 1989), which can be enhanced by inoculating seedlings as trees are established. Mycorrhizal inoculation with suitable fungi has been proposed as a promising tool for improving restoration success in semi-arid areas especially where soils are degraded (Barea et al. 2011; Garbaye 2000). To improve our ability to predict where inoculation is most likely to be beneficial, knowledge is needed about effects of site effects on AMF inoculum potential. Response to inoculation with AMF in field soils depends upon the degree of mycorrhizal dependence of the host plant, the density and effectiveness of propagules of indigenous fungi, soil nutrient concentrations, and rates of fertilizer application (Camprubí et al. 2008; Clark 1997; Seckbach and Grube 2010; Shepherd et al. 1996).

In Northern Ethiopia, deforestation and poor land management has resulted in environmental degradation. To rehabilitate degraded communal grazing lands, exclosures are established by communities and local authorities (Mekuria and Yami 2013). Exclosures are areas from which animals and humans are excluded with the goal of promoting natural regeneration of plants and reducing land degradation of formerly degraded communal grazing lands (Aerts et al. 2009; Mekuria et al. 2011; Seyoum et al. 2015). In the different land uses of the study area, be it grazing or cultivated land or exclosures, important, multipurpose agroforestry tree species, such as *Faidherbia albida (Del.) A. Chev*., have long been used by farmers for soil fertility enhancement, crop yield improvement, and fodder for livestock (Birhane et al. 2016). In these areas, drought and low soil fertility are two major soil rehabilitation constraints as they have a negative impact on soil biodiversity (including beneficial root symbionts) and plant physiological processes that affect establishment and survival of seedlings (Cardoso and Kuyper 2006).

Improvement of soil nutrient availability through application of nitrogen (N), phosphorus (P) or potassium (K) fertilizer and water may increase

establishment success and growth of dry tropical seedlings of various species (Khurana and Singh 2001). P and water uptake might be improved by mycorrhizal inoculation (Mahdi and Atabani 1992). However, the interactive effect of water stress and soil P levels on plant responses to AMF is unclear. Studies have examined growth responses following inoculation of tree species with AMF (Bati et al. 2015; Chev et al. 2009; Stevens et al. 2011; Xie et al. 2014), but limited information is available on the growth of *F. albida* seedlings inoculated with AMF from different land uses, under varying water availability or with different P applications. In this study, we hypothesized that (i) field-collected inocula from the rhizosphere soils of *F. albida* trees grown on different land uses could enhance growth of *F. albida* seedlings and (ii) growth of *F. albida* seedlings will vary depending on the AMF status of inoculum soils, soil water availability and phosphorus levels. The objectives of the study were: (i) to investigate the growth of *F. albida* seedlings inoculated with AMF from different inoculum sources and under different soil water levels and (ii) to investigate the growth of *F. albida* seedlings inoculated with AMF from different inoculum sources and with different P application levels.

Methods

Sources of AMF inoculum

Soil inocula were collected from the Kilite Awulaelo District (39°30′E–39°45′E and 13°45′N–14°00′N, altitude 1980–2500 m above sea level (m.a.s.l.) in northern Ethiopia. The average daily air temperature ranges between 15 and 30 °C, and the mean annual rainfall is 558 mm. The greenhouse experiments were conducted at Mekelle University (13°29′N and 39°28′E altitude 2200 m.a.s.l.) from July to November 2012. The mean daily temperature of the greenhouse was 27 °C during the day and 22 °C during the night with the mean daily average relative humidity of 51% for the study period.

Soil sampling

Soil samples were collected 1 m from the trunk of six *F. albida* trees per land use system (LUS) (cultivated land, grazing land and exclosure) for soil physical and chemical analysis and as the sources of inocula for the greenhouse experiment. Four insertions were made around each tree at 0–30 cm depth using a cylindrical soil core with a 10 cm internal diameter and soil from these four insertions was thoroughly mixed together to form a composite soil sample. A total of 18 composite soil samples (from near 6 trees in each of 3 land use systems) were thus collected. Approximately 1 kg of soil was taken for soil physical and chemical analysis and 10 kg retained for the pot experiments.

Physical and chemical analysis of soil samples

The 18 soil samples were analyzed for pH, electrical conductivity (EC), available P, total nitrogen (TN), organic matter (OM), exchangeable bases (Na, K, Ca and Mg), cation exchange capacity (CEC), bulk density (BD) and soil texture. OM was determined by the wet combustion procedure of Walkley–Black (Van Ranst et al. 1999). TN was determined by the wet-oxidation procedure using the Kjeldahl method (Bremner and Mulvaney 1982). Available P content was determined by the P-Olsen method (Olsen and Sommers 1982). Na, K, Ca and Mg, and CEC were determined by the 1 M ammonium acetate (pH 7) method using the percolation tube procedure (Van Reeuwijk 1995). The effective CEC was calculated as the sum of exchangeable cations extracted by the ammonium acetate method plus 1 M KCl extractable Al. BD was determined by the core method (Blake and Hartge 1986). pH and EC were determined using a suspension of 1:2.5 soil: water ratio. Soil texture was determined using the hydrometer method (Gee and Bauder 1986).

Greenhouse pot experimental design

In this study, two greenhouse experiments were conducted. The first was a three-factorial experiment with two levels of AMF treatments (inoculated = AMF+ and non-inoculated = AMF−), three levels of water availability (field capacity (FC), 60% of FC representing moderate water deficit and 20% of FC, representing a severe water deficit), and three soil inoculum sources (soil inocula collected from cultivated land, grazing land and area exclosure).

The second experiment also had a three-factorial experimental design with two AMF levels (AMF+ and AMF−), four levels of P application (0, 25, 50,

and 100 mg kg^{-1}), and three soil inoculum sources (cultivated land, grazing land and area exclosure). Soil in this experiment was maintained at field capacity.

The treatment units were arranged on a greenhouse bench in a completely randomized design (CRD) with three replications using a total of 108 seedlings. The treatment combinations common to both experiments, i.e. the zero P and at field capacity for both AMF+ and AMF− (a total of 18 pots) were used within both analyses.

AMF inoculum preparation

Composite soil samples that were used as inocula for this study were collected during the dry season from the area surrounding *F. albida* trees grown on different land uses. Inocula production followed the method of Brundrett et al. (1996). The inocula were trapped and multiplied using *Sorghum bicolor* plants grown on sterilized sand and field-collected soil that was autoclaved at 121 °C for 2 h before filling plastic pots with 10 kg of soil. About 50 g of fungal inocula consisting of a mixture of soil, spore and root fragments produced from the rhizosphere of soil and roots of pre-colonized *Sorghum bicolor* plants was added near the roots of each treated (AMF+) seedling. The controls were prepared without AMF propagules.

Pot experiment

Seeds of *F. albida* were surface sterilized and allowed to germinate on the surface of moist filter paper in sealed 15 cm petri dishes at room temperature. Four germinating seeds of uniform size were transplanted into each pot. Potted seedlings were maintained in a greenhouse until 20 days after sowing. Then, the seedlings were thinned to select the most vigorous plant in each pot. In experiment one, the soil water availability factor was applied by 20% FC, 60% FC and FC. In experiment two, the P (P_2O_5) level treatment was applied to each pot using four different concentrations (0, 25, 50, and 100 mg kg^{-1}) in a deionized water mixture.

Harvest and measurements

The plants were harvested 20 weeks after planting. For each harvested pot, plant shoots were cut at the base, and roots separated from the soil by washing over a 1–2 mm sieve into a container and retained. Total root length was measured using the grid line transect method (Tennant 1975). Plant height, root collar diameter, leaf dry mass, stem dry mass, fine root dry mass, coarse root dry mass, shoot and root dry mass, root length and leaf number were thus determined for each plant. Plant dry weight was determined after drying at 65 °C for 24 h to constant mass.

Assessment of mycorrhizal colonization

Mycorrhizal colonization was assessed as the presence or absence of arbuscules, vesicles and hyphae using the grid line intersect method (Giovannetti and Mosse 1980). Collected subsample roots were chopped into 1 cm segments and placed in 50% ethanol and stored at room temperature until clearing and staining. After decanting and rinsing the ethanol solution, roots were treated with 10% KOH and autoclaved at 121 °C for 15 min. Roots were acidified with 3% HCl (v/v) for 30 min at room temperature and stained overnight in a staining solution of Trypan blue (0.01% w/v) in lactoglycerol (5:1:1, lactic acid: glycerol: distilled water) (Brundrett et al. 1996). Afterwards, stained roots were left in a de-staining solution (50% glycerol) to remove colorations from empty root cells. Finally, six randomly selected stained roots from each replicate were prepared and examined at 100–400× magnification under a microscope. The mycorrhizal colonization by the different AMF structures was recorded using root length data.

Statistical analysis

Data were subjected to analysis of variance using SAS statistical software (version 9) (SAS 2002). Analysis of variance (ANOVA) including all two- and three-way interactions was used to test for differences in the seedling growth parameters and root colonization among AMF inoculation, land use, water level and P application. A mean separation was made using Duncan's multiple range test after ANOVA showed significant differences ($P < 0.05$).

Results

Soil properties of the three land use systems

The three soils used to collect the AMF inoculum sources differed in their mean characteristics for all parameters except for pH, EC and BD (Table 1). OC, Total N, available K, Ca, Mg and Na were greater in cultivated land and lowest in exclosure. CEC was significantly higher in grazing land than in exclosure. Soil from cultivated land had a significantly higher silt and lower sand fraction than the other land uses.

Effect of AMF, water level and AMF inoculum source on *F. albida* seedling growth

Shoot height, total dry mass, root collar diameter, total root length and leaf number of *F. albida* were significantly affected by AMF inoculation, water availability and AMF inoculum source (Table 2). Significant interactions were observed for AMF × - land use for plant dry mass, AMF × water and land use × water for all growth parameters, and AMF × - land use × water for root dry mass. AMF inoculation increased seedling growth, regardless of inoculum origin and water status. Generally, seedling growth increased significantly with increasing soil water availability (Fig. 1). However, the improved growth with AMF inoculation was more pronounced at FC and at 60% FC than under 20% FC where, presumably, water was limiting growth and thus AMF inoculation had less effect. Growth was lowest on soil from cultivated land. Seedling growth was highest on soils collected from area exclosure followed by grazing land, and the lowest was on cultivated land soils. However, for the 20% field capacity treatment, seedlings grown on grazing land soil, whose soils had a higher silt and clay content than exclosure land, performed better than those on exclosure land, presumably because of higher water holding capacity.

Effect of AMF, P application level and AMF inoculum source on *F. albida* seedling growth

Inoculation of AMF, P application, and soil source led to significant effects on the *F. albida* seedling growth (Table 3). AMF inoculation, and increasing P application significantly increased plant height, root collar diameter, total dry mass, total root length, and leaf number of *F. albida* seedlings. *F. albida* seedling

Table 1 Mean soil characteristics of each land use type used for the pot experiments (Mean SE of six replicates)

Soil properties	Unit	Land use type			*F*	*P*
		Cultivated land	Grazing land	Area exclosure		
pH	(H_2O, 1:2.5)	$6.9^{a} \pm 0.1$	$6.7^{a} \pm 0.3$	$6.9^{a} \pm 0.2$	0.16	0.8522
EC	(ds/m)	$0.15^{a} \pm 0.03$	$0.18^{a} \pm 0.05$	$0.11^{a} \pm 0.03$	1.12	0.3857
O.C	(%)	$1.01^{a} \pm 0.02$	$1.03^{a} \pm 0.06$	$0.8^{b} \pm 0.05$	7.16	0.0257
N	(%)	$0.07^{a} \pm 0.01$	$0.06^{a} \pm 0.06$	$0.035^{b} \pm 0.01$	19.68	0.0023
Av.P	(ppm)	$13.1^{a} \pm 0.9$	$10.2^{a} \pm 1.5$	$1.5^{b} \pm 0.5$	25.68	0.0011
K	(centmol(+)/kg	$1.09^{a} \pm 0.06$	$0.78^{b} \pm 0.08$	$0.22^{c} \pm 0.03$	55.68	0.0001
Ca	(centmol(+)/kg	$2.7^{a} \pm 0.29$	$2.6^{a} \pm 0.21$	$1.4^{b} \pm 0.12$	10.8	0.0103
Mg	(centmol(+)/kg	$2.6^{a} \pm 0.27$	$1.78^{b} \pm 0.1$	$1.18^{c} \pm 0.26$	10.09	0.0121
Na	(centmol(+)/kg	$0.5^{a} \pm 0.02$	$0.36^{ba} \pm 0.03$	$0.22^{b} \pm 0.01$	45.96	0.0002
CEC	meq/100gm	$6.2^{ba} \pm 0.38$	$7.73^{a} \pm 0.69$	$4.8^{b} \pm 0.38$	8.33	0.0185
BD	(g/cm^3)	$1.62^{a} \pm 0.04$	$1.47^{ab} \pm 0.04$	$1.53^{a} \pm 0.04$	3.64	0.0924
Sand	%	$68.3^{b} \pm 0.7$	$86.33^{a} \pm 2.9$	$91.0^{a} \pm 1.2$	42.04	0.0003
Silt	%	$19.0^{a} \pm 1.2$	$5.7^{b} \pm 1.8$	$3.0^{b} \pm 1.6$	38.15	0.0004
Clay	%	$12.7^{a} \pm 0.7$	$8.0^{b} \pm 1.2$	$6.0^{b} \pm 0.1$	19.75	0.0023
Textural class		Sandy loam	Sandy	Sandy		

Means in the same rows followed by same letter do not differ significantly at $P < 0.05$

Table 2 Three-way ANOVA assessing the effects of water availability at field capacity (FC), 60% of FC and 20% of FC, AMF inoculation (AMF+, AMF−), and soil inoculum source (cultivated land, grazing land and area exclosure = land use) on *F. albida* seedlings

Parameter	Unit	AMF		Land use		Water		AMF × land use		AMF × water		Land use × water		AMF x land use × water	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Height	cm	142.71	< .0001	41.89	< .0001	312.28	< .0001	1.59	0.2187	16.87	< .0001	3.67	0.0132	1.04	0.4014
Root collar diameter	cm	96.18	< .0001	5.43	0.0087	130.70	< .0001	0.11	0.8997	11.92	0.0001	9.93	< .0001	1.04	0.4014
Coarse root dry mass	gm	442.74	< .0001	305.55	< .0001	489.92	< .0001	27.55	< .0001	56.96	< .0001	24.86	< .0001	7.85	0.0001
Fine root dry mass	gm	66.40	< .0001	153.06	< .0001	255.77	< .0001	0.73	0.4882	7.56	0.0018	9.81	< .0001	1.28	0.2953
Leaf dry mass	gm	84.89	< .0001	3.44	0.0431	562.99	< .0001	0.40	0.6752	14.85	< .0001	3.95	0.0093	0.36	0.8368
Stem dry mass	gm	311.32	< .0001	302.61	< .0001	429.55	< .0001	6.63	0.0035	59.52	< .0001	26.77	< .0001	1.31	0.2858
Root dry mass	gm	387.95	< .0001	377.68	< .0001	635.40	< .0001	9.97	0.0004	44.34	< .0001	29.09	< .0001	3.36	0.0196
Shoot dry mass	gm	373.18	< .0001	182.35	< .0001	881.52	< .0001	4.24	0.0223	67.86	< .0001	17.21	< .0001	1.38	0.2595
Plant dry mass	gm	659.23	< .0001	475.66	< .0001	1282.30	< .0001	9.22	0.0006	91.71	< .0001	29.45	< .0001	2.20	0.0882
Root: shoot	gg^{-1}	65.58	< .0001	135.63	< .0001	92.37	< .0001	2.00	0.1505	3.27	0.0496	15.74	< .0001	2.12	0.0990
Total root length	cm	143.73	< .0001	156.75	< .0001	392.90	< .0001	0.03	0.9658	20.75	< .0001	6.20	0.0007	0.73	0.5749
Leaf number	Number	95.41	< .0001	48.13	< .0001	456.56	< .0001	1.76	0.1860	13.04	< .0001	7.26	0.0002	0.89	0.4826

$P < 0.05$ indicates significant sources of variation between treatments

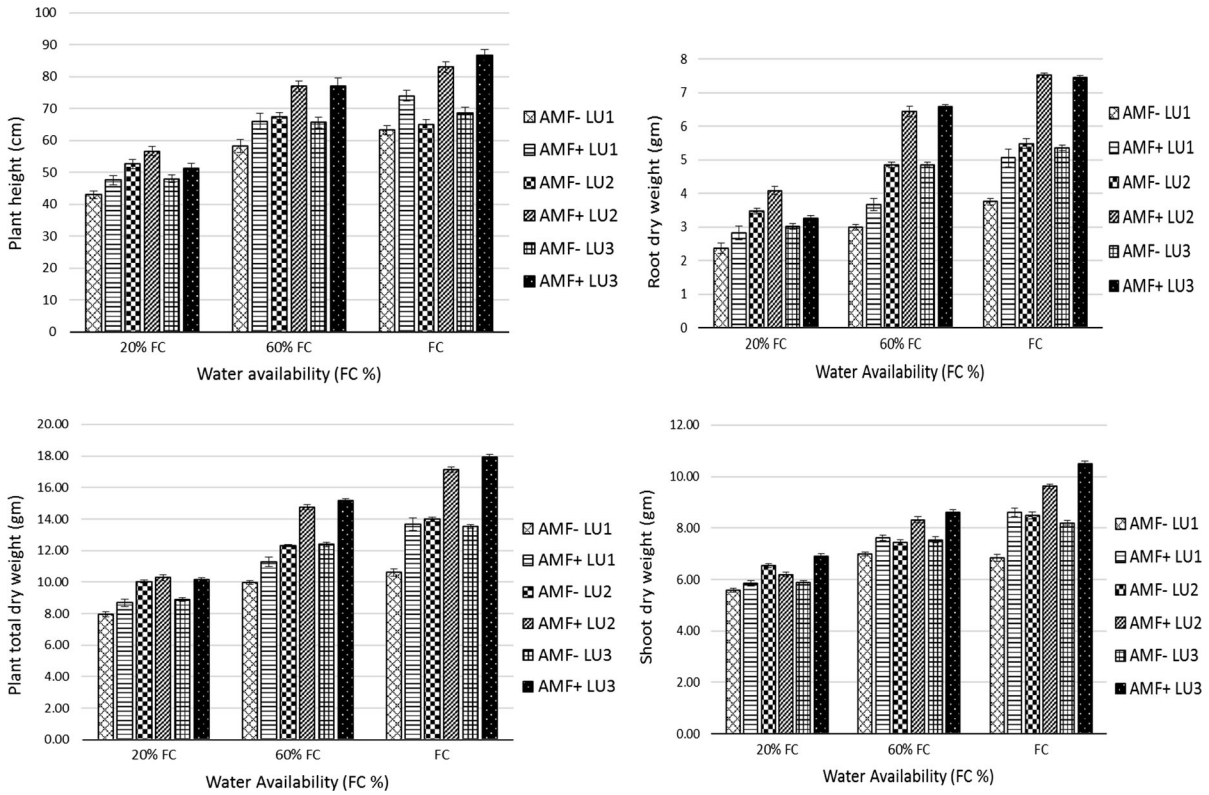

Fig. 1 Effect of water availability (FC, 60% FC and 20% FC), AMF inoculation (AMF+ and AMF−), and soil inoculum source (*LU1* cultivated land, *LU2* grazing land and *LU3* area exclosure) on size and growth of *F. albida* seedlings

growth significantly increased with increasing P application (Fig. 2). *F. albida* seedlings grown on soils collected from area exclosure followed by grazing land had significantly greater growth, and the lowest growth was on soil from cultivated land.

Effect of soil water level and inoculum source on AMF colonization

All *F. albida* seedlings inoculated with AMF inocula were colonized by AMF structures (arbuscules, vesicles, and hyphae) regardless of water level (Fig. 3, Table 4). None of the seedlings from the control group were colonized by AMF structures. Greater growth was attained by the plants that were colonized by AMF. The AMF colonization was found to increase with increasing soil water for all inoculum sources. However, the highest percentages of hyphae and arbuscule fungal structures were observed on seedlings grown on soils from area exclosure at FC and 60% FC, whereas for vesicular structures, for the drought treatments (20% FC and 60% FC) the highest percentages were observed on seedlings grown on soils from cultivated land. For the FC treatment, seedlings grown on grazing land soil had the highest colonization (Fig. 3).

Effect of phosphorus application level and soil inoculum source on AMF colonization

All *F. albida* seedlings receiving different P application levels were colonized by AMF structures. The level of P application and inoculum source significantly affected the AMF root colonization percentage of *F. albida* seedlings ($P < 0.05$) (Table 5). The highest percentage of hyphae and arbuscule colonization was observed on seedlings grown on soils collected from area exclosure and with the lowest P application rate (Fig. 4). Hyphae root colonization decreased with increasing P application rates, whereas plant growth was enhanced with increasing P application rates for all soil inoculum sources.

Table 3 Three-way ANOVA assessing the effects of P application levels (0, 25, 50, and 100 mg kg^{-1} = Fertilizer), AMF inoculation (AMF+, AMF−), and soil inoculum source (cultivated land, grazing land and area exclosure = land use) on the plant size and growth of *F. albida* seedlings

Parameter	Unit	AMF		Land use		Fertilizer		AMF × land use		AMF × fertilizer		Land use × fertilizer		AMF × land use × fertilizer	
		F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Height	cm	496.65	< .0001	75.71	< .0001	115.63	< .0001	0.25	0.7831	1.50	0.2266	1.50	0.1995	2.50	0.0344
Root collar diameter	cm	233.47	< .0001	7.47	0.0015	19.03	< .0001	1.77	0.1821	1.87	0.1468	1.10	0.3786	0.73	0.6268
Coarse root dry mass	gm	913.09	< .0001	377.44	< .0001	168.59	< .0001	21.48	< .0001	1.46	0.2367	1.91	0.0986	3.12	0.0115
Fine root dry mass	gm	151.47	< .0001	108.11	< .0001	85.28	< .0001	0.44	0.6477	0.94	0.4264	5.36	0.0003	1.57	0.1758
Leaf dry mass	gm	364.08	< .0001	146.70	< .0001	455.31	< .0001	13.76	< .0001	10.66	< .0001	54.14	< .0001	3.39	0.0072
Stem dry mass	gm	1617.83	< .0001	316.11	< .0001	193.72	< .0001	18.74	< .0001	49.32	< .0001	6.49	< .0001	3.76	0.0038
Root dry mass	gm	990.34	< .0001	472.02	< .0001	252.16	< .0001	10.85	0.0001	1.74	0.1722	2.57	0.0305	1.85	0.1092
Shoot dry mass	gm	1797.94	< .0001	418.19	< .0001	482.28	< .0001	28.89	< .0001	48.44	< .0001	13.79	< .0001	5.28	0.0003
Plant dry mass	gm	2907.59	< .0001	923.04	< .0001	763.09	< .0001	39.94	< .0001	31.23	< .0001	9.04	< .0001	2.40	0.0418
Root: shoot	gg^{-1}	0.02	0.9018	34.96	< .0001	1.74	0.1716	1.88	0.1634	17.00	< .0001	8.78	< .0001	2.82	0.0197
Total root length	cm	568.85	< .0001	407.68	< .0001	200.70	< .0001	0.95	0.3935	0.22	0.8853	19.94	< .0001	0.76	0.6068
Leaf number	number	707.76	< .0001	53.60	< .0001	87.70	< .0001	12.33	< .0001	13.83	< .0001	3.46	0.0064	2.47	0.0369

$P < 0.05$ indicates significant sources of variation between treatments

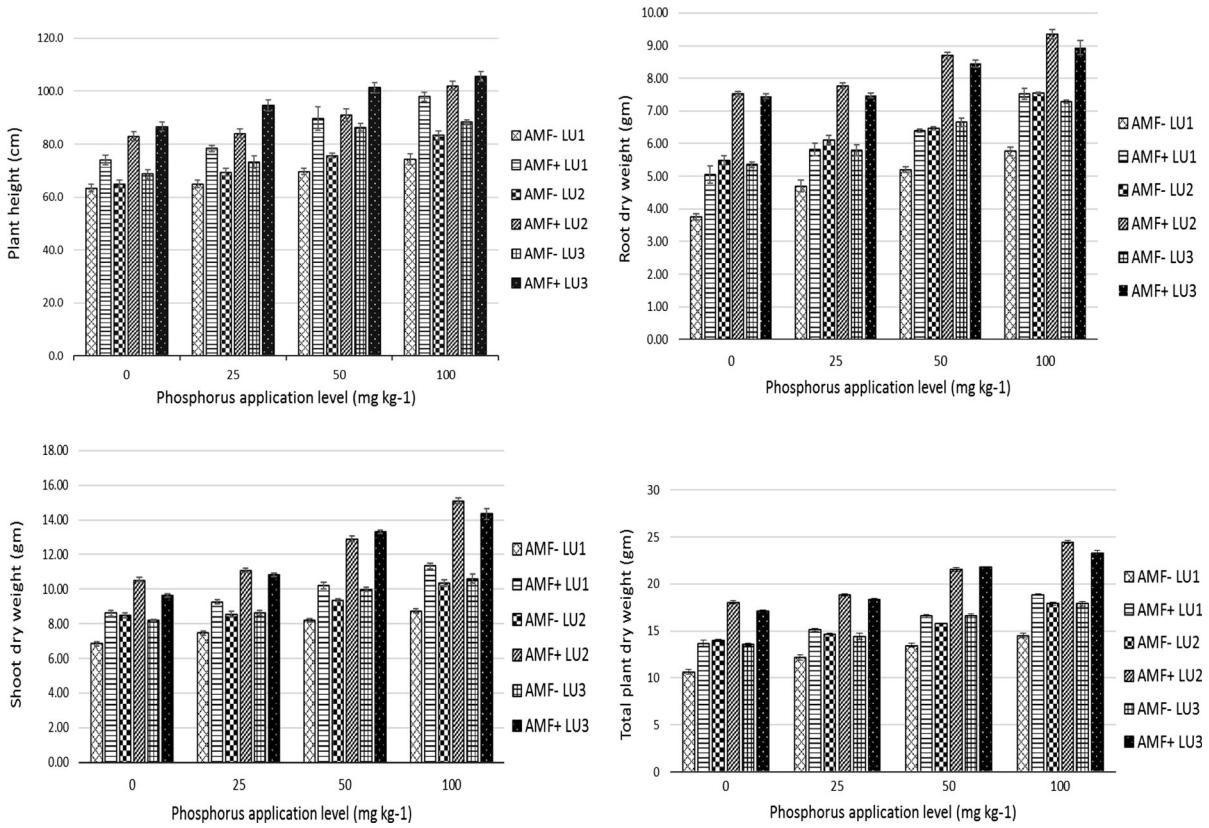

Fig. 2 Effect of P application levels (0, 25, 50, and 100 mg kg^{-1}), AMF inoculation (AMF+ and AMF−), and soil inoculum source (*LU1* cultivated land, *LU2* grazing land, *LU3* area exclosure) on the plant size and growth of *F. albida* seedlings

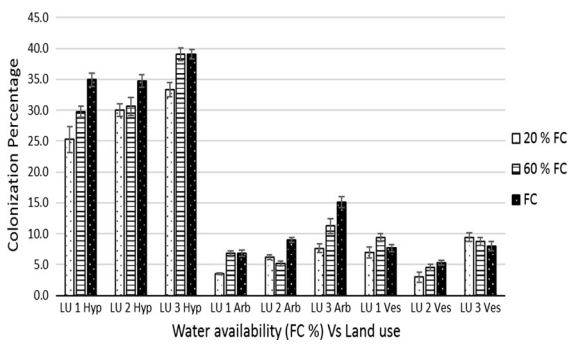

Fig. 3 Effects of water availability (FC, 60% FC and 20% FC) and soils inoculum sources (*LU1* cultivated land, *LU2* grazing land, *LU3* area exclosure) and their interaction on *Arb* arbuscular, *Ves* vesicular and *Hyp* hyphal colonization percentage of *F. albida* seedlings

Discussion

We observed a positive effect of mycorrhizal symbiosis on the growth and biomass increment of *F. albida* seedlings under greenhouse conditions using surface sterilized seeds inoculated with AMF from local soils. Increased growth and development in AMF plants compared to non-mycorrhizal ones has been reported for other species (Birhane et al. 2012; Hailemariam et al. 2013; Smith and Read 2008; Turjaman et al. 2006). The greater plant biomass measured from treatments inoculated with AMF could be due to enhanced nutrient uptake due to increased root surface area that ultimately improved plant growth rate (Haselwandter & Bowen, 1996; Jayachandran and Shetty, 2003; Kahiluoto et al. 2009; Ortas and Ustuner 2014; Xie et al. 2014). Birhane et al. (2012) reported a positive mycorrhizal effect on the growth of *Boswellia papyrifera* seedlings over control seedlings, due to significantly improved P nutrition.

Seedlings grown at field capacity grew better than those under water stress. This suggests a probable increase in water and P uptake by AMF (Birhane et al. 2012). Plants that store more water can maintain open stomata resulting in increased assimilation and

Table 4 Two-way ANOVA assessing the effects of water availability (field capacity (FC), 60% FC and 20% FC) and soil inoculum sources (cultivated land, grazing land and area exclosure) and their interaction on arbuscular, vesicular and hyphal colonization percentage of *F. albida* seedlings

Colonization	Water		Land use		Water × land use	
	F	*P*	F	*P*	F	*P*
Arbuscular	38.57	< .0001	65.85	< .0001	7.41	0.001
Vesicular	1.93	0.1745	37.65	< .0001	2.82	0.0561
Hyphal	23.03	< .0001	28.2	< .0001	2.41	0.0868

$P < 0.05$ indicates significant sources of variation between treatments

Table 5 Two-way ANOVA assessing the effects of P application levels (0, 25, 50, and 100 mg kg^{-1}) and soil inoculum sources (cultivated land, grazing land and area exclosure) and their interaction on arbuscular, vesicular and hyphal colonization percentage of *F. albida* seedlings

Colonization	Fertilizer		Land use		Fertilizer × land use	
	F	*P*	F	*P*	F	*P*
Arbuscular	14.6	< .0001	36.67	< .0001	26.51	0.001
Vesicular	5.8	0.0041	34.07	< .0001	15.82	< .0001
Hyphal	45.1	< .0001	4.9	0.0165	9.86	0.001

$P < 0.05$ indicates significant sources of variation between treatments

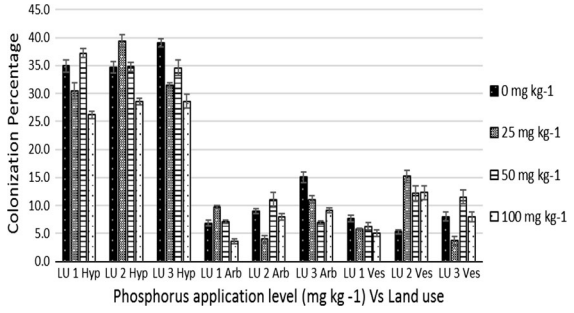

Fig. 4 Effects of phosphorus application levels (0, 25, 50, and 100 mg kg^{-1}) and soils inoculum sources (*LU1* cultivated land, *LU2* grazing land, *LU3* area exclosure) and their interaction on *Arb* arbuscular, *Ves* vesicular and *Hyp* hyphal colonization % of *F. albida* seedlings

transpiration rates (Birhane et al. 2012). In agreement with this study, Birhane et al. (2012) reported that biomass increment of *Acacia etbaica* and *A. senegal* seedlings increased with increasing water availability.

Seedlings grown on soils collected from area exclosures had the highest growth and AMF root colonization percentages and seedlings grown on soil from cultivated lands had the lowest. Within the exclosures, grazing and other agricultural activities are not allowed. This promotes natural regeneration of vegetation, degradation (Mekuria et al. 2011), and results in a positive impact on biophysical properties of formerly degraded communal grazing lands (Mengistu et al. 2005). Therefore, a low level of soil disturbance and high understory vegetation in exclosures (Birhane et al. 2010) can improve AMF propagation and occurrence of AMF in the plant roots, thereby resulting in greater biomass production of inoculated seedlings. Grazing lands of the study area are managed with medium grazing pressure, maintaining a diverse community of herbs and grasses that might promote the occurrence of indigenous AMF propagules. These combined practices resulted in better seedling growth than cultivated land inoculum sources. Conversely, seedlings grown on soil from cultivated land were smallest, whether inoculated or not, despite the cultivated soil having higher N, P and K contents and being less sandy with a probable higher water holding capacity. Where plants were inoculated, growth was better than non-inoculated plants but still less than those inoculated with other inocula sources. Thus there were factors other than those measured limiting growth on cultivated land and the inoculum

derived from cultivated land did not have as great an effect as that from the other land uses. In agricultural practices, use of heavy fertilizers and fungicides, and frequent soil disturbance/tillage reduces the lengths of extra-radical mycelium of AMF and colonization of roots (Boddington and Dodd 2000; Gosling et al. 2006), and the infectiveness of indigenous mycorrhizal populations (Schreiner and Bethlenfalvay 1995; Eason et al. 1999; Friberg 2001; Gosling et al. 2014; Martinez and Johnson 2010; Onguene et al. 2011; Ortas, 2015). This suggests that land use variations could be attributed to differences in the number of infective AMF spores and hyphae in the colonized roots of the trees grown on the different land use types (Gai et al. 2006; Jefwa et al. 2009; Ndoye et al. 2012; Tchabi et al. 2008).

Inoculating *F. albida* seedlings and applying P fertilizer resulted in an additive effect on biomass production, thus biomass increment was higher than with P application on non-inoculated seedlings. The increase of phosphatase activity in mycorrhizal plants, which has been reported by several other researchers (Dodd et al. 1987; Khalil et al. 1994), is most likely due to higher phosphatase activity of the internal hyphae produced by mycorrhizal fungi (Saito 1995). Inoculated *F. albida* seedling growth increased with increasing level of P application, yet the level of AMF colonization decreased with increasing P application rates. In this investigation the mycorrhizal dependency in seedlings was high at the lowest level of P application. This positive effect on plant growth is in agreement with the studies of Gnekow and Marschner (1989), in which mycorrhizal growth enhancement of *Malus domestica* (apple) remained significant in substrates containing high levels of extractable P. Results of the present study demonstrate mycorrhizal symbiosis and suggest P nutrition as an important benefit. Greater responsiveness to and dependence of AMF is characteristics of mycorrhizal plants grown at lower soil P concentrations and low tissue P concentration (Smith and Read 1997).

Conclusion

The present study suggests a positive effect on *F. albida* trees if properly inoculated with AMF, although percentage colonization was lower under the highest rates of P fertilizer application (100 mg kg^{-1}). AMF/inoculated seedlings show significant growth increment and increased colonization with increasing soil water availability. The highest growth of AMF inoculated seedlings was recorded at field capacity, using AMF from area exclosure. The lowest growth was recorded under 20% field capacity and with cultivated land inoculum sources. P application resulted in significant increases in plant height and dry mass. Plant growth and biomass increased with increasing level of P application, yet the AMF colonization percentage decreased with increasing P application. However, the highest growth parameters of AMF inoculated seedlings was recorded on *F. albida* seedlings grown on soil collected from area exclosure followed by grazing land, and the lowest was on soil inoculum from cultivated land. Generally, this emphasizes the importance of prior native soil mycorrhizal potentials of area exclosure and grazing land to enable screening for better combinations of *F. albida* seedlings with AMF inoculation, under low water stress and low P application rate to achieve optimum plant growth improvement and environment protection. This knowledge is essential for rehabilitation efforts of dryland areas. Hence, further field studies are needed to confirm the beneficial effects of AMF inoculum because there might be other biotic and abiotic factors interacting with AMF.

Acknowledgements The financial assistance provided by Mekelle University recurrent budget (CDANR/RB/14/2012) is gratefully acknowledged. We are grateful to the two anonymous referees for constructive comments on an earlier version of this manuscript.

References

Aerts R, Nyssen J, Haile M (2009) On the difference between "exclosures" and "enclosures" in ecology and the environment. J Arid Environ 73:762–763

Alho L, Carvalho M, Brito I, Goss MJ (2015) The effect of arbuscular mycorrhiza fungal propagules on the growth of subterranean clover (*Trifolium subterraneum* L.) under Mn toxicity in ex situ experiments. Soil Use Manag 31(2):337–344. https://doi.org/10.1111/sum.12183

Badege B (2001) Deforestation and land degradation in the Ethiopian highlands: a strategy for physical recovery. Northeast Afr Stud 8(1):7–25. https://doi.org/10.1353/nas.2005.0014

Barea JM, Palenzuela J, Cornejo P, Estrada B, Azcón R, Ferrol N (2011) Ecological and functional roles of mycorrhizas in semi-arid ecosystems of Southeast Spain. J Arid Environ

75(12):1292–1301. https://doi.org/10.1016/j.jaridenv.2011.06.001

Bati CB, Santilli E, Lombardo L (2015) Effect of arbuscular mycorrhizal fungi on growth and on micronutrient and macronutrient uptake and allocation in olive plantlets growing under high total Mn levels. Mycorrhiza 25:97–108. https://doi.org/10.1007/s00572-014-0589-0

Birhane E, Kuyper TW, Sterck FJ, Bongers F (2010) Arbuscular mycorrhizal associations in *Boswellia papyrifera* (frankincense-tree) dominated dry deciduous woodlands of Northern Ethiopia. For Ecol Manag 260(12):2160–2169. https://doi.org/10.1016/j.foreco.2010.09.010

Birhane E, Sterck FJ, Fetene M, Bongers F, Kuyper TW (2012) Arbuscular mycorrhizal fungi enhance photosynthesis, water use efficiency, and growth of frankincense seedlings under pulsed water availability conditions. Oecologia 169(4):895–904. https://doi.org/10.1007/s00442-012-2258-3

Birhane E, Gebremeskel K, Taddesse T, Hailemariam M, Hadgu KM, Norgrove L, Negussie A (2016) Integrating *Faidherbia albida* trees into a sorghum field reduces striga infestation and improves mycorrhiza spore density and colonization. Agrofor Syst. https://doi.org/10.1007/s10457-016-0027-8

Bishaw B (2001) Deforestation and land degradation in the Ethiopian Highlands: A strategy for physical recovery. Northeast African Studies 8(1):7–25. https://doi.org/10.1353/nas.2005.0014

Blake GR, Hartge KH (1986) Bulk Density 1. In: Klute A (ed) Methods of soil analysis: part 1-physical and mineralogical methods. SSSA Book Ser. 5.1. SSSA, ASA, Madison, pp 363–375. https://doi.org/10.2136/sssabookser5.1.2ed.c13

Boddington CL, Dodd JC (2000) The effect of agricultural practices on the development of indigenous Arbuscular mycorrhizal fungi. I. Field studies in an Indonesian ultisol. Plant Soil 218:137–144

Bremmer JM, Mulvaney CS (1982) Nitrogen total. In: Page AL (ed) Methods of soil analysis, part 2 chemical and microbiological properties ASA monograph, number 9. Madison, WI, USA, pp 595–624

Bremner JM, Mulvaney CS (1982) Nitrogen total. In: Page AL (ed) Methods of soil analysis, part 2, chemical and microbiological properties. SSSA, Madison, pp 595–641

Brundrett M, Bougher N, Dell B, Grove T, Malajczuk N (1996) Working with mycorrhizas in forestry and agriculture. ACIAR Monograph. J Biol Chem 32(June 1982):374. https://doi.org/10.1046/j.1469-8137.1997.00703-7.x

Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. New Phytol 173:11–26

Cameron DD, Neal AL, Van Wees SCM, Ton J (2013) Mycorrhiza-induced resistance: more than the sum of its parts? Trends Plant Sci 18(10):539–545. https://doi.org/10.1016/j.tplants.2013.06.004

Camprubí A, Estaún V, Nogales A (2008) Response of the grapevine rootstock Richter 110 to inoculation with native and selected arbuscular mycorrhizal fungi and growth performance in a replant vineyard. Mycorrhiza 18:211–216. https://doi.org/10.1007/s00572-008-0168-3

Cardoso IM, Kuyper TW (2006) Mycorrhizas and tropical soil fertility. Agric Ecosyst Environ 116:72–84. https://doi.org/10.1016/j.agee.2006.03.011

Chev DA, Shinkafi MA, Aduradola AM (2009) Effects of Mycorrhiza on the growth and productivity of *Faidherbia albida* (Del.) A. Chev. Niger J Basic Appl Sci 17(2):198–201

Clark RB (1997) Arbuscular mycorrhizal adaptation, spore germination, root colonization, and host plant growth and mineral acquisition at low pH. Plant Soil 192(1):15–22. https://doi.org/10.1023/A:1004218915413

Dodd JC, Burton CC, Burns RG, Jeffries P (1987) Phosphatase activity associated with the rhizosphere of plants infected with vesicular-arbuscular mycorrhizal fungi. New Phytol 7:163–172

Eason WR, Scullion J, Scott EP (1999) Soil parameters and plant responses associated with arbuscular mycorrhizas from contrasting grassland management regimes. Agric Ecosyst Environ 73(3):245–255. https://doi.org/10.1016/S0167-8809(99)00054-7

Friberg S (2001) Distribution and diversity of arbuscular mycorrhizal fungi in traditional agriculture on the Niger inland delta, Mali, West Africa, 53–80

Gai JP, Feng G, Cai XB, Christie P, Li XL (2006) A preliminary survey of the arbuscular mycorrhizal status of grassland plants in southern Tibet. Mycorrhiza 16(3):191–196. https://doi.org/10.1007/s00572-005-0032-7

Garbaye J (2000) The role of ectomycorrhizal symbiosis in the resistance of forests to water stress. Agric 29:63–69

García IV, Mendoza RE (2007) Arbuscular mycorrhizal fungi and plant symbiosis in a saline-sodic soil. Mycorrhiza 17:167–174. https://doi.org/10.1007/s00572-006-0088-z

Gee GW, Bauder JW (1986) Particle-size analysis 1. In: Klute A (ed) Methods of soil analysis: part 1—physical and mineralogical methods, vol 5. Soil Science Society of America, Fitchburg, pp 383–411. https://doi.org/10.2136/sssabookser5.1.2ed

Giovannetti M, Mosse B (1980) An evaluation of techniques for measuring vesicular Arbuscul. New Phytol 84:489–500

Gnekow MA, Marschner H (1989) Role of VA-mycorrhiza in growth and mineral nutrition of apple (*Malus pulmilavar*. domestica) rootstock cuttings. Plant Soil 119:285–293

Gosling P, Hodge A, Goodlass G, Bending GD (2006) Arbuscular mycorrhizal fungi and organic farming. Agric Ecosyst Environ 113:17–35

Gosling P, Proctor M, Jones J (2014) Distribution and diversity of *Paraglomus* spp. in tilled agricultural soils. Mycorrhiza 24:1–11. https://doi.org/10.1007/s00572-013-0505-z

Hailemariam M, Birhane E, Asfaw Z, Zewdie S (2013) Arbuscular mycorrhizal association of indigenous agroforestry tree species and their infective potential with maize in the Rift Valley, Ethiopia. Agrofor Syst 87(6):1261–1272. https://doi.org/10.1007/s10457-013-9634-9

Haselwandter K, Bowen GD (1996) Mycorrhizal relations in trees for agroforestry and land rehabilitation. For Ecol Manag 81:1–17

Jama B, Zeila A (2005) Agroforestry in the drylands of eastern Africa: (a call to action. ICRAF Working Paper—no. 1. World Agroforestry Centre), Nairobi

Jasper DA, Abbott LK, Robson AD (1989) Acacias respond to additions of phosphorus and to inoculation with VA mycorrhizal fungi in soils stockpiled during mineral sand mining. Plant Soil 108:99–108

Jayachandran K, Shetty KG (2003) Growth response and phosphorus uptake by arbuscular mycorrhizae of wet prairie sawgrass. Aquat Bot 76:281–290. https://doi.org/10.1016/S0304-3770(03)00075-5

Jefwa JM, Mung'atu J, Okoth P, Muya E, Roimen H, Njuguini S (2009) Influence of land use types on occurrence of arbuscular mycorrhizal fungi in the high altitude regions of Mt. Kenya. Trop Subtrop Agroecosyst 11: 277–290. http://redalyc.uaemex.mx/redalyc/pdf/939/93913057004.pdf

Joseph S, Martin G (2010) Symbiosis and stress. Springer, Berlin. https://doi.org/10.1007/978-90-481-9449-0

Kahiluoto H, Ketoja E, Vestberg M (2009) Contribution of arbuscular mycorrhiza to soil quality in contrasting cropping systems. Agric Ecosyst Environ 134(1–2):36–45. https://doi.org/10.1016/j.agee.2009.05.016

Khalil S, Loynachan TE, Tabatabia MA (1994) Extension of the phosphorus depletion zone in VA mycorrhizal white clover in a calcareous soil. Plant Soil 136:41–48

Khurana E, Singh JS (2001) Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ Conserv 28:39–52. https://doi.org/10.1017/S0376892901000042

Mahdi AA, Atabani IMA (1992) Response of *Bradyrhizobium* inoculated soybean and lablab bean to inoculation with vesicular mycorrhizae. Exp Agric 28:399–407

Marschner H (1998) Role of root growth, arbuscular mycorrhiza, and root exudates for the efficiency in nutrient acquisition. Field Crops Res 56(1–2):203–207. https://doi.org/10.1016/S0378-4290(97)00131-7

Martinez TN, Johnson NC (2010) Agricultural management influences propagule densities and functioning of arbuscular mycorrhizas in low- and high-input agroecosystems in arid environments. Appl Soil Ecol 46(2):300–306. https://doi.org/10.1016/j.apsoil.2010.07.001

Mekuria W, Yami M (2013) Changes in woody species composition following establishing exclosures on grazing lands in the lowlands of Northern Ethiopia. Afr J Environ Sci Technol 7:30–40. https://doi.org/10.5897/AJEST11.378

Mekuria W, Veldkamp E, Tilahun M, Olschewski R (2011) Economic valuation of land restoration: the case of exclosures established on communal grazing lands in Tigray, Ethiopia. Land Degrad Dev 22:334–344

Mengistu T, Teketay D, Hulten H, Yemshaw Y (2005) The role of enclosures in the recovery of woody vegetation in degraded dryland hillsides of central and northern Ethiopia. J Arid Environ 60:259–281

Ndoye F, Kane A, Ngonkeu Mangaptché EL, Bakhoum N, Sanon A, Diouf D, Sy MO, Baudoin E, Noba K, Prin Y (2012) Changes in land use system and environmental factors affect arbuscular mycorrhizal fungal density and diversity, and enzyme activities in rhizospheric soils of *Acacia senegal* (L.) Willd. ISRN Ecol. https://doi.org/10.5402/2012/563191

Olsen SR, Sommers LE (1982) Phosphorus. In: Page AL (ed) Methods of soil analysis, part 2 chemical and microbiological properties. ASA Monograph, Number 9. Madison, WI, USA, 403–430

Onguene NA, Kuyper TW (2005) Growth response of three native timber species to soils with different arbuscular mycorrhizal inoculum potentials in South Cameroon: indigenous inoculum and effect of addition of grass inoculum. For Ecol Manag 210(1–3):283–290. https://doi.org/10.1016/j.foreco.2005.02.038

Onguene NA, Ngonkeu LEM, Kuyper TW (2011) Growth response of *Pterocarpus soyauxii* and *Lophira alata* seedlings to host soil mycorrhizal inocula in relation to land use types. Afr J Microbiol Res 5(17):2391–2398. https://doi.org/10.5897/AJMR10.061

Ortas I (2015) Comparative analyses of Turkey agricultural soils: potential communities of indigenous and exotic mycorrhiza species' effect on maize (*Zea mays* L.) growth and nutrient uptakes. Eur J Soil Biol 69:79–87. https://doi.org/10.1016/j.ejsobi.2015.05.006

Ortas I, Ustuner O (2014) Determination of different growth media and various mycorrhizae species on citrus growth and nutrient uptake. Sci Hortic 166:84–90. https://doi.org/10.1016/j.scienta.2013.12.014

Pellegrino E, Bosco S, Ciccolini V, Pistocchi C, Sabbatini T, Silvestri N, Bonari E (2015) Agriculture, ecosystems and environment agricultural abandonment in mediterranean reclaimed peaty soils: long-term effects on soil chemical properties, arbuscular mycorrhizas and CO_2 flux. Agric Ecosyst Environ 199:164–175. https://doi.org/10.1016/j.agee.2014.09.004

Saito M (1995) Enzyme activities of the internal hyphae and germinated spores of an arbuscular mycorrhizal fungus, *Gigaspora margariata* Becker and Hall. New Phytol 129:425–431

SAS (2002). User's guide: statistics version 9.00. SAS Institute, Inc., Cary, North Carolina

Schreiner RP, Bethlenfalvay GJ (1995) Mycorrhizal interactions in sustainable agriculture. Crit Rev Biotechnol 15:271–285

Seckbach, Grube (2010) Symbiosis and stress: joint ventures in biology, cellular origin, life in exetereme habitats, astrobiology. Springer, Berlin pp 359–374

Seyoum Y, Birhane E, Mengistu T, Esmael N, Hagazi N, Kassa H (2015) Enhancing the role of the forestry sector in building climate resilient green economy in Ethiopia: scaling up effective forest management practices in Tigray National Regional state with emphasis on area exclosure. Center for international Forestry Research, Ethiopia Offices, Addis Ababa

Shepherd KD, Jefwa J, Wilson J, Ndufa JK, Ingleby K, Mbuthu KW (1996) Infection potential of farm soils as mycorrhizal inocula for Leucaena leucocephela. Biol Fertil Soils 22:16–21

Siddiqui ZA, Pichtel J (2008) Mycorrhixae: an overview. In: Siddiqui ZA, Akhtar MS, Futai K (eds) Mycorrhizae: Sustainable Agriculture and Forestry. Springer, Dordrecht pp 1–36

Smith SE, Read DJ (1997) Mycorrhizal symbiosis, 2nd edn. Academic Press, London

Smith SE, Read DJ (2008) Mycorrhizal symbiosis. Soil Sci Soc Am J. https://doi.org/10.1097/00010694-198403000-00011

Stevens KJ, Wall CB, Janssen JA (2011) Effects of arbuscular mycorrhizal fungi on seedling growth and development of two wetland plants, *Bidens frondosa* L., and *Eclipta prostrata* (L.) L., grown under three levels of water availability. Mycorrhiza 21:279–288. https://doi.org/10.1007/s00572-010-0334-2

Tchabi A, Coyne D, Hountondji F (2008) Arbuscular mycorrhizal fungal communities in sub-Saharan savannas of Benin, West Africa, as affected by agricultural land use intensity and ecological zone. Mycorrhiza 18(4):181–195. https://doi.org/10.1007/s00572-008-0171-8

Tennant D (1975) A test of modified line intersect method of estimating root length. J Ecol 63:995–1001

Turjaman M, Tamai Y, Santoso E (2006) Arbuscular mycorrhizal fungi increased early growth of two non-timber forest product species *Dyera polyphylla* and *Aquilaria filaria* under greenhouse conditions. Mycorrhiza. https://doi.org/10.1007/s00572-006-0059-4

Van Ranst E, Verloo M, Demeyer A, Pauwels JM (1999) Manual for the soil chemistry and fertility laboratory: analytical methods for soils and plants, equipment and management of consumables. University of Gent, Belgium

Van Reeuwijk LP (1995) Procedures for soil analysis, 5th ed. Technical Paper 9, International Soil Reference & Information Centre (ISRIC), Wageningen, The Netherlands

Varma A, Kharkwal AC (2009) Symbiotic fungi. Springer, Berlin. https://doi.org/10.1007/978-3-540-95894-9

Veresoglou SD, Chen B, Rillig MC (2012) Arbuscular mycorrhiza and soil nitrogen cycling. Soil Biol Biochem 46:53–62. https://doi.org/10.1016/j.soilbio.2011.11.018

Xie X, Weng B, Cai B, Dong Y, Yan C (2014) Effects of arbuscular mycorrhizal inoculation and phosphorus supply on the growth and nutrient uptake of *Kandelia obovata* (Sheue, Liu & Yong) seedlings in autoclaved soil. Appl Soil Ecol 75:162–171. https://doi.org/10.1016/j.apsoil.2013.11.009