Environmental and Experimental Biology (2015) 13: 139–145 *Original Paper*

Arbuscular mycorrhizal colonization in roots of sand dune plants in relation to soil factors

Ligita Liepiņa, Arta Dimbiere, Brigita Laime, Didzis Tjarve, Didzis Elferts, Guntis Tabors, Guntis Brūmelis*

University of Latvia, Faculty of Biology, Jelgavas 1, Riga, LV 1004, Latvia

*Corresponding author, E-mail: guntis.brumelis@lu.lv

Abstract

Seacoast plant communities represent primary successions characterized by a harsh environment in which mycorrhizal symbioses are known to be important for plant survival and growth. The study was carried in two grey dune areas (Užava and Pāvilosta) on the western coast of Latvia by the Baltic Sea. We examined how root colonization and abundance of arbuscular mycorrhiza differed along a primary dune succession from an early successional primary dune to an overgrowing grey dune, in relation to soil factors. We hypothesized that plant species growing on soil with a poorly developed soil horizon and low C, P and N concentration would have a higher extent of arbuscular mycorrhiza colonization. We also tested the relationship of soil factors and fungal abundance in roots within specific plant species. In a total of 93 plots among 5 habitats, we determined soil carbon, phosphorus and nitrogen concentrations and sampled roots of dominant plants for determination of arbuscular mycorrhizal (vesicules and hyphae) frequency, abundance of arbuscular mycorrhizal vesicules and hyphae, and abundance of arbuscules. The results showed that extent of mycorrhizal colonization was related to soil development, being more important in the most nutrient poor habitats, compared to grassland habitats. However, slight increases in P and N concentration were associated in increased mycorrhizal colonization in early successional stages and disturbed habitats.

Key words: carbon, dunes, mycorrhiza, nitrogen, phosphorus, sand texture, seacoast communities.
Abbreviations: AM, arbuscular mycorrhiza.

Introduction

About 80% of vascular plant species are known to have arbuscular mycorrhizal symbioses, which is particularly important in conditions of nutrient deficiency and water stress (Smith et al. 2010). Arbuscular mycorrhiza (AM) have an important role in nitrogen and phosphorus acquisition by plants (Hodge et al. 2010; Smith et al. 2011). However, plant species differ in mycorrhizal response in complex ways across gradients of N and P availability (Hoeksema et al. 2010). AM abundance decreases with higher P (Richardson et al. 2011) and also N concentration (Treseder 2004) in soil, while soil pH affects mostly fungal community composition (Dumbrell et al. 2010).

Seacoast plant communities are characterized by poorly formed soils and in this nutrient poor environment with shifting sands, mycorrhizal symbioses might be crucial for plant survival and growth. Most of the plant species of dune communities are known to have symbioses with AM with variable degrees of colonization (Logan et al. 1989; Druva-Lusite, Ievinsh 2010). AM have a role in stabilization of dune soil indirectly by increased performance of dune plants due to improved P nutrition, and also directly by forming aggregations of soil particles (Koske, Polson 1984). Other suggested functions of AM in poor and dry environments include deposition of C beyond the rhizosphere, symbiotic adaptation to dry conditions via, for example, better access of AM to water-filled pores, increased resistance of plants to root pathogens and greater plant success in resource-mediated competition. However, on the heterogeneous and unpredictable seacoast, AM colonization might be expected to be greater in the more stable habitats (Ievinsh 2006).

Primary plant successions are associated with pedogenesis by development of an organic horizon, changes in nutrient availability and pH, and these soil factors interact with the mycorrhizal community (Dickie et al. 2013). AM community composition changes during primary dune succession, which might not be linked with improved plant growth (Sikes et al. 2012). AM abundance in these successions seems to be more associated with soil factors than to plant community composition (Sikes et al. 2014). Previous study has shown increased AM colonization in fixed-dunes with higher organic matter and N concentration (Sridhar 2006). Here we examined how root colonization by AM differed along a primary dune succession from an early successional primary dune to an overgrowing grey dune, in relation to soil factors. We hypothesized that plant species growing on soil with a poorly developed soil horizon and low C, P and N concentration would have a higher degree of AM colonization. We also tested the relationship of soil factors and fungal abundance in roots within specific plant species.

Materials and methods

Description of study area

The study was carried on the western coast of Latvia. Mean temperature in July and January is +16.5 and −3.0 °C, respectively, and precipitation is 600–700 mm yearly (www.meteo.lv). Dominating westerly winds cause regular transport of sand from the beach zone to the grey dune area (Eberhards 2003). Two grey dune areas (Užava and Pāvilosta) on the western coast of Latvia by the Baltic Sea were selected for the study. The area of both selected dune sites is mostly within nature reserves included in the Natura 2000 network. These sites were chosen, as they are the best examples of natural dune systems in the Baltic region. Both are representative of the European Union habitat 2130* fixed coastal dunes with herbaceous vegetation (grey dunes)". The grey dune area consists of a vegetation mosaic with patches of moss, lichens, and herbs. Wave and wind erosion, as well as human caused disturbance has created patches of bare sand. Over time the habitat has partly overgrow with short shrubs and pine (*Pinus sylvestris*). Other grey dune habitats in Latvia form small remnants altered by human activity, and thus were not considered in the study.

Plot location with habitats

A total of 93 plots were established, 50 in Pāvilosta and 43 in Užava. Habitats within each site with different vegetation structure (density and cover), level of disturbance (overblowing sand) and soil development were chosen. Within these habitats, plots with radius 1.5 m (7.07 m^2) were established randomly. Plots randomly falling in places with no vegetation, and those overgrown with trees or Calluna vulgaris, were omitted and the next random location was chosen. A map of plot locations is shown in Fig. 1. Description of vegetation in these habitat types is given in Table 1.

In Pāvilosta, the existing (and chosen) habitat types were: (1) early successional grey dune stage dominated by pioneer herbaceous species and moss and lichen species typical of xeric habitats, (2) grassland type grey dune with dense vegetation dominated by graminoid species and pleuropcarpous moss species, and (3) disturbed grey dune with actively overblowing sand behind a foredune, vegetation dominated by xeric moss species and typical fore-dune species.

In the Užava site, two grey dune habitat types were distinguished: (1) overgrowing xerophytic grey dune on pebble-gravel-sand substrate with little overblowing sand and dominated by typical grey dune herbaceous species and *Cladonia* spp. lichens, with scattered low shrubs and

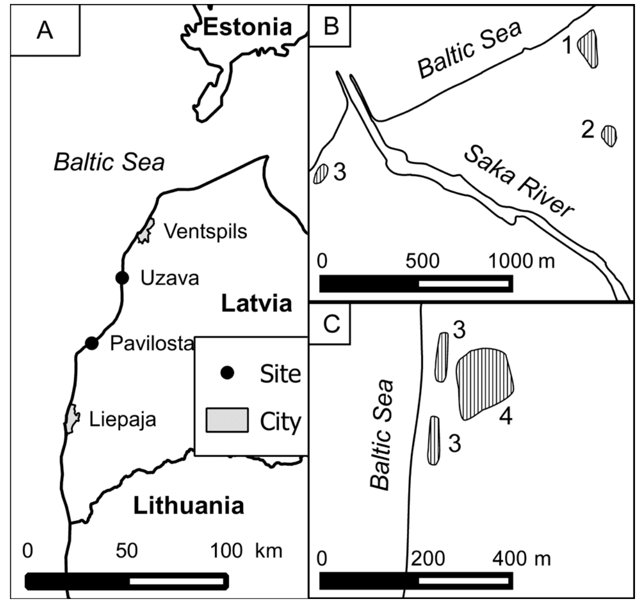

Fig. 1. Map of the study area showing location of sites and habitats. A, location of the sites in Latvia; B, habitats in the Pavilosta site; C, habitats in the Uzava site. 1, early successional grey dune; 2, grassland type grey dune; 3, disturbed grey dune; 4, overgrowing grey dune.

(2) disturbed grey dune with actively overblowing sand at a bluff edge, behind a fore-dune, vegetation dominated by xeric moss species and typical fore-dune species.

Soil and root sampling

In October 2014, samples of the surface soil layer to 10-cm depth were removed by trowel from five random locations within each plot and collected together. For each of the most frequent plant species in plots, root samples from three individuals were removed by carefully digging and removing loose soil. The samples were placed in bags and transported to the laboratory, where they washed under tap water. The roots were then cut into 1-cm-long segments and stained with trypan blue according to the method of Phillips and Hayman (1970). The number of species in plots differed and therefore the number of species sampled varied from 1 to 11. In total 501 plant root samples from 33 species were collected.

Soil analysis

Soil samples were dried for 48 h at 80 °C and then sieved using a 2-mm mesh to remove roots and pebbles. Sand texture was described as fine, medium or coarse. Soil pH was determined with a glass electrode in 1 M KCl solution (2 g soil and 20 mL solution). Phosphorus concentration was determined in soil extracts by colorimetric analysis using the ascorbic acid method (Egner et al. 1960). Nitrogen and carbon concentrations were determined using a CHNS-O EA3000 Elemental Analyser.

Table 1. Description of sampled habitat types within sites. Coordinates (LKS92) are given in brackets

Habitat type	Number of plots	Structure and composition
Pāvilosta site		
Early successional grey dune (328735, 6309040)	20	Dominant cover of lichens (mainly *Cladonia* spp.) and acrocarpic xerophytic mosses (*Racomitrium canescens, Ceratodon purpureus*) and sparse herbaceous pioneer species (*Corynephorus canescens, Carex arenaria*).
Grassland-type grey dune (328853, 6308675)	20	Dense vegetation patches (mean about 60% cover) dominated by graminoid species (*Festuca sabulosa, Calamagrostis epigeios*) and herbaceous species among patches of pleurocarpous mosses (*Hypnum cupressiforme, Dicranum scoparium*).
Disturbed grey dune (327319, 6308503)	10	Patches of acrocarpic xerophytic mosses (*Syntrichia ruralis, Ceratodon purpureus*). Herbaceous layer composed of foredune (*Ammophila arenaria, Festuca arenaria*) and grey dune species are common.
Užava site		
Overgrowing grey dune (343606, 6341549)	23	Stable xerophytic grey dune (minimally overblown with sand) on pebble-gravel-sand substrate overgrowing in patches with *Pinus sylvestris* and low shrubs (Arctostaphylos uva-ursi), herbaceous layer dominated by *Festuca sabulosa, Koeleria glauca, Thymus serpyllum* and *Anthyllis maritima*, lichen cover mainly *Cladonia* spp. 10 to 60%.
Disturbed grey dune (343508, 6341512)	20	Herbaceous layer with mean cover. Herbaceous layer dominated by *Festuca sabulosa, Koeleria glauca, Thymus serpyllum* and *Anthyllis maritima*, mixed with foredune species *Ammophila arenaria* and *Festuca arenaria*. Patches of acrocarpic xerophytic mosses (*Syntrichia ruralis, Ceratodon purpureus*). Lichens absent.

Arbuscular mycorrhizal analysis

Roots were stained with trypan blue according to the method of Phillips and Hayman (1970). Fifteen root tips with length 1 cm were placed on glass slides. By fields of view at magnification 200 ×, amount of vesicules and hyphae was assessed in intensity classes of zero to five and amount of arbuscules in classes of zero to three as described by Trouvelot et al. (1986). Using the MYCOCALC program (Trouvelot et al. 1986), the following parameters were determined: arbuscular mycorrhizal (vesicules and hyphae) frequency (percent of fields of view with mycorrhizal colonization) of colonization in whole root systems (F), abundance of arbuscular mycorrhizal vesicules and hyphae (percent of fields of view with mycorrhizal colonization weighted by intensity classes) in whole root systems (M), and abundance of arbuscules (percent of fields of view with arbuscules weighted by intensity classes in whole root systems (A).

Statistical analysis

Arbuscular mycorhization parameters (F, M, A) were arcsine square root transformed before statistical analysis. The Chi-square test was used to compare differences in sand texture class distribution between sites and between habitat types. One-way ANOVA and the Tukey HSD test as a post-hoc test was used to compare differences in arbuscular mycorhization parameters (F, M, A) and soil parameters between sites, habitat types and sand texture classes. Pearson's correlation coefficients between soil parameters were determined. Linear regression analyses was used to determine relationship between soil parameters (independent variables) and arbuscular mycorhization parameters (F, M, A) (dependent variables); a separate model was developed for each combination of soil and arbuscular mycorhization parameter. ANOVA and linear regression analysis of arbuscular mycorhization parameters was performed in two ways: (1) calculating mean parameter value for each plot from all collected plant species; (2) doing separate analysis for plant species (*Festuca sabulosa, Hieracium umbellatum, Koeleria glauca* and *Thymus serpyllum*) that were found in more than 30 plots. As *Koeleria glauca* was not found in the grassland habitat (the only fixed dune habitat) at Užava, to avoid bias, the analysis was conducted for *Festuca sabulosa*, *Hieracium umbellatum*, and *Thymus serpyllum* using data from all habitats, and repeated again for all four plant species without data for the grassland habitat. All statistical analyses were performed at significance level $p < 0.05$ in program R 3.2.1. (R Core Team 2015).

Results

Soil characteristics

The sites and habitats differed in soil development stage. The grassland habitat had the highest C, P and N concentrations (Table 2). Among the other habitats, the overgrowing habitat had higher C and the early succession habitat had higher P concentration. Soil pH was in the neutral range, but significantly differed between sites and habitats. Lower pH levels occurred at Pāvilosta, and particularly in

Table 2. Soil chemical characteristics. Letters show significant differences (Tukey HSD test as a post-hoc test when ANOVA indicated significant differences) between sites and between habitats.

		C (%)	pH	P (mg kg^{-1})	N (%)
Site	Pāvilosta	0.57	6.3 a	1.07 a	0.038 a
	Užava	0.58	7.5 b	0.24 b	0.009 b
Habitat	Early (Pāvilosta)	0.14 a	5.7 a	0.60 a	0.009 a
	Grassland (Pāvilosta)	1.15 c	6.6 b	1.96 b	0.080 b
	Disturbed (Pāvilosta)	0.26 ab	7.0 c	0.22 a	0.012 a
	Overgrowing (Užava)	0.74 d	7.6 b	0.29 c	0.013 c
	Disturbed (Užava)	0.39 b	7.4 d	0.19 c	0.005 c

the early successional habitat. C, P and N concentrations were significantly positively correlated (Table 3). There was a weak significant positive correlation of pH with C concentration and negative with P concentration, but this was due to severe outliers, presumably due to sea shell deposits and considered to be artefacts. For this reason, pH was not used in further analysis.

Sand texture indicated spatial sorting of deposited material in the habitats (Table 4). Distribution of sand texture was rather uneven among habitats at Pāvilosta. At that site, fine texture sand dominated in early succession plots, medium texture in grassland plots, and coarse texture in disturbed plots. At the Užava site, most plots in the overgrowing habitat had medium texture sand, and coarse sand was lacking in the disturbed habitat.

Arbuscular mycorrhizal colonization

Arbuscular mycorrhizal colonization (F, M and A) for plant species by habitat is given as supplementary data. Arbuscular mycorrhizal colonization was observed in most roots of the sampled plants and frequency of occurrence by field of view (F) was high (Table 5). Analysis of variance showed that mean extent of mycorrhizal colonization in roots of the sampled plants significantly differed between sites (M and A) and habitats (F and A), but the Tukey post-hoc test failed to show significant differences between habitats. No significant differences in mycorrhizal colonization in individual species between habitats were observed (not shown). However, mean frequency of colonization of vesicules and hyphae (F) in roots of plant species of the dune communities was significantly higher in medium and coarse sands compared to fine sand (Table 5). Linear regression analysis showed some significant effects of C, N and P concentration on colonization frequency (F), abundance of vesicules and hyphae (M) and arbuscules (A) in roots of plants in the dune communities (Table 6). When data from all habitats were used (Table 6), the significant regressions of soil variables (C, P and N concentrations) with F and/or M were consistently negative for *Festuca sabulosa, Hieracium umbellatum* and *Thymus serpyllum*. However, when the richer grassland habitat was excluded, the significant regressions of soil variables (C, P and N concentrations) with F and M for all species and separately for the tested species were positive. The regressions of soil variables with A had a contrasting effect: negative effect of P for *Thymus serpyllum* and the mean for all species, and positive effect of N for *Festuca sabulosa*.

Table 3. Statistically significant Pearson's correlations between soil variables

Parameter	C	P	N
C	***		
P	0.605	***	
N	0.704	0.723	***

Discussion

Early successional sand dunes are poor in nutrients and erosion of established dunes can cause loss of accumulated organic material in soil. Thus, it might be expected that in these poor conditions mycorrhiza play a crucial role in survival (Logan et al. 1989). No significant differences occurred in extent of mycorrhizal colonization between habitats. The lack of significant differences between pairs of habitats might be due to heterogeneity of the habitats created by spatial variation in sand texture and nutrient concentrations. In this regard, the observed significant relationships of soil variables (P, N and C concentration and sand texture) with F (arbuscular mycorrhizal frequency), M (amount of arbuscular mycorrhizal vesicules and hyphae) and A (amount of arbuscules) in whole root systems suggests fine spatial structure of mycorrhizal interactions with soil properties. Mean M and A for all selected plant were higher in the Užava site where soil P and N concentrations were lower. This is in contrast to previous observations that showed increased AM colonization in fixed-dunes with higher organic matter and N concentration (Sridhar 2006). When data for all habitats were used, significant regressions were not found between the mycorrhizal colonization parameters and P and N concentrations when mean values were calculated for all sampled plants, but for specific plant species (*Festuca sabulosa, Hieracium umbellatum* and *Thymus serpyllum*) significant negative

Table 4. Sand texture. Number of plots with fine, medium or coarse texture in sites and habitats. Different letters indicate significant differences (Chi-square test) in distribution by sand texture between sites and habitats. Significant differences area indicated by different letters

		Sand texture			Significant differences
		Fine	Medium	Coarse	
Site	Pāvilosta	14	21	15	a
	Užava	7	33	3	b
Habitat	Early (Pāvilosta)	14	6	0	a
	Grassland (Pāvilosta)	0	13	7	b
	Disturbed (Pāvilosta)	0	2	8	c
	Overgrowing (Užava)	3	17	3	d
	Disturbed (Užava)	4	6	0	d

relationships between C, P or N and F or M did occur. The proportion of root colonized by AM is known to be higher when concentrations of P in soil are low (Smith et al. 2010; Richardson et al 2011), as also suggested in this study. Mycorrhizal abundance is known to decrease also under increased N concentration (Treseder 2004). However, it is considered that AM do not transport N to host plants, as is the case for ectomycorrhiza (Hodge and Fitter 2010). In our study, significant correlation occurred between P, N and C, and thus it was not possible to partition the partial effects of these elements. As plants supply the C needed for fungal growth (Smith et al 2011), and N-fixing bacteria are common in dune ecosystems (Dalton et al. 2004), the observed relationship of mycorrhizal colonization with C and N concentration might be an artefact due to their correlation with P concentration in soil. However, AM can utilize organic matter patches in soil for supply of N that is transferred to plants (Leigh et al. 2009) and this might be important in the seacoast communities. The higher mycorrhizal colonization frequency (mean for all species) in sands with medium and coarse texture might also be due to interaction with nutrient concentrations, as leaching of P would be expected to be less in fine-textured sands. Experimental studies using nutrient additions (Treseder 2004) in the existing non-stratified design of the seacoast communities would be needed to determine effects of each soil parameter and their interactions.

When only the poorest habitats were considered, i.e. excluding the grassland habitat, the results suggested that a slight increase of P and/or N concentration is needed to promote fungal colonization (F) and abundance of arbuscular mycorrhizal vesicules and hyphae (M). Sikes et al. (2012) observed in a very long dune succession (>800 years) that fungi that participate in late succession produce more arbuscules and soil hyphae than fungi of early and mid-dune succession. However, in our study, which likely represents a relatively short succession, we did not observe a significant relationship of P and N concentration with

Table 5. Extent of arbuscular mycorrhizal colonization in roots of plants by site and habitat. F, arbuscular mycorrhizal (vesicules and hyphae) frequency (percent of fields of view with mycorrhizal colonization) of colonization in whole root systems; M, abundance of arbuscular mycorrhizal vesicules and hyphae (percent of fields of view with mycorrhizal colonization weighted by intensity classes) in whole root systems; A, and abundance of arbuscules (percent of fields of view with arbuscules weighted by intensity classes in whole root systems). Means and standard deviations for F, M and A of all species sampled in the plots are given. *P* values of ANOVA tests for significant differences between sites and habitats are shown. Different letters indicate significant differences in the Tukey HSD post-hoc test

		Extent of mycorrhizal colonization		
		F	M	A
Significant differences	site		P < 0.001	P < 0.001
	habitat	P = 0.017		P = 0.042
Site	Pāvilosta	42.34 (9.84)	1.28 (0.82) a	0.10 (0.22) a
	Užava	44.19 (11.23)	2.69 (2.45) b	0.35 (0.46) b
Habitat	Early (Pāvilosta)	42.81 (11.65)	1.16 (0.84)	0.08 (0.26)
	Grassland (Pāvilosta)	40.24 (7.99)	1.29 (0.58)	0.09 (0.07)
	Disturbed (Pāvilosta)	44.41 (8.71)	1.55 (1.27)	0.19 (0.31)
	Overgrowing (Užava)	48.35 (9.10)	2.22 (1.51)	0.19 (0.20)
	Disturbed (Užava)	39.15 (11.65)	3.28 (3.20)	0.54 (0.59)
Sand texture	fine	36.75 (10.96) a	1.43 (1.45)	0.14 (0.33)
	medium	45.16 (10.02) b	2.36 (2.18)	0.28 (0.41)
	coarse	45.20 (8.29) b	1.19 (0.82)	0.12 (0.20)

Table 6. Linear regression results of for soil parameters versus extent of arbuscular mycorrhizal colonization (all habitats). Coefficients of variation (R^2) and direction of slope (+ve or –ve) are shown only for significant regressions. F, arbuscular mycorrhizal (vesicules and hyphae) frequency (percent of fields of view with mycorrhizal colonization) of colonization in whole root systems; M, abundance of arbuscular mycorrhizal vesicules and hyphae (percent of fields of view with mycorrhizal colonization weighted by intensity classes) in whole root systems; A, abundance of arbuscules (percent of fields of view with arbuscules weighted by intensity classes in whole root systems

Species	Extent of mycorrhizal colonization	C	P	N
Mean (all species)	M			
	A			
Festuca sabulosa	F	(-ve) 0.049		
	M		(-ve) 0.055	(-ve) 0.062
Hieracium umbellatum	F			(-ve) 0.065
Thymus serpyllum	F	(-ve) 0.326	(-ve) 0.249	(-ve) 0.253
	M		(-ve) 0.093	

Table 7. Linear regression results of for soil parameters versus extent of arbuscular mycorrhizal colonization (excluding grassland habitat). Coefficients of variation (R^2) and direction of slope (+ve or –ve) are shown only for significant regressions. F, arbuscular mycorrhizal (vesicules and hyphae) frequency (percent of fields of view with mycorrhizal colonization) of colonization in whole root systems; M, abundance of arbuscular mycorrhizal vesicules and hyphae (percent of fields of view with mycorrhizal colonization weighted by intensity classes) in whole root systems; A, abundance of arbuscules (percent of fields of view with arbuscules weighted by intensity classes in whole root systems

Species	Extent of mycorrhizal colonization	C	P	N
Mean (all species)	F			(+ve) 0.103
	M			(+ve) 0.059
	A		(-ve) 0.083	
Festuca sabulosa	F			(+ve) 0.151
	M			(+ve) 0.143
	A			(+ve) 0.162)
Hieracium umbellatum	F		(+ve) 0.225	
Koeleria glauca	F	(-ve) 0.164	(+ve) 0.215	
	M		(+ve) 0.160	
Thymus serpyllum	F		(+ve) 0.132	
	A		(-ve) 0.083	

abundance of arbuscules (A) when data from all habitats were used, and a contrasting effect depending on species when the grassland habitat was excluded.

It is known that AM communities composition changes during primary dune succession (Sikes et al. 2012), which we did examine in this preliminary study. It is also know that AM colonization changes seasonally with a peak in summer (Druva-Lūsīte et al. 2008), but within the confines of the study we conducted sampling in autumn. However, the results do show that mycorrhizal colonization was related to soil development, being more important in the most nutrient poor habitats, compared to grassland habitats. However, mycorrhizal colonization appeared to be promoted by slight increases in P and perhaps N concentration in the successional stages before the grassland habitat. The seacoast communities thereby provide the opportunity for further study of successions of AM communities and using experimental field trials to determine specific effects and interactions of soil factors.

Acknowledgements

The study was funded by the European Regional Development Fund project "New concepts for using root endophytes in ecological long term agriculture" 2014/0032/2DP/2.1.1.1.0/14/APIA/VIAA/089. The Nature Conservation Agency of Latvia kindly allowed the study to be conducted in the nature reserves. The technical support by Anete Rateniece and Anna Žeiviniece is much appreciated.

References

Dalton D.A., Kramer S., Azios N., Fusaro S., Cahill E., Kennedy C. 2004. Endophytic nitrogen fixation in dune grasses (*Ammophila arenaria* and *Elymus mollis*) from Oregon. *FEMS Microbiol. Ecol.* 49: 469–479.

Dickie I.A., Martínez-Garcia L.B., Koele N., Grelet G-A., Tylianakis J.M., Peltzer D.A., Richardson S.J. 2013. Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development (Marscher Review). *Plant Soil* 367: 11–39.

Druva-Lūsīte I., Karlsons A., Osvalde A., Ņečajeva J., Ievinsh G. 2008. Photosynthetic performance and mycorrhizal symbiosis of a coastal marsh plant, *Glaux maritima*, in conditions of fluctuating soil salinity. *Acta Univ. Latv.* 745: 155–164.

Druva-Lusite I., Ievinsh, G. 2010. Diversity of arbuscular mycorrhizal symbiosis in plants from coastal habitats.

Environ. Exp. Biol. 8: 17–34.
Dumbrell A.J., Nelson M., Helgason T., Dytham C., Fitter A.H. 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. *ISME J.* 4:337–345.
Eberhards G. 2003. Seacoast of Latvia. Latvijas Universitāte, Rīga. 292 p. /in Latvian/
Egner H., Riehm H., Domingo W.R. 1960. Untersuchungen über die chemische Boden-analyse als Grundlage für die Beurteilung des Nährstoffzustandes der Boden. *Kungliga Landbrukshögskolans Annaler* 26: 199–215.
Hodge A., Fitter A.H. 2010. Substantial nitrogen acquisition by arbuscular mycorrhizal fungi from organic material has implications for N cycling. *Proc. Natl. Acad. Sci. USA* 107: 13754–13759.
Hodge A., Helgason T., Fitter A.H. 2010. Nutritional ecology of arbuscular mycorrhizal fungi. *Fungal Ecol.* 3: 267–273.
Hoeksema J.D., Chaudhary V.B., Gehring C.A., Johnson N.C., Karst J., Koide R.T., Pringle A., Zabinski C., Bever J.D., Moore J.C., Wilson G.W.T., Klironomos J.N., Umbanhowar J. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol Let*t. 13: 394–407.
Ievinsh G. 2006. Biological basis of biological diversity: physiological adaptations of plants to heterogeneous habitats along a sea coast. *Acta Univ. Latv.* 710: 53–79.
Koske R.E., Polson W.R. 1984. Are VA mycorrhizae required for sand dune stabilization? *BioScience* 34: 420–424.
Leigh J., Hodge A., Fitter A.H. 2009. Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host Plant from organic material. *New Phytol.* 181: 199–207.
Logan V.S., Clarke P.J., Allaway W.G. 1989. Mycorrhizas and root attributes of plants of coastal sand-dunes of New South Wales. *Austr. J. Plant Physiol. 16*: 141–146.
Phillips J.M., Hayman D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of colonization. *Transact. British Mycol. Soc.* 55: 158–161.
R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.
Richardson A.E., Lynch J.P., Ryan P.R., Delhaize E., Smith F.A., Smith S.A., Harvey P.R., Veneklaas E.J., Lambers H., Oberson A., Culvenor R.A., Simpson R.J. 2011. Plant and microbial strategies to improve the phosphorus efficiency of agriculture. *Plant Soil* 349: 121–156.
Sikes B.A., Maherali H., Klironomos J.N. 2012. Arbuscular mycorrhizal fungal communities change among three stages of primary sand dune succession but do not alter plant growth. *Oikos* 121: 1791–1800.
Sikes B.A., Maherali H., Klironomos J.N. 2014. Mycorrhizal fungal growth responds to soil characteristics, but not host plant identity, during a primary lacustrine dune succession. *Mycorrhiza* 24: 219–226.
Smith S.E., Facelli E., Pope S., Smith F.A. 2010. Plant performance in stressful environments: interpreting new and established knowledge of the roles of arbuscular mycorrhizas. *Plant Soil* 326: 3–20.
Smith S.E., Jakobsen I., Gronlund M., Smith F.A. 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: Interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. *Plant Physiol.* 156: 1050–1057.
Sridhar K.R. Arbuscular mycorrhizal fungi of coastal sand dunes. 2006. In: Bukhari M.J., Rodrigues B.F. (eds) *Techniques in Mycorrhizae*. Department of Botany, Government College of Arts, Science and Commerce, Quepem, Goa.
Treseder K.K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO_2 in field studies. *New Phytol.* 164: 347–355.
Trouvelot A., Kough I.L., Gianinazzi-Pearson V. 1986. Mesure du taux de mycorization Va ďun système radiculaire. Recherche de methods ďestimation ayant une signification fonvtionelle. In. Gianinazzi-Pearson V., Gianinazzi S. (eds) *Physiological and Genetical aspects of Mycorrhizae*. INRA Press, Paris, pp. 217–221.

Received 8 September 2015; received in revised form 15 September 2015; accepted 16 September 2015