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Original article

Mycorrhizal community structure, microbial biomass P and phosphatase activities under *Salix polaris* as influenced by nutrient availability

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ABSTRACT

Low supply of the nutrients nitrogen (N) and phosphorus (P) limit plant growth and spreading, and increase the plant-microbial nutrient competition in subarctic and arctic regions. We investigated the mycorrhizal community structure of a polar shrub willow (*Salix polaris*) and the microbial turnover in its rhizosphere to explore the adaptation of a mycorrhizal plant in the subarctic tundra. The ectomycorrhizal colonisation ranged from 35 to 64% of the fine root tips and decreased with an increasing soil C/N ratio. In total, 16 ectomycorrhizal morphotypes were found under *S. polaris* (eight to 13 morphotypes per site, five morphotypes at all four sites). *Cenococcum* sp. was the most common EM fungus (32% of the ectomycorrhizal fine roots). The abundance of *Cenococcum* sp. increased with an increasing organic matter content and N/P ratio in the soil. Arbuscular mycorrhizal colonisation of *S. polaris* was absent or less than 1% of the fine root length. Microbial biomass P accounted for 21–75% of the organic soil P and 6–49% of the total soil P. Microbial biomass P, alkaline and acid phosphatase activities in the rhizosphere increased with increasing soil N concentration. We conclude that a higher N supply decreases the diversity in the mycorrhizal community on polar willows and increases the role of P turnover from the soil microbial biomass for the nutrient supply.

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1. Introduction

The growth of the tundra vegetation often is limited by the soil nitrogen (N) and/or phosphorus (P) availability [41]. A greater P availability increases the plant species cover and density of the tundra vegetation [27]. Additionally, it can strongly increase the P accumulation in the microbial biomass [39,40]. The microbial biomass can be an important sink for nutrients and can withdraw substantial amounts of nutrients from the plant-available pool in arctic soils [20]. However, mycorrhizal fungi can effectively transfer microbially accumulated P to the vegetation [5]. They can affect the rates and pattern of P cycling [10,19]. Furthermore, ectomycorrhizal (EM) fungi are also important for plant N uptake in tundra ecosystems [30]. This provides EM plants with an advantage compared to their non-mycorrhizal competitors. A reduced spread of arbuscular mycorrhiza was described for several host plants in arctic and subarctic regions and therefore a lower importance for the

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plant nutrition than in tropic and temperate climates was hypothesised [20,51]. On the other hand, dwarf shrubs and trees in the arctics and subarctics had a relatively high EM colonisation [51]. The arctic flora is not diverse and a few genera such as *Empetrum*, *Eriophorum*, *Carex*, *Betula* and *Salix* dominate large areas [8]. The polar dwarf shrub willow (*Salix polaris*) is a typical pioneer coloniser of arctic and subarctic tundra substrates at high-altitude fell sites. *Salix* spp. are known to be dual mycorrhizal plants which have the capacity to form arbuscular mycorrhizas and ectomycorrhizas [26]. However, their fine roots are mainly colonised by EM fungi, irrespective of different environmental conditions [33,48]. They enhance the nutrient supply of their host plants especially in nutrient deficient conditions, e.g. by more efficient soil exploitation compared to roots without mycorrhiza and excretion by mycorrhizal symbionts of significant quantities of phosphatases [45,47]. Mechanisms of EM fungi for adaptation on N and P limitation at arctic sites, e.g. by the utilisation of seed protein N were demonstrated by Tibbett et al. [45,46] but only *in vitro*. However, very little information is available on the ecological role of mycorrhizal fungi in arctic conditions [20]. Therefore, the aims of the present study at subarctic tundra sites were: (1) to assess the mycorrhizal community structure, biomass P and phosphatase activities under *S. polaris*; and (2) to disclose the adaptation of a mycorrhizal plant to an increased nutrient supply.

2. Materials and methods

2.1. Test plant, site description and sampling

Salix polaris was selected as an example of a dual symbiotic plant which is well-adapted to the arctic and subarctic environment. It belongs to the characteristic pioneer vegetation in this environmental and is able to grow and build up organic layers directly on weathering rock. Intersexual physiological differences of arctic willows as observed by Jones et al. [21] were considered by selection of exclusively female test plants during flowering. Twenty root and soil samples (20 cm × 20 cm, 10 cm deep or to the bedrock) were taken at four sites (five per site) in July 2006 near Abisko in the tundra of northern Swedish Lapland. The climate is montane subarctic, with a growing season of approximately 3 months, from mid-late June to early–mid September [29]. The mean annual temperature is −0.9 °C and the mean annual precipitation about 400 mm. The co-ordinates, altitudes and chemical soil properties of the four test sites are summarised in Table 1.

The four test sites were characterised by increasing C_{org}, N_{tot} and P_{org} concentrations of the soil and an increasing soil pH from sites 1 to 4, whereas the P_{tot} concentration of the soil differed not significantly between the sites (Table 1).

2.2. Soil analyses

The soil properties of each replicate were investigated separately. Rhizosphere soil was carefully separated from the roots and used at field-moist status for the investigation of the soil microbial properties. Reference samples were air-dried and sieved (2 mm) for chemical analyses. The C, N and S contents of the soils were determined with Foss Heraeus CNS – Vario EL (Elementar Analysentechnik GmbH, Germany). Total phosphorus content (P_t) of the soil was determined according to Dick and Tabatabai [11]. Organic phosphorus content (P_{org}) of the soil was determined with the method of Olsen and Sommers [35]. The concentration of P was analysed by inductively coupled plasma-optical emission spectroscopy (ICP-OES, JY 238, Jobin Yvon, France) at 214.914 nm wave length. Determination of soil pH was performed electrometrically using a glass electrode in 0.01 M $CaCl_2$ at a soil:solution ration of 1:2.5.

2.3. Determination of the mycorrhizal colonisation

Roots from each sample were carefully separated and washed with de-ionised water for microscopic examination. Roots of *S. polaris* were separated from other roots in the sample by their morphology and connection to the shoots. Three subsamples of 20 randomly selected 1 cm-rootlets per site were cleared in 10% KOH for 24 h and in 10% H_2O_2 for 1 h, acidified in 1% HCl for 15 min and stained with Trypan blue [36]. A minimum of 200 line intersections per subsample was investigated for arbuscular mycorrhizal colonisation according to McGonigle et al. [28].

Living roots were identified on the basis of a turgid appearance and possessing white cortical cells. EM frequencies were calculated microscopically (numbers of EM root tips × 100%/total numbers of root tips). A minimum of 1500 root tips was investigated per sample (7500 per site). The morphological-anatomical EM types were distinguished by macroscopic characteristics of the fungal mantle, such as colour, surface appearance, presence of emanating hyphae and hyphal strands, as well as microscopic features such as mantle type and hyphal connections [2,3]. The EM types were classified into contact, short-distance, medium-distance and long-distance exploration types [1]. Two to five root tips per EM type were frozen in Eppendorf-tubes and stored at −20 °C for extraction of DNA analyses separately from each test site and sampling date.

2.4. Molecular analysis of the EM fungi

Analyses of the DNA sequences of the D1/D2 region of the nuclear-encoded large subunit RNA gene (LSU) and of the internal transcribed spacer (ITS) region were used to identify the ectomycorrhiza forming fungi of these samples. DNA was isolated from frozen mycorrhizal samples using the DNAeasy Plant Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. Part of the LSU was amplified by the polymerase chain reaction (PCR) with the primer-pair NL1–NL4 [34]. The ITS region within the ribosomal RNA genes was amplified using the primers ITS1 or ITS1F and ITS4 or ITS4B [15,52]. The PCR reaction volume and PCR conditions were as proposed by Haug [17]. The PCR products obtained were purified using QIAquick protocol (Qiagen, Hilden, Germany). Direct sequencing of PCR products was performed using the PCR primers as sequencing primers. Cycle sequencing was conducted using the ABI PRISM Dye-Terminator Cycle Sequencing Ready Reaction Kit (Applied

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