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Residual Effect of Induced Water Stress and Nitrogen Addition on the Mycobiota in Scots Pine Stands[1]

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Abstract—Mycobiota (fungi, lichens and myxomycetes) was examined in permanent plots following experiments of artificial drought (D) and nitrogen addition (N) and compared with untreated forest (C), in Scots pine stand planted on Arenosols. Species diversity and relationships between fungal community structure and environmental variables (plant species numbers and cover, bryophyte cover, soil and bark pH, tree mortality) were explored. Both D and N treatments lead to decrease of fungal species in general, however, responses of individual trophic and ecological groups varied. The strongest effect of the treatments was observed for soil fungi, especially mycorrhizal: numbers of fruiting species and ectomycorrhizal root tips decreased, and species composition has changed. Saprotrophic fungi reacted by changes in species composition but not in numbers. Of the studied environmental variables, the most significant effect on mycobiota had bryophyte and vascular plant cover as well as vascular plant species numbers.

Keywords: fungi, lichens, myxomycetes, ectomycorrhizal root tips, artificial drought, nitrogen fertilization experiment

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INTRODUCTION

Water and nitrogen are important determinants for vegetation and cryptogamic organisms, influencing biodiversity patterns and relationships inside an ecosystem. Water availability appears to be a limiting factor to diversity and indeed the existence of fungi. Drought has been shown to be an important factor decreasing species diversity of both of litter decomposers [1] and of mycorrhizal fungi [2]. However, other studies indicate that the reaction of fungi may be more complex than just a decrease in diversity. Saprotrophic fungi in soil were found to be less susceptible to water stress than ectomycorrhizal (ECM), besides, variation in tolerance to water stress and post-drought recovery exists among different ECM species and drought may result in shifts of soil fungal communities [3, 4]. Nitrogen content is further vital determinant of fungal community structures [5], although the impact of raised N contents was found to be even more complicated and contradictory for various groups of fungi [6, 7] than the impact of drought. According to Lilleskov [8], the differences in experimental outcomes of N addition may stem from the high variation of environmental factors involved, experiment timing and conditions, methods of fungal identification, and possibly other factors.

Drought manipulation and/or nitrogen fertilization experiments in forests have been carried out in several European and extra-European countries [9–11]. However, only a few drought experiments include or deal specifically with forest fungi. Studies on nitrogen addition experiments on fungi are more frequent, but only a few included parallel drought and nitrogen addition manipulations [2, 3]. Among these, however, there are practically no studies that would include several functional and ecological groups of fungi.

The goal of our study was to compare species diversity and structure of wood, bark and soil/litter inhabiting fungi (saprotrophic, mycorrhizal and lichenized) and myxomycetes in the post-experimental plots following manipulation of artificial drought and N addition in managed Scots pine (*Pinus sylvestris*) stands. The experiment was set to investigate the impact of these factors on the forest vegetation and performance of trees and after the manipulations were ceased, the residual effect of water stress and increased N input on mycobiota was investigated, to obtain more complete

[1] The article is published in the original.

[†] Deceased.

picture of the impact of both experiments on the biotic components of the pine forest ecosystem.

MATERIALS AND METHODS

The artificial drought and nitrogen addition experiment was set in Kaunas district, central Lithuania (54°50′ N, 24°2′ E), in a 65-year-old Scots pine stand (mean DBH 22 cm, mean height 25 m), planted on Arenosols. For details of the site characteristics and vegetation see Ozolinčius et al. [11]. The climate of the study area is subcontinental with an annual precipitation of 650–750 mm, mean annual temperatures ranging from 15.8 to 18.5°C in June–August to –2.2 and –2.8°C in December–February, and annual snow cover lasting 70–80 days [12].

The experiments of artificial drought (D) and nitrogen addition (N) had a randomized block design with the two treatments and control (no treatment) (C) and three replicates for each, nine permanent 15 × 20 m sample plots in total. Artificial drought was induced by using transparent roof constructions installed below the stand canopy [11], from spring of 2003 till the autumn of 2005. For the N addition experiment, the following total amounts of ammonium nitrate were applied: 400 kg N/ha in 2003 (200 kg N/ha per application, two applications); 600 kg N/ha in 2004 (150 kg N/ha per application, four applications), and 600 kg N/ha in both 2005 and 2006 (150 kg N/ha per application, four applications).

Pine tree mortality, defoliation and ground vegetation were monitored from 2003 until 2008. For mortality rates, the number of living trees in every plot was recorded annually from 2003 to 2008. Methods for defoliation assessment and ground vegetation monitoring were described in Ozolinčius et al. [11]. The amount of woody debris (WD) was evaluated in four 1.5 m^2 quadrats situated randomly in each treatment plot (once, in 2008). The length and diameter of all WD ≥ 0.5 cm diam. was measured, but not differentiated by decay stage. Field sampling of mycobiota was performed from May 2008 until October 2009. The study plots were inspected three times per year during one visit in spring (May) and two visits in autumn (September-October), except for epiphytic lichens and ECM root tips both of which were sampled only once in 2008. Additionally, samples of litter and bark of pine were collected in the field for further preparation of moist chamber cultures to study myxomycetes (following [13]). Litter samples were collected randomly in every plot (five samples per plot), and bark was collected from five pine trunks per plot at 120–150 cm height, sampling was performed during every visit. For ECM root tip calculations, five core samples of topsoil (15 cm) were taken from every plot and pooled into one sample per plot. From this, the number of ECM roots in 50 cm^3 of soil was counted. For the lichens, 10 pine trees were chosen randomly in every plot. All lichen species were registered on a tree trunk from its base to a height of 170 cm. Fungal specimens were identified following routine methods [14]. Taxa identified only to genus rank were treated further as single species every (e.g. *Russula* sp. or *Lepraria* spp.). Voucher specimens were deposited in the Herbarium of the Institute of Botany of Nature Research Centre (BILAS). Fungal names mostly follow Index Fungorum database (http://www.indexfungorum.org/), names of myxomycetes follow Lado (2005–2016) (http://www.nomen.eumycetozoa.com). All recorded fungi were divided into the trophic groups: saprotrophs, mycorrhizal symbionts, lichens and phagotrophs (myxomycetes) and into the ecological groups according to the occupied substrates: bark-, wood- and soil/litter-inhabiting species. Litter and bark pH was measured following the methods described in Motiejūnaitė et al. [15].

Annual tree mortality rate was calculated following the formula by Sheil et al. [16]; the WD volume was calculated with the Smalian's formula [17]. To test whether fungal communities and environmental variables were statistically different across the treatment types, multiresponse permutation procedure (MRPP) in PC-ORD v. 6 [18] was used. Species presence/absence data at each plot and environmental variables (vascular plant species number (Vasc no), vascular plant cover (Vasc cov), bryophyte cover (Bryo cov), tree mortality (Tree mor), pine bark pH (bark pH), litter pH (litt pH), WD volume and ECM root tips) were analysed using nonmetric multidimentional scaling (NMS) analysis based on the Sørensen distance in PC-ORD v. 6. The Pearson correlation coefficient (r) value between environmental and fungal community variables and ordination axes was calculated. The final stable solution was derived from 250 runs using real data and was subjected to 250 randomized runs using the Monte Carlo test to evaluate the strength of patterns in the NMS solutions.

RESULTS AND DISCUSSION

Pine tree mortality rate was highest in the drought treatment, lowest – in N treatment. In both treatments tree mortality ranges were wider between individual plots compared to the control: from 1.8% to 7.42% per plot in D, from 0% to 2.72% per plot in N and from 2.63% to 3.58% in C. Defoliation followed tree mortality pattern, but it remained as this only until 2007; afterwards, this index evenned out in all variants (Fig. 1).

By the end of the experimental treatment and during mycobiota investigations, the cover of vascular plants in both N (MRPP test; effect size A = 0.127; $p = 0.043$) and D (MRPP test; effect size A = 0.428; $p = 0.022$) treatments; and of bryophytes in N (MRPP test; effect size A = 0.428; $p = 0.022$) and D (MRPP test; effect size A = 0.428; $p = 0.023$) treatments decreased and was significantly lower compared to control. The

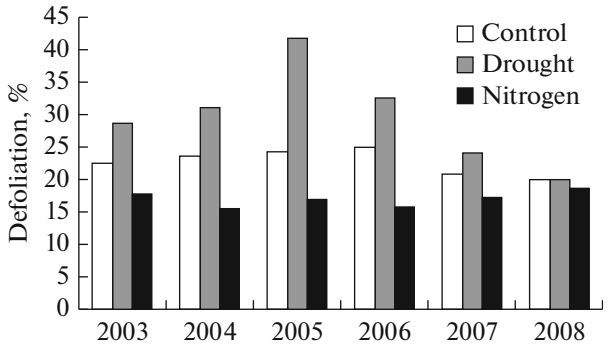

Fig. 1. Tree defoliation in the different treatments during 2003–2008.

number of vascular plants was significantly lower in D treatment (MRPP test; effect size A = 0.489; $p = 0.025$). There was also an obvious (though not significant) difference in the quantities of ECM root tips for D treatment (MRPP test; effect size A = 0.111; $p = 0.062$), when compared with the control. Differences in bark or litter pH values were not obvious. Wood debris was sparse and of small dimensions, which is characteristic to industrial pine plantations in Lithuania (Table 1).

Drought manipulation and/or nitrogen fertilization experiments worldwide have demonstrated that drought had detrimental effect on forests and wood production, but fertilization, especially in coniferous forests showed positive results for timber productivity [19]. In our study, the impact of drought and nitrogen addition showed similar effects on trees (see also [11]). However, a disquietingly high detrimental effect of fertilization on other forest biota and processes was noted, too, and, as demonstrated by Strengbom et al. [20], residual influence of nutrient addition persisted a long time after the last input of fertilizers. In our study, experimental impact on ground vegetation was obvious three years after the cessation of the experiments, though the impact on trees (defoliation) appeared to be lessened by the year 2008.

In total, 223 taxa of mycobiota were recorded across all plots during the study period. The majority were common species typically encountered in Lithuanian pine forests. The highest total number of species was observed in C plots (Table 2). Thirty-eight species were recorded only in C plots, and 29 and 32 only in D and N plots respectively. Only 17 species were recorded in every plot of all treatments, among them lichens predominated. The MRPP test confirmed that the different treatments significantly influenced fungal community composition (effect size A = 0.333, $p = 0.004$). All treatments held the same trophic groups of mycobiota (Table 2) and there was only a slight difference in their relative structure: the percentage of lichens in D plots and the percentage of mycorrhizal fungi in N plots were somewhat lower.

NMS analysis of all fungal species (main matrix) and environmental variables (second matrix) resulted in a four-dimensional solution with a final stress of 0.34018 and a final instability <0.000001. The majority of variability (81.7%) was explained by three axes. Of all environmental variables, herb and dwarf shrub species number and bryophyte cover had the strongest negative correlation with Axis 1 ($r = -0.766$; $r = -0.731$), and the herb and dwarf shrub cover ($r = 0.601$) strongly correlated with Axis 2; the amount of WD ($r = -0.561$) and bark pH ($r = -0.465$) had weaker (negative) correlations with Axis 2 (Fig. 2a). Almost all bark dwellers (myxomycetes and lichens) did not demonstrate affinities to any of the treatments. Lack of evident response of corticolous mycobiota to fertilization can be explained by little or no impact of granular fertilizers on the substrata that are above the forest floor, as was noted in the study of corticolous bryophytes [9]. The effect of the experiments on xylotrophic mycobiota was rendered intangible by the extremely low amounts and diversity of deadwood. Most of the xylotrophic

Table 1. Environmental variables in the studied plots (abbreviations as in Materials and Methods). All calculations were made from the data of year 2008, except for pH which was calculated from all samplings in 2008 and 2009. Mean values (±standard deviations) are presented

Environmental variables	Treatments		
	control	drought	nitrogen
Bryo cov, %	90.38(±5.22)	11.17(±4.53)*	7.50 ±2.59)*
Vasc cov, %	38.04(±22.82)	1.25 (±0.75)*	6.34(±8.01)*
Vasc no	7.00 (±1.00)	3.33 (±0.58)*	4.00(±2.65)
Bark pH	3.47 (±0.34)	3.45 (±0.22)	3.63 (±0.40)
Litter pH	4.73 (±0.41)	4.25 (±0.21)	4.84 (±0.40)
ECM tips/50 cm^3	378.67(±293.16)	125.67(±71.53)	206.67(±61.58)
WD, m^3/plot	0.082 (±0.017)	0.141 (±0.044)	0.078 (±0.015)

* Significant difference between treatment and control (MRPP test).

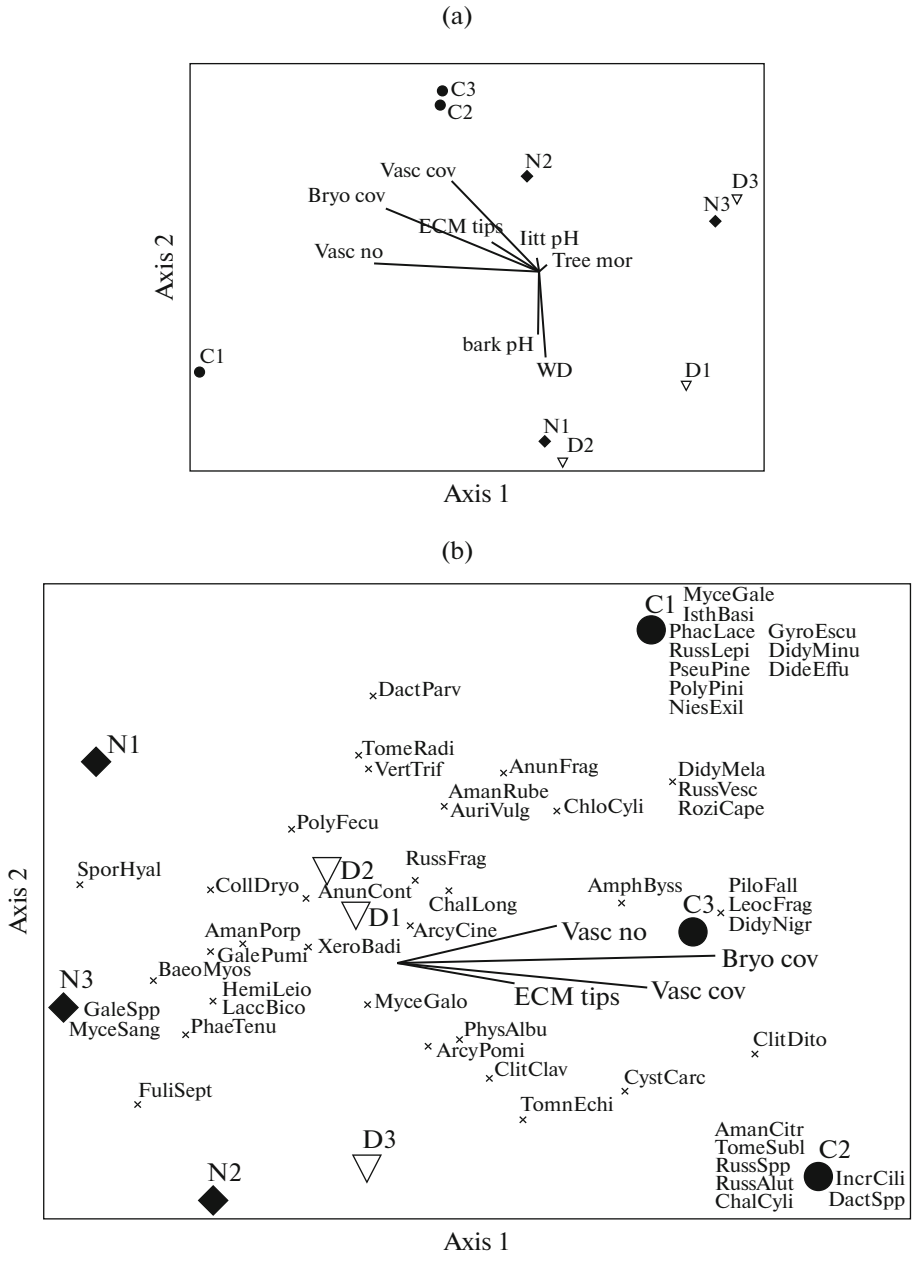

Fig. 2. (a) NMS joint plot of 9 treatment plots based on presence/absence of fungal species. Correlation of environmental variables is shown as vectors (b). NMS joint biplot of soil/litter fungal community from different treatments with environmental variables (abbreviations as in Materials and Methods). Abbreviations of fungus species: AmanCitr—*Amanita citrina*, AmanPorp—*Amanita porphyria*, AmanRube—*Amanita rubescens*, AmphByss—*Amphinema byssoides*, AnunCont—*Anungitea continua*, AnunFrag—*Anungitea fragilis*, ArcyCine—*Arcyria cinerea*, ArcyPomi—*Arcyria pomiformis*, AuriVulg—*Auriscalpium vulgare*, BaeoMyos—*Baeospora myosura*, ChalCyli—*Chalara cylindrica*, ChalLong—*Chalara longipes*, ChloCyli—*Chloridium cylindrosporum*, ClitClav—*Clitocybe clavipes*, ClitDito—*Clitocybe ditopus*, CollDryo—*Gymnopus dryophilus*, CystCarc—*Cystoderma carcharias*, DactParv—*Dactylaria parvispora*, DactSpp—*Dactylaria* sp., DideEffu—*Diderma effusum*, DidyMela—*Didymium melanospermum*, DidyMinu—*Didymium minus*, DidyNigr—*Didymium nigripes*, FuliSept—*Fuligo septica*, GalePumi—*Galerina pumila*, GaleSpp—*Galerina* sp., GyroEscu—*Gyromitra esculenta*, HemiLeio—*Hemitrichia leiotricha*, IncrCili—*Incrucipulum ciliare*, IsthBasi—*Isthmolongispora basitruncata*, LaccBico—*Laccaria bicolor*, LeocFrag—*Leocarpus fragilis*, MyceGale—*Mycena galericulata*, MyceGalo—*Mycena galopus*, MyceSang—*Mycena sanguinolenta*, NiesExil—*Niesslia exilis*, PhacLace—*Phacidium lacerum*, PhaeTenu—*Phaeostalagmus tenuissimus*, PhysAlbu—*Physarum album*, PiloFall—*Piloderma fallax*, PolyFecu—*Polyscytalum fecundissimum*, PolyPini—*Polyscytalum pini*, PseuPine—*Pseudohelotium pineti*, RoziCape—*Cortinarius caperatus*, RussAlut—*Russula alutacea*, RussFrag—*Russula fragilis*, RussLepi—*Russula lepida*, RussVesc—*Russula vesca*, RussSpp—*Russula* sp., SporHyal—*Sporidesmiella hyalosperma*, TomeRadi—*Tomentella radiosa*, TomeSubl—*Tomentella sublilacina*, TomnEchi—*Tomentellopsis echinospora*, VertTrif—*Verticicladium trifidum*, XeroBadi—*Xerocomus badius.*

species were too patchily distributed to allow any conclusions to be drawn.

Evident effect of the treatments was observed only for soil and litter mycobiota. The most prominent negative reaction to the experimental disturbances was demonstrated by mycorrhizal fungi, though quantity of ECM root tips and number of fruiting mycorrhizal species differed for D and N treatments: ECM roots were more numerous in N than in D plots, contrary to fruiting mycorrhizal species. The separate NMS ordination was run to compare distribution of soil and litter inhabiting species in different treatment variants with respect to the environment variables that were found to be most strongly related to the treatments (Fig. 2b). NMS resulted in a two-dimensional solution with the final stress of 8.01783 and a final instability <0.000001. Two axes explained the majority of the variability in fungal communities (axis 1, $r^2 = 0.624$; axis 2, $r^2 = 0.221$). The joint plot illustrates the strength and correlation of environmental variables to each ordination axis. The correlation of bryophyte cover with axis 1 was strongest ($r = 0.904$), followed by cover of herbs and dwarf shrubs ($r = 0.823$) and with their species number ($r = 0.626$). The number of ECM tips also correlated significantly with axis 1 ($r = 0.575$). Axis 2 showed no association with any variable employed and appeared to be mainly associated with characteristics of individual plots. These differences were somewhat lessened by drought experiment.

Among the species correlating positively with C plots ($r \geq 0.542$), the most common were the mycorrhizal basidiomycetes and two saprotrophic agaricoid fungi *Clitocybe ditopa* and *Cystoderma carcharias*. Mycorrhizal *Amphinema byssoides, Piloderma fallax* and *Cortinarius caperatus*, that showed the strongest affinities to C plots in our study, are characterized as nitrophobic by Kuyper [6] and Lilleskov et al. [21, 22]. These and a few other species that also preferred C plots, avoided both N and D plots, both of which showed loss of bryophyte and ground vegetation cover and diversity. Meanwhile *Laccaria bicolor*, termed as nitrotolerant by Kuyper [6], showed a clear preference for both N and D treatments but correlated negatively with C plots ($r \geq -0.614$). Such behaviour patterns of reputedly nitrophobic and nitrotolerant fungi may suggest that the changes in cover and composition of ground vegetation could be as responsible for some of the deviations in mycobiota species structure as the direct impact of the nutrient itself. Similar relationship between ECM fungus diversity and ground vegetation changes were observed by Tarvainen et al. [23].

Myxomycetes, frequently found on bryophyte cover (i. e., *Didymium melanospermum* or *Leocarpus fragilis*), were also positively associated with C plots ($r \geq 0.542$) where bryophyte cover percentage remained high. Saprotrophic fungi (i. e., *Baeospora myosura* or *Gymnopus dryophilus*), showed a strong negative correlation with C plots ($r \geq -0.511$), and generally were more common in N plots. In N plots, apart from typical saprotrophs of coniferous litter, species preferring litter of deciduous woodlands and grasses (i. e., *Phaeostalagmus tenuissimus* or *Mollisiopsis lobkovicensis*) were found. A higher richness of plant species should provide a higher diversity of litter which subsequently should be inhabited by more diverse species of decomposers; however, although the number of herb and dwarf shrub species in N plots was almost half of that in C plots (Table 1), the number of saprotrophic fungi was slightly higher in N treatment (Table 2).

Table 2. Mycobiota species numbers in the studied plots. Data derived from all recorded fructifications in years 2008 and 2009

Species of mycobiota	Treatments		
	control	drought	nitrogen
All species	137	124	126
Mycorrhizal	21	18	13
Saprotrophic	70	72	74
Lichens	21	16	20
Myxomycetes	25	18	19
Wood inhabiting	41	44	41
Bark inhabiting	31	24	28
Soil/litter inhabiting	65	56	57

CONCLUSIONS

Induced drought and nitrogen addition lead to decrease of mycobiota species in general, however, responses of individual trophic and ecological groups varied. Corticolous and lignicolous mycobiota showed little or no response to any of the treatments, effect on xylotrophic fungi was rendered intangible by scarceness of suitable substrata. The strongest effect of both treatments was observed for soil fungi, especially mycorrhizal: numbers of fruiting species and ectomycorrhizal root tips decreased, and species composition has changed. Meanwhile, saprotrophic fungi reacted by changes in species composition but not in numbers.

The different treatments (nitrogen addition, drought and no treatment) significantly influenced fungal community composition. Both treatments and the control held the same trophic groups of mycobiota and there was only a slight difference in their relative structure. The strongest effect was observed in species compositions. Of the studied environmental variables, tree mortality and litter pH had the least significant impact on the species distribution; the strongest effect had changes in bryophyte and vascular plant cover as well as vascular plant species number in ground vegetation.

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