The influence of contrasting ground cover vegetation on soil properties in the NJ pine barrens

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\textbf{Abstract}

Upland forests of the New Jersey pine barrens are characterized by a pine and oak forest canopy. The herbaceous layer consists primarily of ericaceous shrub species. Scattered throughout the region grass-sedge and lichen–moss dominated patches under a pine canopy can also be found. It is generally believed these patches come about after severe disturbance. These patches can persist even in the absence of further disturbance. In this study, examples of three herb layer community types: ericaceous (predominantly Gaylussacia borealis Wang.), graminoid (almost exclusively Carex pensylvanica Lam.) and lichen–moss dominated communities (Cladonia spp. and Polytrichum juniperinum Hedw.), in close proximity to one another, from three different forest locations were examined. We determined whether graminoid and lichen-dominated communities differ significantly in edaphic factors from the surrounding forest herbaceous layer vegetation matrix (ericaceous dominated community). In order to characterize the sites canopy and herbaceous layer vegetation and surface cover were assed. Soil particle size, soil carbon, respiration, microbial biomass and extractable nitrogen were also determined. Our analysis found only minor differences in forest canopy vegetation and no difference in soil particle size among forests or among communities. The results further suggest that differences in soil chemical parameters are the result of differences in the vegetation rooting architecture and decomposability. The lichen–moss dominated communities are distinguished by more bare ground, low bulk density, low nitrogen availability and a preponderance of microbial biomass in the upper 5 cm of the soil profile. The high soil bulk density in the lichen communities is presumably a function of its smaller root biomass content, greater percent bare ground cover and lower litter inputs. The ericaceous dominated communities are distinguished by greater presence of tree seedlings, low bulk density, lower nitrogen availability a large above ground biomass (AGB) and below ground biomass (BGB). Despite a significantly greater overall AGB the ericaceous community leaf mass is no greater than the graminoid community leaf mass or lichen–moss dominated community AGB. The graminoid dominated communities were distinguished by higher levels of extractable ammonium, soil organic matter (SOM) as represented by loss on ignition (LOI). Although the communities did not vary significantly in soil particle size the Pearson correlation analysis indicates that the significantly greater levels of soil carbon, ammonium and nitrate characteristic of the graminoid community are positively correlated with % silt–clay and negatively correlated with sand. Our results suggest that the subtle physical and chemical property differences between each of the communities may be due to a biogenic origin. This may explain, at least in part, the persistence of differing herb layer community type dominance.

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1. Introduction

The New Jersey Pinelands National Reserve is approximately 1.1 million acres in size and lies toward the northern end of the Atlantic Coastal Plain (New Jersey Pinelands Commission, 1980). The soils are sandy and nutrient-poor (Tedrow, 1986). The forests are characterized by a dense pine and oak forest canopy, commonly underlain by an ericaceous understory. Frequently grass-sedge, and lichen–moss dominated understory communities can be found scattered throughout the forest matrix. These patches can persist for decades or longer when established after a disturbance such as a fire (Forman, 1979; Ehrenfeld et al., 1995). However it is unclear what conditions or circumstances lead to establishment of a grass-sedge or lichen–moss dominated understory community following disturbance.
Two of these understory communities, ericaceous and lichen–moss, present a significant impediment to forest regeneration in Sweden (Zackrisson et al., 1997) and in North American boreal forests (Mallick, 2003). In the case of ericaceous species, dense clonal spread and a nearly impenetrable root mat preempts tree seedlings establishment space (Mallick, 2003) and through their mycorrhizae negatively influence nutrient availability (Zackrisson et al., 1997). The litter of some species in this family have been found to inhibit seedling growth (Nilsson et al., 1998), seed germination (Mallick, 2003; Zackrisson and Nilsson, 1992) or both (Zackrisson et al., 1997). Inhibition of soil microbial activity has also been found (Wardle et al., 1997). Several species of Cladonia lichens have also been shown to inhibit seed germination (Seda and Ehrenfeld, 2003; Crittenden, 1999) and reduce plant growth and negatively influence nutrient acquisition (Fisher, 1979).

This study was performed to characterize the individual plant communities and to determine to what extent soil properties and nutrient dynamics vary among them. To do this we selected three locations where all three community types were found in close proximity to one another. The origin of these communities is unclear but they have clearly persisted with little change and in the absence of significant disturbance for over 20 years (personal observation). By studying these sites we have attempted to determine if forest location or community type exert a greater influence on soil physical and chemical properties.

We first hypothesized that there would be no difference in soil physical characteristics among communities within a forest and little or no difference between forests. We hypothesized that differing nutrient use efficiency (NUE) and rooting depth characteristics of community constituent plant species would influence soil microbial and faunal communities and soil nutrient mineralization pathways, resulting in significantly different soil biogeochemical characteristics among communities. We believe that in ericaceous plant dominated communities the shrubs maintain site dominance by germination space and nutrient preemption. This community is characterized by positive feedbacks that limit nitrogen availability (sensu Latham et al., 1996; Johnson and Wedin, 1997). Low soil nutrient availability results in small bacterial populations and a microbial community with a significant ericoid mycorrhizal fungal component. The lichen–moss dominated communities are characterized by slow growing high NUE species that do not contribute to significant stores of soil carbon or available nutrients advantageous to other species establishment, and may also maintain site dominance by production of secondary antimicrobial or allelopathic compounds (Armstrong and Welsh, 2007; Seda and Ehrenfeld, 2003; Lawrey, 1995). Due to low levels of nutrient availability (recalcitrant litter and low levels of mineralization) microbial population sizes are predominantly comprised of the lichen fungal symbiont. We hypothesized that graminoid herb layer species, once ascendant at a site, preempt space by producing a large root mass through extensive clonal propagation and abundant litter (Matlack and Good, 1989). From this we predict that pioneer low C:N litter produced in the graminoid community will support a significant saprotrophic microbial community, resulting in increased rates of litter decomposition and consequently greater extractable nitrogen, SOM, microbial biomass, and rates of soil respiration.

2. Materials and methods

Three forest locations were studied in Burlington County NJ, Chatsworth (39°48′50″ 74°32′50″), Woodmansie (39°52′00″ 74°29′00″), and McDonald (39°54′50″ 74°32′25″). The soil at all three sites were classified in the Woodmansie–Lakehurst association according to the Burlington County soil Survey (Markley, 1971). Three distinct herbaceous layer plant communities were identified at each forest location: ericaceous dominated community type, primarily Gaylussacia baccata Wang., Vaccinium palidum Ait. and Gaultheria procumbens L.; graminoid dominated community type, almost exclusively Carex pensylvanica Lam., and lichen–moss dominated community type, Cladonia sp. and Polytrichum juniperinum Hedw. In July 2010, within each of the 9 communities the percent cover of bare ground, litter cover and live above ground biomass (AGB) cover for each herbaceous layer species were determined in four randomly placed 1 m × 1 m quadrats per community. The quadrats were further divided into 10 cm × 10 cm cells. From two randomly assigned cells per quadrat, the individual cells live AGB percent cover was determined for each plant species and the live AGB was clipped and collected. Following AGB removal 0−5 and 15−20 cm depth soil samples were collected using a 5 cm diameter steel coring device. The plant material and soil samples from the two 10 cm × 10 cm cells in each quadrat were pooled and returned to the lab for further analysis.

To determine canopy layer species composition, dominance and frequency the nearest neighbor tree species distance and diameter at breast height (DBH) were recorded in each of the 4 cardinal quadrants from the edge of each quadrat. Twenty random canopy cover observations within a 45° vertical cone were made at each quadrat. Species richness, Shannon–Wiener species diversity and species evenness, based Shannon–Wiener index, were determined based on herbaceous layer cover data (Southwood and Henderson, 2000).

In the laboratory live AGB dry weight, soil moisture content, bulk density and root dry weight biomass were determined gravimetrically. Soil sand/silt/clay content was determined by hydrometry (Robertson et al., 1999). Soil particle size distribution of: gravel (>2.0 mm), coarse sand (1–2 mm), medium sand (0.5–1 mm) and fine sand (0.125–0.5 mm) was determined by serial sieving of air dried soil samples using (2.0, 1.0, 0.5 and 0.125 mm mesh) USA Standard Testing Sieves. Soil aggregation is not a characteristic of these sandy soils.

Soil organic matter (SOM) was determined by loss on ignition (LOI) (Robertson et al., 1999). Microbial Biomass Carbon (MBC) was determined by IR following UV and persulphate oxidation using a Dohrmann Xertex Carbon analyzer with a Horiba PIR 2000 IR detector (Santa Clara, CA). The samples were prepared by the chloroform fumigation and extraction method (Robertson et al., 1999; Brookes et al., 1985). Soil extractable ammonium and nitrate + nitrite concentrations were determined from 1 M KCl extracts (Allen, 1989). Two additional soil samples were collected from each community in August 2010 extracted and analyzed for inorganic nitrogen content. Sample results from both dates were pooled for statistical analysis. All extractions were made within 12 h of soil sampling. Soil extractable ammonium and nitrate + nitrite concentrations were determined using the Astoria Pacific AP3 auto-analyzer (Astoria Pacific Inc., Clackamas, OR).

Soil respiration was determined by EGM-3 Soil Respiration Chamber, Infra-red Gas analyzer (PP Systems Inc., Boston, MA). Measures were performed on four occasions: mid afternoon July 19, 2010, early morning July 20, 2010, 2 days after a rainfall event, mid morning August 11, 2010, 8 days after a rainfall event, and mid morning April 10, 2011. Soil moisture was determined at the time of the July and August respiration sampling events. Sampling order was randomly assigned by forest and community within forest.

2.1. Statistical methods

Data were tested for homogeneity of variance by the Brown Forsythe HOV test and for normality by the Proc Univariate command. To achieve homoscedasticity and normality data were transformed before analysis. Where simple arcsin and log
transformation could not entirely resolve this the data were rank transformed before an ANOVA was performed (Sokal and Rohlf, 1995; Conover and Iman, 1981). Where appropriate data were statistically analyzed by ANOVA using the Proc GLM command. The experimental design comparing communities was a block design comparing communities nested within forest. Repeated measures statistical analyses were performed by two way ANOVA of forest and community using the Proc Mixed command with date as the repeated group (Sokal and Rohlf, 1995; SAS Inst., Cary, NC). The statistical significance α level was 0.1.

To identify relationships between environmental parameters Pearson’s correlation matrices were created. The analyses above were performed using SAS 9.2 2002–2008 (SAS Inst., Cary, NC). To identify relationships between biological species and environmental parameters Canonical correspondence analysis (CCA) was performed with PC-Ord vs. 3.01 (MJM Software, Glendenen Beach, OR).

3. Results

3.1. Community characteristics

Within each community type the nominal species group predominated with less than 5% representation of either opposing community type dominant represented (Table 1a). Within the lichen–moss community type mosses made up nearly 50% of the lichen plus moss cover in two of the forests lichen–moss communities, but at the McDonalds forest site mosses made up 16% of the total lichen plus moss cover.

There was no significant difference among forest sites in measured canopy parameters. The graminoid and ericaceous dominated communities had significantly greater stem density (stems ha$^{−1}$) ($F_{2,4}$ 4.36, $p = 0.09$), tree stem basal coverage (m$^2$ ha$^{−1}$) ($F_{2,4}$ 6.30, $p = 0.058) and % canopy cover ($F_{2,4}$ 5.43, $p = 0.072) than the lichen–moss dominated community (Table 1b). Canopy tree species richness did not vary among communities.

Herbaceous layer cover, Shannon–Wiener species diversity, Evenness and Richness did not vary significantly among forests or communities. Aboveground biomass (AGB) was significantly greater in the ericaceous community type than the graminoid or lichen–moss dominated community types (Fig. 1a). AGB in McDonald was greater than that of Woodmansee and Chatsworth forests ($F_{2,4}$ 9.90, $p = 0.033). The root biomass to a depth of 20 cm did not vary significantly among forests, but was significantly greater in the ericaceous and graminoid community than the lichen–moss dominated community type (Fig. 1b). Proceeding incrementally down the soil profile; root biomass per unit volume of soil did not significantly vary among forests or communities at 0–5 cm depth. At 5–10 cm depth forests did not vary but the ericaceous and graminoid communities had greater root biomass than the lichen dominated community ($F_{2,4}$ 7.76, $p = 0.041), at 10–20 cm depth the ericaceous community had significantly greater root biomass than the graminoid or lichen dominated communities ($F_{2,4}$ 20.6, $p = 0.008) and McDonalds had significantly more root than Woodmansee or Chatsworth ($F_{2,4}$ 12.20, $p = 0.020).

3.2. Soils

Percent bare ground was significantly greater at the lichen–moss dominated communities than at the ericaceous communities ($F_{2,4}$ 5.19, $p = 0.077) and percent litter cover was significantly lower at the lichen–moss dominated communities than at the ericaceous and graminoid communities ($F_{2,4}$ 25.20, $p = 0.005). There were no significant differences in either percent bare ground or percent litter cover between forests. Woody debris was greater at the ericaceous communities than at the lichen–moss dominated communities ($F_{2,4}$ 5.47, $p = 0.072). Woody debris did not vary significantly among forests.

Bulk density at the lichen–moss dominated communities was significantly greater than that of the ericaceous communities at 5–10 cm depth ($F_{2,4}$ 7.86, $p = 0.041) and greater than that of the ericaceous and graminoid communities at 0–20 cm depths (Fig. 2). Bulk density did not vary among communities at 0–5 or 10–20 cm soil depths or among forest sites at any measured depth. Soil particle size analysis of the 0–5 cm and 10–20 cm soil fractions revealed no significant differences in gravel (>20 mm), sand (0.125 – 2.0 mm), silt + clay or SOM among forests or communities at 0–5 cm depth. At 10–20 cm soil depth there were no significant differences in gravel content among forests or communities. At the level of forest SOM did not differ but the McDonalds sand content was greater than the Chatsworth forest site ($F_{2,4}$ 7.80, $p = 0.042) and the silt–clay content at Chatsworth was greater than that of McDonalds ($F_{2,4}$ 6.24, $p = 0.059). At the level of community silt + clay content did not vary but the ericaceous community sand content was greater than that of the graminoid community ($F_{2,4}$ 6.20, $p = 0.059), and the graminoid community SOM was greater than either the ericaceous or lichen dominated communities ($F_{2,4}$ 7.24, $p = 0.047). The moisture content 2 or 8 days post rainfall event did not significantly vary among forests or communities.

Division of the sand fraction into coarse (1–2 mm), medium (0.5–1 mm) and fine particle sizes (0.125–0.5 mm) found no
Table 1a
Community composition percent cover per m². Values presented are mean and SD in parentheses; n = 3.

<table>
<thead>
<tr>
<th>Species</th>
<th>% cover</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ericaceous community</td>
<td>Graminoid community</td>
<td>Lichen–moss community</td>
</tr>
<tr>
<td>Graminoid sp.</td>
<td>0.35 (0.42)</td>
<td>23.6 (7.92)</td>
<td>1.85 (1.59)</td>
</tr>
<tr>
<td>Ericaceous sp.</td>
<td>73 (0.90)</td>
<td>0.06 (0.06)</td>
<td>0.75 (0.90)</td>
</tr>
<tr>
<td>Lichen sp.</td>
<td>2.6 (4.2)</td>
<td>0.33 (0.52)</td>
<td>28.5 (20.3)</td>
</tr>
<tr>
<td>Moss sp.</td>
<td>0.58 (0.63)</td>
<td>0.60 (1.0)</td>
<td>16.5 (19.4)</td>
</tr>
<tr>
<td>Herb sp.</td>
<td>0.29 (0.40)</td>
<td>0.06 (0.06)</td>
<td>0.10 (0.18)</td>
</tr>
<tr>
<td>Tree seedling</td>
<td>0.04 (0.07)</td>
<td>0.02 (0.04)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Shrub tree</td>
<td>3.8 (4.4)</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
</tbody>
</table>

Table 1b
Tree canopy layer characteristics: stem density (ha⁻¹); stem cover (m² ha⁻¹); canopy cover (%), among forest location: Chatsworth, McDonald, Woodmansee; and herb layer community type; ericaceous dominated, graminoid dominated, lichen–moss dominated. Values presented are mean and SEM in parentheses; n = 12. Means separation determined by Tukey’s HSD test following statistically significant ANOVA results (α = 0.1). Significantly different group means indicated by different lower case superscript letters following SEM value in parentheses; a > b > c.

<table>
<thead>
<tr>
<th>Location</th>
<th>Stem density</th>
<th>Stem cover</th>
<th>Canopy cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chatsworth</td>
<td>410 (149)</td>
<td>77.0 (27.7)</td>
<td>57.1 (13.1)</td>
</tr>
<tr>
<td>McDonald</td>
<td>552 (143)</td>
<td>84.3 (10.7)</td>
<td>49.2 (3.70)</td>
</tr>
<tr>
<td>Woodmansee</td>
<td>532 (233)</td>
<td>109 (36.8)</td>
<td>45.8 (12.0)</td>
</tr>
</tbody>
</table>

Significant differences among forests or communities. Overall gravel content ranged from 0.32 to 3.4%; sand content from 93 to 96%, and silt clay from 4.7 to 6.9%. Within the sand fraction the overall range was: coarse sand (3-9%), medium sand (23-34%) and fine sand (60-68%).

Soil extractable ammonium per gram of soil was significantly greater in soils of the graminoid dominated communities than the lichen dominated communities 0–5 cm depth and from 10 to 20 cm soil depth (Fig. 3a and b). Among forests extractable ammonium concentrations per gram of soil was significantly greater in Chatsworth than in McDonald at the 0–5 cm soil depth (F_{2,4} 5.29, p = 0.075), but did not vary significantly at 10–20 cm soil depth. Extractable nitrate + nitrite was greater in soils of the ericaceous and graminoid dominated communities than in the lichen dominated communities at 0–5 cm soil depth (Fig. 3c). No significant differences in nitrate + nitrite concentration per gram of soil were found among communities at 10–20 cm soil depth. Nitrate + nitrate was greater at both Chatsworth and Woodmansee than at McDonald at 0–5 cm soil depth (F_{2,4} 5.29, p = 0.075), and greater at Woodmansee than at McDonald at 10–20 cm soil depth (F_{2,4} 7.54, p = 0.044).

Microbiological activity as measured by MBC per gram of soil did not vary significantly among communities in the 0–5 cm depth samples (Fig. 4a), but was greater in the McDonald and Woodmansee sites than at the Chatsworth sites (F_{2,4} 12.74, p = 0.020). MBC per gram of soil was significantly lower at the lichen–moss dominated community type than either ericaceous or graminoid community types at 10–20 cm depth (Fig. 4b), but did not vary significantly among forests.

Microbiological activity and root activity as measured by soil respiration demonstrates significantly less activity at the lichen–moss dominated community type than either the graminoid or ericaceous community types (Fig. 5). The forests did not significantly vary and there was no significant forest by community interaction. The non-significant forest by community interaction indicates that respiration within communities varied similarly among the forests examined.

The Pearson correlation matrix (α 0.05) created for the 0–5 cm soil samples (Table 2a) revealed several consistent results, i.e.: soil moisture was positively correlated with silt–clay content; ammonium concentration positively correlated with nitrate concentration and both negatively correlated with sand content. There was a significant negative correlation of SOM, as measured by LOI, with sand content and a positive correlation of SOM with ammonium and nitrate concentration, both of which were significantly greater in the graminoid community type than in the lichen dominated community type (Fig. 3a and c). This finding suggests that the graminoid community also tends to have more SOM and less sand than the other communities. Bulk density and MBC did not correlate with any measured parameter. The Pearson correlation matrix for the 10–20 cm soil samples (Table 2b) similarly revealed several consistent results, i.e.: silt–clay content was positively correlated with soil moisture content and sand was negatively correlated with SOM. Silt–clay content was also positively correlated with SOM. Bulk density, which was significantly greater in the lichen–moss community (Fig. 2), was negatively correlated with MBC, which

![Fig. 2](image-url)
Table 2a
Pearson’s correlation matrix for 0–5 cm soil depth, % moisture (moisture); % loss on ignition (LOI), ammonium nitrogen (µg g⁻¹) (NH₄-N); nitrite + nitrate nitrogen (µg g⁻¹) (NO₂-N); % sand (sand); % silt + clay (silt-clay). r² value presented above p value. Significant p values (α < 0.1) in italics. Bulk density (g cm⁻³), root mass (mg cm⁻²) and microbial biomass carbon (µg g⁻¹) did not correlate significantly with other measured parameters.

<table>
<thead>
<tr>
<th>0–5 cm</th>
<th>Moisture</th>
<th>LOI</th>
<th>NH₄-N</th>
<th>NO₂-N</th>
<th>Sand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture</td>
<td>1.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>LOI</td>
<td>0.523</td>
<td>1.000</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>NH₄⁻</td>
<td>0.134</td>
<td>0.812</td>
<td>1.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0.732</td>
<td>0.0078</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NO₂⁻</td>
<td>0.286</td>
<td>0.769</td>
<td>0.886</td>
<td>1.000</td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0.456</td>
<td>0.0154</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand</td>
<td>−0.433</td>
<td>−0.880</td>
<td>−0.921</td>
<td>−0.856</td>
<td>1.000</td>
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<tr>
<td>Silt-clay</td>
<td>0.845</td>
<td>0.5812</td>
<td>0.340</td>
<td>0.274</td>
<td>−0.602</td>
</tr>
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<td>0.004</td>
<td>0.101</td>
<td>0.371</td>
<td>0.475</td>
<td>0.0860</td>
</tr>
</tbody>
</table>

was lower in the lichen–moss community at 0–20 cm soil depth (Fig. 4b). Ammonium and nitrate did not correlate with any measured parameter at this depth.

 Canonical correspondence analysis (CCA) separation of community types according to measured community constituents and edaphic factors explained 51.4% of the variation by axis 1 and 37% of the variation by axis 2 (Fig. 6). Overall the CCA clearly separated the communities. In terms of species composition the assigned names indicate the dominant herb layer species (Table 1a), and these communities align more clearly with one another than to their respective forests.

The lichen–moss dominated communities are distinguished by greater % bare ground, low bulk density intermediate levels of extractable ammonium and greater presence of non-graminoid herb species. The graminoid dominated communities are distinguished by the highest levels of extractable ammonium concentrations and higher SOM. The ericaceous dominated communities are distinguished by low bulk density, low extractable ammonium availability and a higher presence of seedlings. The canopy characteristics were centered between communities along both axes.

4. Discussion

Reduced stem density, basal coverage, canopy cover, herbaceous cover and litter cover in the lichen dominated community indicate that these communities are subject to greater desiccation due to increased sun exposure. Reduced competition for water and nutrients from surrounding trees may explain the lack of soil moisture differences among communities at either two or eight days after a rainfall event. The CCA found that tree seedlings clustered with the ericaceous community, contrary to our expectations and contrary to that suggested by Mallick (2003). These deciduous ericaceous species may not exert as significant impediment to tree species regeneration as evergreen or more sclerophyllous ericas.

In terms of soil particle size distribution, our first hypothesis, that there would be no difference in soil physical characteristics among communities within a forest was supported by the results. Reductions in soil bulk density in the ericaceous community appear to more heavily influenced by the greater root biomass, litter inputs or both than by soil particle size distribution.

Significantly greater root biomass in the ericaceous and graminoid communities along with significantly greater SOM content in the graminoid community at the 10–20 cm depth coupled with the finding of significantly greater extractable ammonium at 0–5 cm and 10–20 cm soil depths and nitrate at 0–5 cm in the ericaceous and graminoid communities suggests that the elevated inorganic nitrogen concentrations in these communities is biogenic in origin, i.e. is derived from the mineralization of root and litter inputs. Sedia and Ehrenfeld (2005) found significantly greater concentrations ammonium in graminoid dominated community soils than in lichen community soils, however they found greater concentrations of nitrate in the soils of lichen dominated communities than under graminoid community soils. This is perhaps indicative of reduced competition between nitrifying bacteria and plant roots for ammonium.

Our finding of similar extractable nitrogen levels among the ericaceous and graminoid communities by ANOVA was also contrary to our expectations. Nevertheless in the CCA the inorganic nitrogen vector aligned more prominently with the graminoid community.

Table 2b
Pearson’s correlation matrix for 10–20 cm soil depth. % moisture (moisture); % loss on ignition (LOI); soil bulk density (g cm⁻³) (BD); microbial biomass carbon (µg g⁻¹) (MBC); % sand (sand); % silt + clay (silt-clay). r² value presented above p value. Significant p values (α < 0.1) in italics. Ammonium nitrogen (µg g⁻¹) (NH₄-N) and nitrite + nitrate nitrogen (µg g⁻¹) (NO₂-N) did not correlate significantly with other measured parameters.

<table>
<thead>
<tr>
<th>10–20 cm</th>
<th>Moisture</th>
<th>LOI</th>
<th>BD</th>
<th>MBC</th>
<th>Sand</th>
</tr>
</thead>
<tbody>
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<td>Moisture</td>
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<tr>
<td>BD</td>
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<td>−0.172</td>
<td>1.000</td>
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</tr>
<tr>
<td></td>
<td>0.0842</td>
<td>0.659</td>
<td></td>
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</tr>
<tr>
<td>MBC</td>
<td>0.591</td>
<td>0.383</td>
<td>−0.809</td>
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<tr>
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<td>0.0937</td>
<td>0.309</td>
<td>0.0083</td>
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<tr>
<td>Sand</td>
<td>−0.125</td>
<td>−0.862</td>
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<td>−0.219</td>
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<td>0.748</td>
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</tbody>
</table>
Fig. 3. Soil extractable ammonium and nitrate + nitrite from studied plant communities. (a) Soil extractable ammonium (μg NH4-N g⁻¹), 0–5 cm soil depth $F_{(2,4)} = 5.57$, $p = 0.070$. (b) Soil extractable ammonium (μg NH4-N g⁻¹), 10–20 cm soil depth $F_{(2,4)} = 7.05$, $p = 0.049$. (c) Soil extractable nitrate + nitrite (μg NO3⁻ + NO2⁻-N g⁻¹), 0–5 cm soil depth $F_{(2,4)} = 4.75$, $p = 0.088$. Means presented are mean with SEM error bars. Means separation determined by Tukey’s HSD test following statistically significant ANOVA results ($α = 0.1$). Significantly different group means indicated by different upper case letters above community histogram, A > B > C.

The findings of reduced root biomass and microbial biomass at 10–20 cm depth at the lichen–moss community suggests that the lichen fungal symbiont may comprise the largest portion of the microbial biomass in that community type. Despite having somewhat similar total microbial biomass concentrations among these communities at 0–5 cm soil depth the microbial communities of these plant communities are by their very nature different. These forests are dominated by fungi (Krumins et al., 2009) and although, in all three communities ectomycorhizal associates of the dominant trees will be found, the ericaceous plant species in these forests

Fig. 4. Microbial biomass carbon (MBC) from studied plant communities. (a) MBC (μg C g⁻¹), 0–5 cm soil depth $F_{(2,4)} = 2.18$, $p = 0.229$. (b) MBC (μg C g⁻¹), 10–20 cm soil depth $F_{(2,4)} = 9.00$, $p = 0.033$. Means separation determined by Tukey’s HSD test following statistically significant ANOVA results ($α = 0.1$). Significantly different group means indicated by different upper case letters above community histogram, A > B > C.

Fig. 5. Soil respiration carbon flux from studied plant communities. Soil respiration carbon flux (g C m⁻² hr⁻¹). Community: $F_{(2,27)} = 26.10$, $p < 0.0001$. Sample dates April 10, 2011, July 19, 20, 2010, August 10, 2010. Values presented are mean with SEM error bars. Means separation determined by Tukey’s HSD test following statistically significant ANOVA results ($α = 0.1$). Significantly different community group means indicated by different upper case letters above community histogram, A > B > C.
are extensively colonized by ericoid mycorrhizae (unpublished data). In the lichen–moss community the microbial community will presumably be dominated by the lichen mycobiont, primarily Euascomycetes (Webster and Webster, 2007), and arbuscular mycorrhizal, frequently of the genus Glomus, through their association with the subdominant mosses (Zhang and Guo, 2007; Rabatin, 1980). As C. pensylvanica is non-mycorrhizal (unpublished data) the microbial community will be largely saprotrophic. Because lichens primarily take up nitrogen from atmospheric deposition (Mallick, 2003) and the microbial communities vary so widely among the plant communities it also seems likely that soil nitrogen dynamics will also vary (Michelsen et al., 1996).

Due to lower root biomass, microbial biomass at 10–20 cm soil depth, more bare ground and less litter cover in the lichen–moss dominated community type it is not surprising that significantly lower rates of respiration were also found. Sedia and Ehrenfeld (2005) also found significantly greater respiration rates in graminoid dominated community soils than in lichen community soils.

In this study we have described some basic edaphic differences between these community types that are irrespective of forest location. Differential natural uptake preferences for ambient N forms among plant species (Nordin et al., 2001) may be important for the continued success of these communities and their apparent self-sustainability in this environment. Further studies should identify the constituent groups of the soil microbial biomass within each herb layer community. Further studies aimed toward identifying the mechanisms of self-sustainability should also be examined. This would include in depth studies of primary productivity and soil carbon accumulation, nutrient cycling pathways and rates of nutrient cycling, and how they are influenced by both mycorrhizal and saprotrophic microorganisms. The identification and influence of potentially allelopathic chemicals in these communities should also be investigated.

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References


Fig. 6. Canonical correspondence analysis (CCA) – separation of community types according to community constituents and edaphic factors. Habitat variables: ericaeous community location: Chatsworth (CE), McDonald (ME), Woodmansee (WE); lichen–moss community location: Chatsworth (CL), McDonald (ML), Woodmansee (WL); graminoid community location: Chatsworth (CG), McDonald (MG), Woodmansee (WG). Matrix 1: community variables: stem density ha−1 (den), stem cover m2 ha−1 (stem cov), % canopy cover (can cov), % herb layer cover (herb cov), % graminoid species cover (g), % lichen cover (lichen), % moss cover (moss), % seedling cover (seed), % shrub cover (shrub). Matrix 2: environmental variables: % bare ground cover (bare), % litter cover (litter), % loss on ignition (LOI), bulk density g cm−3 (BD), ammonium nitrogen (μg g−1) (NH4-N), nitrite + nitrate nitrogen μg g−1 (NO3-N), microbial biomass carbon (μg g−1) (MBC). Edaphic factors explained 51.4% of the variation along axis 1 and 37% of the variation along axis 2.


