

North American Fungi



Volume 5, Number 5, Pages 205-213
Published December 22, 2010

Nitrogen concentration does not increase in ectomycorrhizal basidiocarps with increasing altitude

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Anna Liisa Ruotsalainen, A. L., and M.-M. Kytöviita. 2010. Nitrogen concentration does not increase in ectomycorrhizal basidiocarps with increasing altitude. *North American Fungi* 5(5): 205-213. doi: 10.2509/naf2010.005.00513

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Abstract: Plants in arctic and alpine environments possess higher nitrogen concentrations (%N) than plants in warmer environments. High nitrogen content is considered an adaptation to nutrient poor and cold environments. Prior studies demonstrate that %N increases in plants with increasing altitude. Since fungal growth should also be limited by harsh environmental conditions that increase with altitude, it was hypothesized that fungi growing at higher altitudes would have higher %N than fungi at lower altitudes. To investigate this hypothesis, we analyzed the total nitrogen concentrations in basidiocarps of two genera of abundant ectomycorrhizal fungi, *Leccinum* and *Lactarius*, growing at different altitudes (85 – 800 m a.s.l.) in several localities of the Fennoscandian subarctic. Contrary to our expectations, results show that nitrogen concentration in *Leccinum* decreases with increasing altitude, whereas there was no change for *Lactarius*. Thus results for fungi were decoupled from that of the associated plants. The %N in *Leccinum* basidiocarps was somewhat higher than that in *Lactarius* species (4.55 ± 1.15 and 3.50 ± 0.58 , respectively). Future studies should include examination of species, host, and soil effects on %N, as well as isotope analysis of carbon and nitrogen in basidiocarps, soil, and root material.

Key words: alpine, ecophysiology, elevation gradient, fungi, nitrogen, subarctic, temperature

Introduction: Alpine gradients bring about two primary environmental changes: the mean temperature is lower at higher altitudes and the atmospheric air pressure decreases i.e. 50 hPa at an altitude of 2600 m compared to an air pressure of 1013 hPa at sea level (Körner 2003). Temperature gradients in soil have also been documented; for example there is a 5.24 °C difference in average growing season temperatures between 2300 m and 1650 m in the Alps (Schinner and Graunthaler 1981). All organisms inhabiting high altitudes must therefore cope with low temperatures and Reduced O₂ and CO₂ in the environment (Larcher 1995, Willmer et al. 2005). Decreases in mean temperature, in particular, affect the whole ecosystem via changes in climatic and edaphic processes (Körner 2003).

Although arctic and alpine ecosystems are nutrient limited (Shaver and Chapin 1980), plants inhabiting these environments possess higher tissue nitrogen concentrations than their temperate and low altitude counterparts (Chapin et al. 1975, Chapin 1983, Chapin and Oechel 1983, reviewed by Körner 1989 and Körner 2003). At high altitudes, plants increase foliar nitrogen concentrations that facilitate CO₂ capture (Körner 1989). This, at least partially compensates for the negative effects of low temperature (Billings and Mooney 1968) and low partial pressure of CO₂ (Friend et al. 1989, Morecroft and Woodward 1996) on enzymatic activities. In addition, nutrient availability typically occurs in flushes in arctic and alpine environments which favor luxury consumption of nutrients and their conservation in plant tissues (Chapin 1980, Van Wijk et al. 2003).

However, there is scant information about potential changes in nutrient concentrations along altitudinal or latitudinal gradients for other groups of organisms such as the fungi. While a set of arctic-alpine fungi are well known, there is only limited information on their physiology in

these cold-dominated habitats. In general most fungi are mesophilic, preferring growth temperatures of 10-40 °C *in vitro* (Deacon 2006). Arctic and alpine species are adapted to temperatures close to zero (Schinner and Graunthaler 1981), however the mechanisms of adaptation are poorly studied (Robinson 2001). Some fungi cope with lower temperatures by induction of cold active enzymes (Tibbett et al. 1998) but increased cellular enzyme activities did not account for higher respiration rates of cold acclimated arctic *Cenococcum* (Antibus 2010). It has also been suggested that low temperatures may limit mycorrhizal fungi more than their host plants (Kytöviita 2005) which could explain why high-arctic plants are increasingly non-mycorrhizal with decreasing latitude (e.g. Bledsoe et al. 1990, Väre et al. 1992). In general, fungi are rich in proteins, but also contain other forms of N such as free amino acids, chitin, nucleic acids and urea (Kurkela et al. 1980). As average temperature and nutrient availability decrease with increasing altitude (Schinner and Graunthaler 1981, Körner 2003), %N might increase as fungi invest in additional protein-based enzymes in response to cold.

In this paper we examined whether fungi express adaptations similar to those of plants at high altitudes, i.e. higher tissue nitrogen (N) concentrations with increasing altitude. To accomplish this, we collected and analyzed the total %N in basidiocarps of two genera of important ectomycorrhizal fungi (*Lactarius* and *Leccinum*) growing at different altitudes in the subarctic Fennoscandian mountains.

Materials and Methods: Material for this study was collected between 2004-2008 at five locations in Fennoscandia and the Kola Peninsula, NW Russia. The major part of the data derives from collections made in autumn 2007 at Utsjoki, Kevo, NE-Finland (Ailigas and Jesnal Mts.). Sampling was carried out in Abisko (Sweden), Tamok (Norway) and Khibiny (NW

Russia) in 2004 and in Kilpisjärvi (Finland) in 2008. Fungi were collected from subalpine to low-alpine zones. Treeline is formed by *Betula pubescens* ssp. *czerepanovii* Orlova (Hämet-Ahti) and lies at about 300 m above sea level (a.s.l.) at Kevo, 500 m a.s.l. in Khibiny, 600 m a.s.l. at Kilpisjärvi, 800 m a.s.l. at Abisko and 900 m a.s.l. at Tamok (Dahl 1975). *Pinus sylvestris* L. was also present at the low altitude sites in the Kevo area (Mt. Jesnal, P. Wäli pers. comm.) and in the Khibiny (160-190 m a.s.l. at Monchegorsk). The number of collections from each locality is given in Table 1. The total number of samples in the analysis was 106 (56 *Lactarius* and 50 *Leccinum*) with each sample consisting of one basidiocarp (or in rare cases of a few adjacent specimens).

Whole basidiocarps were picked and cleaned and only young or intact basidiocarps with no major signs of insect-damage were included.

Basidiocarps were dried with a mushroom dryer at 40°C until air dry and preserved in paper bags at room temperature for subsequent C/N analysis. To avoid contamination by pests, the material was frozen (-18°C) for two weeks once or twice during the preservation period.

The ectomycorrhizal genera *Lactarius* and *Leccinum* were selected as the focal taxa because (i) they are abundant in the research area, (ii) the same species can be found over a wide elevational range and (iii) they are easy to identify to genus level. A genus level analysis was necessary since obtaining representative collections at the species level would not have been possible due to the sparse occurrence of basidiocarps and the limitations of sampling efforts. Although much of the material was not identified to species level, 42 of the 106 collections were named (Table 2); no major bias was found for any particular species due to altitudinal distribution.

The C/N analysis was carried out on dried and homogenized caps (pilei) of the basidiocarps using a dynamic flash combustion technique (CE Instruments EA 1110 Elemental Analyzers).

Statistical analysis

The study material was analyzed in two portions which correspond to the structure of our data. The data collected from Utsjoki, Kevo (hereafter referred as Kevo data) constituted a major part of this study since it was collected in a systematic factorial manner at two altitudes, high vs low, for

Table 1. Localities, altitudes, number of samples and sample years for fruiting bodies in nitrogen concentration study in 2004-2008. Each sample represents either one fruiting body or a small, closely associated group of fruiting bodies.

Locality	Country	Altitude m a. s. l.	No. Samples <i>Lactarius</i>	No. Samples <i>Leccinum</i>	Sample year
Kevo, Jesnal, high	Finland	310	10	12	2007
Kevo, Jesnal, low	Finland	85	10	19	2007
Kevo, Ailigas, high	Finland	330	10	1	2007
Kevo, Ailigas, low	Finland	90	10	4	2007
Kilpisjärvi ¹	Finland	470 -800	7	11	2004, 2008
Abisko & Tamok ²	Sweden, Norway	233 - 600	5	1	2004
Khibiny ³	Russia	190 - 615	4	2	2004

¹Samples from mountains Jehkats, Pikku-Malla and Saana.

²Samples from Låktajohka and Tamokdalen.

³Samples from Monchegorsk and mountains Rasvumchorr and Hipik

Table 2. Nitrogen concentrations (%N) for collections identified to species (some tentative names).

Species	No. collections	Ave. %N	Range %N	Elevation range	Locations
<i>Lactarius mammosus</i> Fr.	1	3.19	3.19	160	Khibiny
<i>Lactarius nanus</i> J. Favre	1	2.86	2.86	500	Tamok
<i>Lactarius rufus</i> (Scop.) Fr.	3	3.72	3.53 - 3.79	190 - 490	Abisko, Khibiny
<i>Lactarius salicis-herbaceae</i> Kühner	2	2.54	2.12 - 2.95	600 - 825	Abisko, Kilpisjärvi
<i>Lactarius scoticus</i> Berk. & Broome	1	2.74	2.74	500	Kilpisjärvi
<i>Lactarius torminosus</i> (Schaeff.) Pers.	1	2.99	2.99	506	Kilpisjärvi
<i>Lactarius trivialis</i> (Fr.) Fr.	4	4.07	3.05 - 4.99	233 - 490	Abisko, Khibiny, Kilpisjärvi, Tamok
<i>Lactarius utilis</i> (Weinm.) Fr.	1	2.86	2.86	630	Kilpisjärvi
<i>Leccinum rotundifoliae</i> (Singer) A.H. Sm.	5	4.23	2.14 - 5.73	610 - 800	Kilpisjärvi
<i>Leccinum scabrum</i> (Bull. : Fr.) Gray coll.	6	4.05	2.54 - 6.57	310 - 470	Kevo (Jesnal), Kilpisjärvi
<i>Leccinum versipelle</i> (Fr. & Hök) Snell	17	4.16	2.71 - 6.55	90 - 621	Kevo (Ailigas, Jesnal), Khibiny, Kilpisjärvi, Tamok

direct comparison. The second portion of the material originated from a geographically large area and altitude was monitored as a continuous variable. First, the Kevo-data was analyzed with a linear mixed effects model (lme) using altitude (high/low) as an explanatory variable and 'mountain' (Mt. Jesnal/Mt. Ailigas) as a random 'block' factor (Crawley 2007). The analyses were carried out separately for *Lactarius* and *Leccinum* basidiocarps. Next, the spatially more variable data collected from different altitudes in Abisko, Tamok, Kilpisjärvi and Khibiny were analyzed with a similar model, except that the explanatory variable was continuous and the locality was a block factor; analyses were done separately for each genus. The applicability of the models was controlled using diagnostic plots. The analyses were carried out with R statistical package (R Development Core Team 2007), version 2.6.2.

Results: In the Kevo material, %N decreased significantly in *Leccinum* specimens at the higher altitude ($F_{(1,33)} = 31.16$, $p < 0.001$, Figure 1A). In contrast, there was no altitudinal difference in %N for the *Lactarius*-specimens ($F_{(1,33)} = 1.63$, $p = 0.210$, Figure 1B) for the Kevo material. These results are supported by observations at the other locations where the %N in *Leccinum* was marginally significantly lower with altitude ($F_{(1,10)} = 3.31$, $p = 0.099$, Fig. 2A) and %N in *Lactarius*

showed no change ($F_{(1,13)} = 1.31$, $p = 0.273$, Figure 2B). The average %N in *Leccinum* basidiocarps was in general higher for the entire data set (4.55 ± 1.15) compared to *Lactarius* species taken altogether (3.50 ± 0.58) ($t = -5.78$, $df = 71.44$, $p < 0.001$).

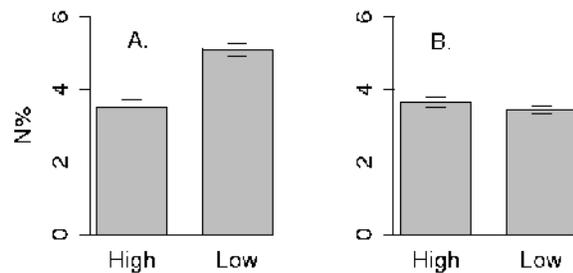


Figure 1. Total nitrogen % (\pm SE) in a) *Leccinum* and b) *Lactarius* caps from Kevo at low (below treeline) and high (above treeline) altitudes.

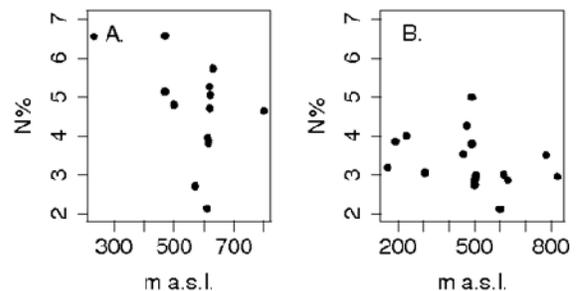


Figure 2. Total nitrogen % in a) *Leccinum* and b) *Lactarius* caps in relation to increasing altitude (m a.s.l.) in subarctic mountains.

Discussion: Although the data set is limited, it suggests that for the ectomycorrhizal fungi tested, %N in the basidiocarps does not increase with the altitude. In actuality, results show that the %N in basidiocarps remained unchanged (*Lactarius* species) and can even decrease with altitude (*Leccinum* species). These data show that ectomycorrhizal fungi do not necessarily follow the same pattern as plants (Körner 1989, 2003) in terms of adaptations to alpine gradients. Also, the average %N is lower in *Lactarius* compared to that for *Leccinum* in the Fennoscandian subarctic.

Several factors should be considered that might qualify the data, including: small sample size limited to two genera, species variation could not be taken into account, and for the larger study, a majority of the *Leccinum* specimens occurred between a narrow altitudinal range, all of which might limit broad conclusions. There was also high variation within genera at particular altitudes. In addition, it is not possible to conclude that the %N in basidiocarps necessarily reflects that of the largest part of the organism, the fungal hyphae in the soil. Comparative studies have not been conducted due to the difficulty of extracting mycelium from the soil but Nilsson and Wallander (2003) found that the average %N for ectomycorrhizal mycelia can be as low as 0.5 % (calculated for a Norway spruce stand). Thus, it is possible that ectomycorrhizal fungi concentrate N in basidiocarps.

The mean %N in *Lactarius* basidiocarps observed in this study (3.5%) is comparable to values reported by Ohtonen (1986) for boreal coniferous forest fungi (2.6-3.8 % in caps) and Edmonds and Lebo (1998) for temperate rain forest *Lactarii* (3.7%) but higher than those reported by Vogt and Edmonds (1980, average 2.8% in whole basidiocarps). Caps (pilei) can be expected to have higher nutrient concentrations due to the fertile hymenium (Rudawska and Leski 2005). The %N in *Leccinum* basidiocarps in this study (4.5%) is comparable to that found in boletes

(Edmonds and Lebo 1998, Gebauer and Taylor 1999) which are considered comparatively protein-rich in general.

Differences in life forms can play a role in %N differences in basidiocarps. Vogt et al. (1981) (also see Hobbie et al. 2009) have shown saprobic fungi to have higher %N compared to ectomycorrhizal fungi. Possible physiological differences in degradative abilities between *Lactarius* and *Leccinum* cannot be ruled out as an explanation for differences in %N as well. Earlier laboratory studies failed to indicate a clear difference in protein utilization capacity between these genera (Abuzinadah and Read 1986, Finlay et al. 1992, Dickie et al. 1998), however a recent study showed heavy protease production in a wide range of *Lactarius* species in culture (Nygren et al. 2007).

In addition to N source use, these differences could reflect the dominant morphology of the ectomycorrhizae themselves as related to the exploration type. *Lactarius* produces a contact exploration type whereas *Leccinum* produces a long range type (Hobbie and Agerer 2010); these also differ in hydrophobicity. Although they don't report %N, Hobbie et al. (2009) do demonstrate significant differences in ¹⁵N abundance in *Leccinum* and *Lactarius* basidiocarps from tundra at Toolik Lake, Alaska. This pattern of ¹⁵N with *Leccinum* higher than *Lactarius* is also evident in boreal forests in Sweden (Taylor et al. 2003).

Host trees also have potential to affect %N in their associated mycorrhizal fungi via nutrient transfer and exchange processes (Smith and Read 1997). Hogberg et al. (1999) for example demonstrated differences in ¹³C abundances in basidiocarps of *Leccinum* and *Lactarius* when associated with different hosts such as birch, pine or spruce. In the area and altitudes studied, *Leccinum* species are associated with *Betula pubescens* Ehrh. at lower altitudes shifting to *B. nana* L. above treeline (Gulden et al. 1985).

Lactarius species are associated either with *P. sylvestris*, *B. pubescens* or *Salix* species below treeline and with *B. nana* and arctic-alpine *Salix* species at higher altitudes (Gulden et al. 1985, Knudsen and Vesterholt 2008). Treeline is formed by *Betula pubescens* ssp. *czerepanovii* Orlova (Hämet-Ahti) on all of our sites, and *Pinus sylvestris* L. was also present at low altitude collecting sites in the Kevo area, at Mt. Jesnal and in the Khibiny area (Monchegorsk). In our alpine sites, the potential hosts for ectomycorrhizal fungi were *B. nana*, *Salix* spp., and *Bistorta vivipara* (L.) Gray.

Differences in soil nutrients might also offer an explanation for altitudinal differences in %N between *Leccinum* and *Lactarius* basidiocarps, with no change for *Lactarius* and a decrease for *Leccinum*. Results could possibly be related to decreasing nitrogen availability in soil with increasing altitude. Lower mean temperatures constrain net primary production of plants (Billings and Mooney 1968, Körner 2003) and nutrient mineralization in soil (Rehder and Schäfer 1978, Schmidt et al. 1999); this implies that in general nutrient availability decreases and the relative proportion of nutrients in organic and recalcitrant forms increases at higher altitudes (Väre et al. 1997, Körner 2003).

Soil nutrient data is available for two of the sites, Khibiny and Kilpisjärvi. In Khibiny, the %N in soils decreases with increasing altitude at one site, whereas at another site the pattern was merely unimodal (Ruotsalainen et al. 2009). In Kilpisjärvi, exchangeable %N and %P (Kyllönen 1988) decrease with increasing altitude (Väre et al. 2007). Shifts in the OM content along the altitudinal gradients (Väre et al. 1997) may complicate the interpretation of altitudinal patterns for %N in the soil, since %N is largely dependent on the amount of the organic matter present. *Leccinum* species appear to have a tendency to accumulate N in higher concentrations compared to those of *Lactarius*,

and could possibly be more limited by the decreasing nutrient availability due to altitude.

The nutrient content of the growth substrate has also been found to affect the %N in basidiocarps of mycorrhizal and decomposer fungi (Vogt and Edmunds 1980). Gebauer and Taylor (1999) observed similar %N between groups of inorganic and organic N-using ECM fungi that could still be separated on the basis of ^{15}N enrichment.

In conclusion, it appears that %N in ECM basidiocarps does not follow that of plants which is consistent with results of Mayor et al. (2009) who found ^{15}N patterns to be uncoupled to those of plants over a latitudinal gradient.

Taken together results show that (i) %N in basidiocarps of two fungus genera either decreases or stays constant along with increasing altitude and (ii) the average %N is lower in *Lactarius* as compared to *Leccinum* in the Fennoscandian subarctic. Future studies aimed at sorting out possible physiological and morphological explanations for the species and the altitudinal differences observed here could incorporate stable isotope analysis of ^{13}C and ^{15}N as well as the C and N concentrations. Examination of soil, plant root and shoot material and basidiocarps should help explain how nitrogen is taken up and partitioned to hosts over the altitudinal gradient in question.

Acknowledgements: We thank Ernest and Valerie Emmett, Riitta Laitinen and Piippa Wäli for collecting a major portion of the samples, and Mikhail Kozlov for practical arrangements in the Kola Peninsula. Esteri Ohenoja is thanked for identifying some specimens and Tuulikki Pakonen and Tarja Törmänen for C/N analysis. We thank Bob Antibus for his input which substantially improved this paper. This study was financed by the Academy of Finland (projects #122 092 and #211 734).

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