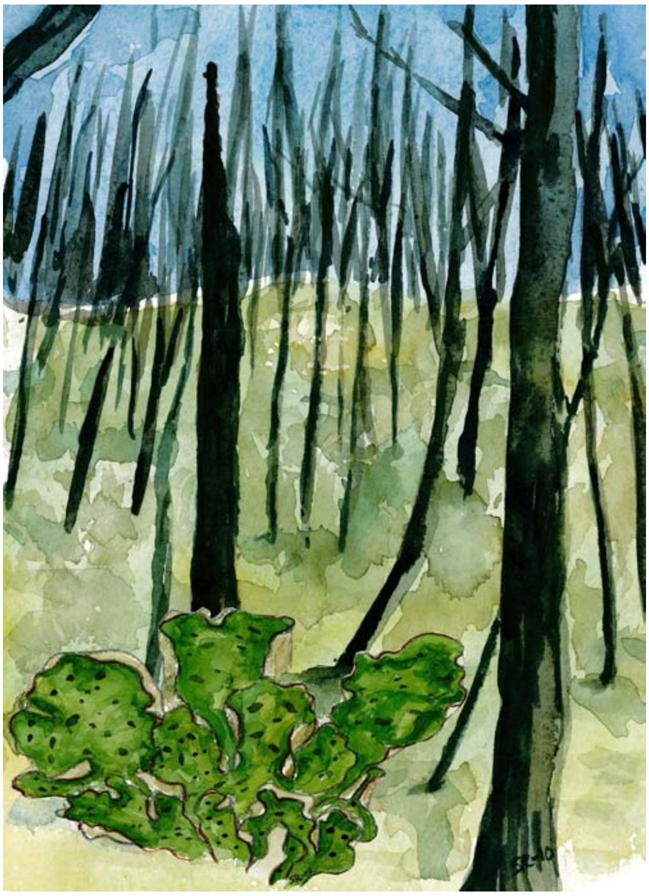
Examensarbeten **2010:01**
Institutionen för skogens ekologi och skötsel

Distribution and nitrogen fixation of terricolous lichens in a boreal forest fire chronosequence



Akvarell: Sara Rundqvist

Aron Sandling

Sveriges Lantbruksuniversitet — Umeå 2010
Examensarbete i biologi, 15 hp, grund C — ISSN 1654-1898
Handledare: Michael Gundale, SLU, Inst för skogens ekologi och skötsel
Examinator: Marie-Charlotte Nilsson Hegethorn, SLU, Inst f skogens ekologi och skötsel

Examensarbeten **2010:01**
Institutionen för skogens ekologi och skötsel

Distribution and nitrogen fixation of terricolous lichens in a boreal forest fire chronosequence

Aron Sandling

Nyckelord / *Keywords:*

Succession, fire chronosequence, nitrogen fixation, boreal forests, lichens, *Peltigera aphthosa*, *Nephroma arcticum*

ISSN 1654-1898 Umeå 2010

Sveriges Lantbruksuniversitet / *Swedish University of Agricultural Sciences*
Fakulteten för skogsvetenskap / *Faculty of Forest Sciences*
Examensarbete i biologi / *Bachelor of Science thesis*, EX0587, 15 hp, C

Handledare / *Supervisor*: Michael Gundale
SLU, Inst för skogens ekologi och skötsel/ *SLU, Dept of Forest Ecology and Management*
Examinator / *Examiner*: Marie-Charlotte Nilsson Hegethorn
SLU, Inst för skogens ekologi och skötsel / *SLU, Dept of Forest Ecology and Management*

I denna rapport redovisas ett examensarbete utfört vid Institutionen för skogens ekologi och skötsel, Skogsvetenskapliga fakulteten, SLU. Arbetet har handletts och granskats av handledaren, och godkänts av examinator. För rapportens slutliga innehåll är dock författaren ensam ansvarig.

This report presents an MSc/BSc thesis at the Department of Forest Ecology and Management, Faculty of Forest Sciences, SLU. The work has been supervised and reviewed by the supervisor, and been approved by the examinator. However, the author is the sole responsible for the content.

Abstract

Given that nitrogen (N) is a limiting nutrient in boreal ecosystems, biological N fixation can have a large influence on primary production and other processes in this ecosystem. To date, most studies focused on N fixation in boreal ecosystems have focused on bryophyte-cyanobacteria associations, whereas relatively few studies have investigated the significance of N fixation by lichens. In this study I examined how biomass and aerial N fixation rates of two common terricolous lichens, *Nephroma arcticum* (L.) Torss. and *Peltigera aphthosa* (L.) Willd., varied across a boreal chronosequence, where time since fire varied from 43 to 362 years. The main objective of the study was to observe how stand age influenced biomass and N fixation rates of terricolous lichens, which has been extensively described in previous studies for bryophyte-cyanobacteria associations. The study revealed that biomass and consequently N fixation rate per unit area for both lichen species significantly increased with time since fire; whereas, lichen N fixation rates per unit mass was unaffected by stand age. *Peltigera aphthosa*, but not *N. arcticum*, demonstrated a significantly higher N fixation rate per unit biomass than the *Pleurozium*-cyanobacteria association. However, on a per unit area basis, both lichen species demonstrated several orders of magnitude lower N fixation rates relative to the *Pleurozium*-cyanobacteria association, which was largely driven by differences in biomass per unit area of lichens and bryophytes. This study demonstrates that lichen biomass and N fixation rates per unit area respond positively to the long term absence of wildfire, and further suggest that the contribution of lichens to total forest N fixation rates is minor relative to bryophytes.

Introduction

Nitrogen is an important component in many biological elements such as amino acids, proteins and nucleic acids (Campbell & Reece 2005). Nitrogen often limits primary production and other processes in cold climate ecosystems (Scimel & Bennett 2004) because the supply of N to plants is slow as a result of slow enzymatic transformation within the N cycle (Tamm 1991). Approximately 78% of the earth's atmosphere is composed of N gas (N_2), but this N is largely unavailable to organisms. Nitrogen must be fixed from the atmosphere to a form that can be used by organisms, which is done through an enzyme mediated reduction reaction. Nitrogen-fixation is carried out exclusively by specialized bacteria that live freely in the soil, in or on plants (associative bacteria) or within lichens (Rai 2002). Biological N-fixation is the main N input in natural ecosystems (Cleveland 1999) and is therefore considered to greatly influence productivity in boreal ecosystems (Vitousek & Hobbie 2000).

In boreal forests, most N fixation occurs in associative N-fixing bacteria that live on feather mosses (DeLuca et al. 2002), and most studies on N fixation have focused on this symbiosis. Yearly N-fixation rates of feather mosses in late successional forests has been estimated to be nearly as large as N inputs via atmospheric deposition (Lagerström et al. 2007; Zackrisson et al. 2004). While it is uncertain how bio-available this N is to vascular plant productivity (Lagerström et al. 2007; Zackrisson et al. 1997), recent studies suggest strong positive interactions between vascular plants and N-fixing feather mosses, suggesting that feather mosses and some vascular plant species may benefit one-another (Gundale et al., In press). The majority of studies on N fixation in boreal forests have focused on feathermoss-cyanobacteria associations, whereas the contribution of other N-fixing organisms remains relatively unexplored. Lichens are a common components of boreal forests (Nash 1996) and some studies have demonstrated that biologically available N in soil is significantly higher close to N-fixing terricolous lichens (Knowles et al. 2006), which may also have a positive effect on vascular plant productivity.

It is well known that lichens generally are sensitive to disturbances such as forestry (Berg et al. 2008), air-pollution (Campbell & Reece 2005) and climate-changes (Epstein et al. 2004). In contrast to these anthropogenic factors, very little is known about how natural disturbances, such as wildfire, influence lichens in boreal forests. The occurrence and long term absence of fire is likely to be an important factor controlling lichen biomass and N fixation rates for several reasons. First, forest fires directly eliminate terricolous lichens and much of the moss layer (Deluca et al. 2002). A second mechanism by which fire may influence lichen biomass and N-fixing activity is by driving changes in N-cycling. Directly following fire, concentrations of inorganic N in the soil greatly increase which promotes a relatively productive community composed of fast growing vascular plant species. In the long term absence of fire, nutrient turnover and availability to plants greatly diminishes, moss biomass increases, and the vascular plant community changes. The reduced rates of nitrogen cycling that occur in the long term absence of wildfire are likely to affect the demand for newly fixed N, and thus provide opportunities for N fixing organisms. Several studies have demonstrated that N fixation in bryophytes increases in response to decreasing N availability (Deluca et al. 2008, Lagerström et al. 2007) and decreasing N deposition (DeLuca et al. 2008). Studies that experimentally evaluated how external N fluxes affect N fixation in lichens have found similar patterns (Rai et al. 1981; Hällbom & Bergman 1983). It is therefore likely that N fixing lichens may respond to forest succession in a similar manner as has been demonstrated for bryophytes.

The objectives of this study were to investigate how time since fire influences the biomass, N fixation rate per unit biomass, and annual N fixation flux per unit area of two common terricolous lichen species in the Swedish boreal forest, *N. arcticum* and *P. aphthosa*. An additional objective was to compare the response of lichens biomass and N-fixation rates to N fixing feather mosses, which have been extensively described. I hypothesized that lichens would demonstrate an increase in biomass, N fixation rate per unit biomass, and N fixation per unit area with increasing time since fire, which has been demonstrated in feathermoss-cyanobacteria associations. Additionally, I hypothesized that the total areal N fixation rate of terricolous lichens will be much lower compared to feathermoss-cyanobacteria associations, due to the relatively low biomass of lichens relative to feather mosses.

Materials and Methods

SITE DESCRIPTION

I conducted this study using 10 forest sites in the northern boreal zone of Sweden (65°35'-66°07' N, 17°15'-19°26' E). The sites vary in time since last fire (43-362 years) and represent a gradient of vegetation development since last fire (Zackrisson 1996). Tree ring scars were used to get estimations when the last fire occurred in the sites (Zackrisson 1996). The selection of the sites were predicated through forest site type classification, a system defining different forest site types based on plant communities that are characteristic in different climatical and edaphical (soil) conditions (Cajander 1949). All sites are of *Empetrum-Vaccinium* type mainly consisting of a mix between *Pinus sylvestris* and *Picea abies* forest. The terricolous lichen flora is dominated by *N. arcticum*, *P. aphthosa* and *Cladina* spp. through the sites, of which *N. arcticum* and *P. aphthosa* are known to fix N, and were the focus species of this study. I quantified the lichen coverage of two species, *N. arcticum* and *P. aphthosa,* by estimating lichen colony sizes in transects at all sites. At each 10m interval along the 100m transect, I created 20m^2 circular plots at random distances (3m or 6m to either left or right) from the central transect. I measured the surface area of all lichen colonies occurring within the borders of these plots. In order to convert surface area to biomass, five colonies of each species in sizes ranging from 0.1 m^2 to 2.5 m^2 were collected to get an estimate of dry weight biomass per unit area.

NITROGEN FIXATION MEASUREMENTS

Nitrogen fixation rates for the lichens were estimated using the acetylene reduction method (Schöllhorn & Burris 1967). When an N-fixing organism is incubated with acetylene gas (C_2H_2), the nitrogenase enzyme reduces acetylene to ethylene gas (C_2H_4), which is directly proportionate to the N fixation rate of the organism. Ethylene is then measured using a gas chromatograph, providing an estimate of N fixation. I collected five thalli of each species from all forest sites for estimation of N fixation rates. *P. aphthosa* was not present in all sites, and therefore was collected only when present. These thalli were placed in vials (22 mL glass tubes), sealed using septa and 2.2ml of air was emptied and replaced with 2.2 ml of acetylene. The lichens were incubated for 24h before measuring the amount of ethylene reduced.

It is well known that moisture content of lichens strongly influences their N fixation rates (Nash 1996). Therefore, in order to scale up N fixation to an annual basis, I used an estimate from Palmqvist & Sundberg (2000) of the annual duration in which lichens are sufficiently moist to fix N. This data was obtained from a nearby location and similar habitat to my study area utilizing one of the same lichen species, *P. aphthosa*, and therefore provide a reasonable estimate of the annual lichen moisture status in my study area.

STATISTICAL ANALYSIS

Biomass and N fixation data was analyzed using linear regressions. N fixation data was log-transformed to receive normality since it is required for the analysis. One-way analysis of variance (ANOVA) with a Tukey's HSD posthoc test was used when comparing N fixation per unit mass for the two lichen species and the bryophyte. Analyses were made in the statistical program R v.2.8.0 for Windows (R-language and environment for statistical computer graphics, Department of Statistics of the University of Auckland).

Results

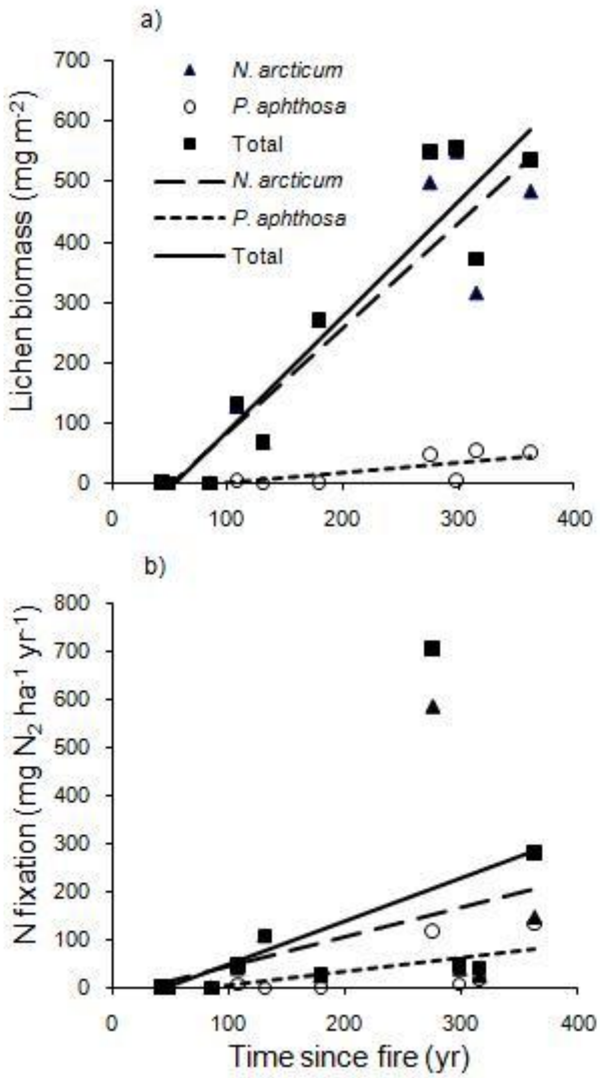


FIG 1. (a) Relationship between biomass and time since fire for *N. arcticum*, *P. aphthosa* and Total biomass for nitrogen fixing terricolous lichens at ten stand in northern Sweden. (b) Relationship between nitrogen fixation and time since fire for *N. arcticum*, *P. aphthosa* and Total nitrogen fixation from terricolous lichens.

The coverage and consequently the biomass of *N. arcticum* and *P. aphthosa* increased linearly with time since fire in the study area (Fig. 1A, Table 1). The nitrogen fixation rate per unit area (expressed as mg N_2 ha^{-1} yr^{-1}) for *N. arcticum* and *P. aphthosa* was found to increase log-linearly with time since fire (Fig. 1B, Table 1). Nitrogen fixation per unit mass had no significant relationship with time since fire for either *N. arcticum* (R^2 = 0.18, P = 0.220) or *P. aphthosa* (R^2 = 0.04, P = 0.692).

Nitrogen fixation per unit mass for terricolous lichens is comparable or higher than *P. schreberi* (Table 2). Nitrogen fixation per unit area was 4 orders of magnitude higher for the bryophyte *P. schreberi* relative to both lichen species, which corresponded closely with differences in percent cover and biomass per unit area between this moss and the lichen species (Table 2).

TABLE 1. Linear regression results for; lichen biomass vs. time since fire, N fixation vs. time since fire and lichen biomass vs. *P. schreberi* % cover fire for *N. arcticum*, *P. aphthosa* and Total values for nitrogen fixating terricolous lichens at 10 sites along a fire chronosequence in a boreal forest in northern Sweden.

	Lichen biomass vs. time since fire		Nitrogen fixation vs. time since fire		Lichen biomass vs. *P. schreberi* % cover	
	R^2	P	R^2	P	R^2	P
N. arcticum	0.86	0.000	0.48	0.025	0.56	0.021
P. aphthosa	0.64	0.005	0.73	0.002	0.34	NS
Total	0.89	0.000	0.55	0.013	0.54	0.023

Notes: Nitrogen fixation data was log transformed; NS, not significant.

TABLE 2. Mean N fixation (μg N_2 g^{-1} d^{-1}), yearly N contribution (g N_2 ha^{-1} yr^{-1}), percent cover (%) and biomass (g/m^2 dry weight) for *N. arcticum*, *P. aphthosa* and *P. schreberi* from the four oldest sites along (>200 years) along a fire chronosequence in a boreal forest in northern Sweden. Mean N fixation values are based on data from all sites collected in September 2009. Mean values followed by the same letters do not differ significantly at P= 0.05 (Tukey's test).

	N. arcticum	*P. aphthosa*	*P. schreberi*
μg N_2 g^{-1} d^{-1}	1.05 (0.35)**a**	3.35 (0.65)**b**	1.39 (0.44)**a**
g N_2 ha^{-1} yr^{-1}	0.20	0.07	†~1500
% cover	3.19	0.20	†70.8
g/m^2	0.46	0.04	†106.2

†Data derived from Zackrisson et al. 2004 and Wardle et al. 1997.

Discussion

This study shows that both the biomass and N fixation rate of two terricolous lichen species, *N. arcticum* and *P. aphthosa*, increases linearly with time since fire, providing support for my hypothesis, and corresponds with the same pattern described for bryophytes in the study system. Several mechanisms may control the increase in lichen biomass and aerial N fixation rates with time since fire, including the combustion of lichens during fire, and increased nutrient availability following fire. As time since fire increases, soil N mineralization and canopy throughfall N greatly diminish (DeLuca et al. 2008) influencing competition for light and the demand for newly fixed N within the system. An additional factor that may be important is moss cover, which also increases with time since fire, and is the main substrate in which these two terricolous lichens grow (Moberg & Holmåsen 1982). However, this is not likely the main factor controlling this relationship, because terricolous lichens are nearly absent in the three youngest sites (43-85 yrs since last fire), whereas aerial coverage of feather mosses is largely re-established in these young stands. This absence of terricolous lichens from these young stands is therefore likely heavily influenced by faster N cycling and more intense light competition in these young stands.

My results also suggest that N fixation rates per unit biomass in *N. arcticum* and *P. aphthosa* does not change with time since fire, which does not support my hypothesis. This pattern is supported by several studies that have demonstrated N fixation per unit biomass for *Peltigera* does not change in response to natural gradients of N and P availability (Chapin et al. 1991; Weiss et al. 2005). It is not clear why N fixation per unit biomass in lichens doesn't respond positively to decreasing N availability, which has been described in bryophytes (Zackrisson et al. 2004; Lagerström et al. 2007). The different pattern in N fixation rates per unit biomass in lichens compared to bryophytes may be the result of a more obligate cyanobacteria association in lichens compared to feathermoss-cyanobacteria associations.

Another pattern that emerged from my data is that N fixation on an aerial basis from terricolous N fixing lichens was very small in comparison to associative cyanobacteria on feather mosses. N fixation from *P. schreberi* is estimated to be between 1.0-2.0 kg N_2 ha^{-1} yr^{-1} in late succession sites (>200 years since fire) in the same fire chronosequence (Zackrisson et al. 2004) (Table 2). In contrast, the stand exhibiting the highest total annual lichen N fixation rate within this study system (Tjadnes, 275 years old) demonstrated only an order of magnitude lower N fixation rate (708 mg N_2 ha^{-1} yr^{-1}) compared to this mean bryophyte N fixation rate. This large difference in aerial N fixation rates between bryophytes and lichens is driven primarily by much greater biomass per unit area of feather mosses compared to terricolous lichens. In late successional forests, coverage was 3.19% for *N. arcticum*, 0.20% for *P. aphthosa* compared to 70.8% for *P. schreberi* (Table 2). Biomass (dry weight) per unit area was 14 g m^{-2} for *N. arcticum*, 20 g m^{-2} for *P. aphthosa* and is approximately 150 g m^{-2} for *P. schreberi* (Wardle et al. 1997). These data demonstrate that lichens likely have a minor effect on the total stand N budget, relative to bryophytes.

Most work focused on lichen responses to successional development are made in primary successional systems (Kurina & Vitousek 1999; Menge & Hedin 2009), whereas my study was conducted in a secondary successional system. Primary succession is characterized by having greatest nutrient limitations at the beginning of ecosystem development (Vitousek & Howarth 1991). This initial lack of nutrients in primary successions often results in high N fixation rates from N-fixing pioneer organisms, such as lichens and mosses. When an adequate nutrient capital becomes established, vascular plants eventually outcompete pioneering N fixing organisms (Campbell & Reece 2005). My study is therefore unique in that very few studies have evaluated the response of lichens to secondary succession, contrary to primary successional studies, my data demonstrates that biomass and aerial N fixation rates of lichens increases with time since disturbance, which coincides with decreasing nutrient availability and retrogression of primary production. This pattern suggests that a common pattern between primary and secondary successional systems is that higher N fixation rates corresponds with N limiting conditions (Zackrisson et al. 2004; Lagerström et al. 2007; Menge & Hedin 2009).

Conclusions

These results have several implications. First, my data clearly support my hypothesis, that terricolous lichen biomass and areal N fixation rates would increase with stand age, which strongly corresponds with increasing nutrient limitation. This strong correlation between nutrient availability and lichen biomass and aerial N fixation rates suggests that anthropogenic factors that influence N availability, such as forest fertilization or increased atmospheric N deposition associated with fossil fuel combustion, may have a detrimental effect on lichen biomass across boreal forest landscapes. A second key finding of my study is that the yearly terricolous lichen N-fixation rate is minor relative to the bryophyte-cyanobacteria association in boreal forests, supporting my second hypothesis. Even though these terricolous lichens did not contribute much to the total forest N budget, other studies have demonstrated that these lichens create micro-sites with higher biologically available N in soil near the lichen colonies. Therefore the ecological importance of the lichens might increase with successional age, where fertile patches associated with terricolous lichen colonies may provide opportunities for some vascular plant species thriving in these micro-site conditions. Much is already known about the sensitivity of lichens to anthropogenic disturbances, whereas relatively little is known about how lichens respond to natural disturbance processes. This study therefore provides an improved understanding of how two common terricolous lichens respond to wildfire and forest succession following wildfire, which is the dominant form of disturbance in boreal ecosystems.

References

Ahmadjian V. 1967. A guide to the algae occurring as lichen symbionts: Isolation, culture, cultural physiology, and identification. *Phycologia*. **6:** 127-160.

Berg A. Östlund L. Moen J. Olofsson J. 2008. A century of logging and forestry in a reindeer herding area in northern Sweden. *Forest Ecology and Management.* **256:** 1009-1020.

Boudreault C. Gauthier S. Bergeron Y. 2000. Epiphytic lichens and bryophytes on Populus tremuloides along a chronosequence in the southwestern boreal forest of Quebec, Canada. *Bryologist*. **103:** 725-738.

Cajander A. K. 1949. Forest types and their significance. *Acta For. Fenn.* **56(5)**: 1-71.

Campbell N. A. & Reece J. B. 2005. Biology (7th edition). Pages: 621-622, 1097. Pearson Education, inc. San Francisco.

Chapin D. M. Bliss L. C. Bledsoe L. J. 1991. Environmental regulation of nitrogen fixation in a high Arctic lowland ecosystem. *Canadian Journal Of Botany*. **69:** 2744–2755.

Cleveland C. C. Townsend A. R. Schimel S. S. Fisher H. Howarth R. W. Hedin L. O. Perakis S. S. Latty E. F. Von Fisher J. C. Elseroad A. Wasson M. F. 1999. Global patterns of terrestrial biological nitrogen (N2) fixation in natural ecosystems. *Global Biogeochemical Cycles*. **13:** 623–645.

DeLuca T. H. Zackrisson O. Nilsson M.-C & Sellstedt A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature,* **419:** 917–920.

DeLuca T. H. Zackrisson O. Gundale M. J. & Nilsson M.-C. 2008. Ecosystem feedbacks and nitrogen fixation in boreal forests. *Science.* **320:** 1181.

Epstein H. E. Calef M. P. Walker M. D. Chapin F. S. & Starfield A. M. 2004. Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology.* **10:** 1325-1334.

Fritz O. Niklasson M. Churski M. 2009. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied vegetation science.* **12:** 93-106.

Galun M. 1988. Handbook of lichenology, vol. 1. CRS Press. Boca Raton, Fla, USA.

Gundale M. J. Wardle D. A. Nilsson M.-C. In press (2010). Vascular plant removal effects on biological N-fixation vary across a boreal forest island gradient. *Journal of ecology*.

Hällbom L. Bergman B. 1983. Effects of inorganic nitrogen on C2H2 reduction and CO2 exchange in *Peltigera praetextata-Nostoc* and *Peltigera aphthosa-Coccomyxa-Nostoc* symbioses. *Planta.* **157:** 441–445.

Jonsson Čabrajić A. 2009. Modeling lichen performance in relation to climate – scaling from thalli to landscapes. Dept. of Ecology and Environmental Science. Umeå. ISBN: 978-91-7264-744-2.

Knowles R. D. Pastor J. Biesboer D. D. 2006. Increased soil nitrogen associated with dinitrogen-fixing, terricolous lichens of the genus *Peltigera* in northern Minnesota. *Oikos*. **114:** 37–48.

Kurina L.M. Vitousek P.M. 1999. Controls over the accumulation and decline of a nitrogen-fixing lichen, Stereocaulon vulcani, on young Hawaiian lava flows. *Journal of ecology*. **87:** 784-799.

Lagerström A. Nilsson M.-C. Zackrisson O. Wardle D. A. 2007. Ecosystem input of nitrogen through biological fixation in feather mosses during ecosystem retrogression. *Functional Ecology.* **21:** 1027–1033.

Larson D. W. 1987. The absorption and release of water by lichens. *Bibliotecha Lichenologia.* **25:** 351-360.

Menge D. N. L. Hedin L. O. 2009. Nitrogen fixation in different biogeochemical niches along a 120 000-year chronosequence in New Zealand. *Ecology*. **90:** 2190-2201.

Moberg R. & Holmåsen I. 1982. Lavar. En fälthandbok. Page: 7. Interpublishing. Stockholm.

Nash T. H. III 1996. Photosynthesis, respiration, productivity and growth. In *Lichen Biology* (ed. T.H. Nash III). 88–119.

Neary D. G. Klopatek C. C. DeBano L. F and Ffolliott P. F. 1999. Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management*. **122:** 51- 71.

Palmqvist K. & Sundberg B. 2000. Light use efficiency of dry matter gain in five macro-lichens. relative impact of microclimate conditions and species-specific traits. *Plant, Cell and Environment* **23:** 1–14.

Rai A. N. Bergman B. Rasmussen U. 2002. Cyanobacteria in symbiosis. Pages: 1-355. Kluwer Academic Pub., Dordrecht.

Rai A. N. Rowell P. Stewart W. D. P. 1981. Nitrogenase Activity and Dark CO2 Fixation in the Lichen *Peltigera aphthosa* Willd. *Planta.* **151:** 256–264.

Schimel J. P. Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology*. **85:** 591–602.

Schöllhorn R. & Burris R. H. 1967. Acetylene as a com-petitive inhibitor of nitrogen fixation. *Proceedings of the National Academy of Science*. **58:** 213-218.

Tamm C. O. 1991. Nitrogen in Terrestrial Ecosystems. 34–49. Springer-Verlag. Berlin.

Vitousek P. M. Cassman K. Cleveland C. Crews T. Field C.B. Grimm N. B. Howarth R. W. Marino R. Martinelli L. Rastetter E. B. & Sprent J. I. 2002. Towards an ecological understanding of biological nitrogen fixation. *Biogeochemistry*. **57:** 1–45.

Vitousek P. M. Field C. B. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry*. **46**: 179-202.

Vitousek P. M. & Hobbie S. 2000. Heterotrophic nitrogen fixation in decomposing litter: Patterns and regulation. *Ecology*. **81:** 2366–2376.

Vitousek P. M. Howarth R.W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*. **13:** 87-1 16.

Wardle D. A. Zackrisson O. Hörnberg G. Gallet C. 1997. The Influence of Island Area on Ecosystem Properties. *Science*. **277:** 1297-1299.

Weiss M. Hobbie S.E. & Gettel G.M. 2005. Contrasting Responses of Nitrogen-Fixation in Arctic Lichens to Experimental and Ambient Nitrogen and Phosphorus Availability. *Arctic, Antarctic, and Alpine Research.* **37:** 396–401.

Zackrisson O. DeLuca T. H. Nilsson M.-C. Sellstedt A. Berglund L. 2004. Nitrogen fixation increases with successional age in boreal forests. *Ecology*. **85**: 3327-3334.

Zackrisson O. Nilsson M.-C. Dahlberg A. Jäderlund A. 1997. Interference mechanisms in conifer-Ericaceae-feathermoss communities. *Oikos.* **78:** 209-220.

Zackrisson O. Nilsson M.-C. Wardle D. A. 1996. Key ecological function of charcoal from wildfire in the Boreal forest. *Oikos.* **77:** 10-19.

SENASTE UTGIVNA NUMMER

2009:8 Författare: Sara M Östh
2000 years of forest dynamics in the Ecopark Raslången, South Sweden – a basis for ecological management

2009:9 Författare: Erik Kretz
Traditional housing in northern Laos – wood preferences and impact on the forest biodiversity

2009:10 Författare: Markus Steén
Forest products and services in northern Laos – Case studies from two forest dwelling villages

2009:11 Författare: Carolina Sundin
Sådd av tallfrön med vattenryggsäck: En laboratoriestudie

2009:12 Författare: Johan Dammström
Rottillväxt och rotmorfologi hos groddplantor av tall och gran efter sådd i humus och mineraljord

2009:13 Författare: Niklas Karlsson
Älgbete och skogsskador på beståndsnivå

2009:14 Författare: Lars Karlsson
Site preparation, planting position and planting stock effects on long-term survival, growth and stem form properties of *Pinus contorta* on southern Iceland

2009:15 Författare: Jennie Sverker
A comparison of protein complexation capacity among six boreal species and the consequences for nitrogen mineralization

2009:16 Författare: Ida Nilsson
Markberedningsresultat och plantbildning med såddaggregaten Humax 2-4 och KSM-såddskopa

2009:17 Författare: Maja Löfstrand
Är förekomst av knäckesjuka i tallföryngringar mindre på stora naturvårdsaspar än på tallsly?

2009:18 Författare: Rose-Marie Kronberg
Importance of mire plant community composition when estimating ecosystem level methane emission

2009:19 Författare: Anna Byström
Skogsbrukets påverkan på fasta fornlämningar – en analys av skador på fasta fornlämningar i Västernorrlands län där avverkning och markberedning utförts

2009:20 Författare: Stefan Ivarsson
Skogstillstånd och skogshistoria i Tyresta nationalpark – en jämförelse mellan nu och då, Haninge och Tyresö

2009:21 Författare: Aida Bargués Tobella
Water infiltration in the Nyando River basin, Kenya

2009:22 Författare: Nils-Olov Eklund
Moose distribution and browsing close to a feeding station

Hela förteckningen på utgivna nummer hittar du på www.seksko.slu.se