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Master's Thesis in

Arctic Landuse and Agriculture

Reindeer faeces and burning alleviates allelopathic effects of *Empetrum* humus on local plants

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May, 2008

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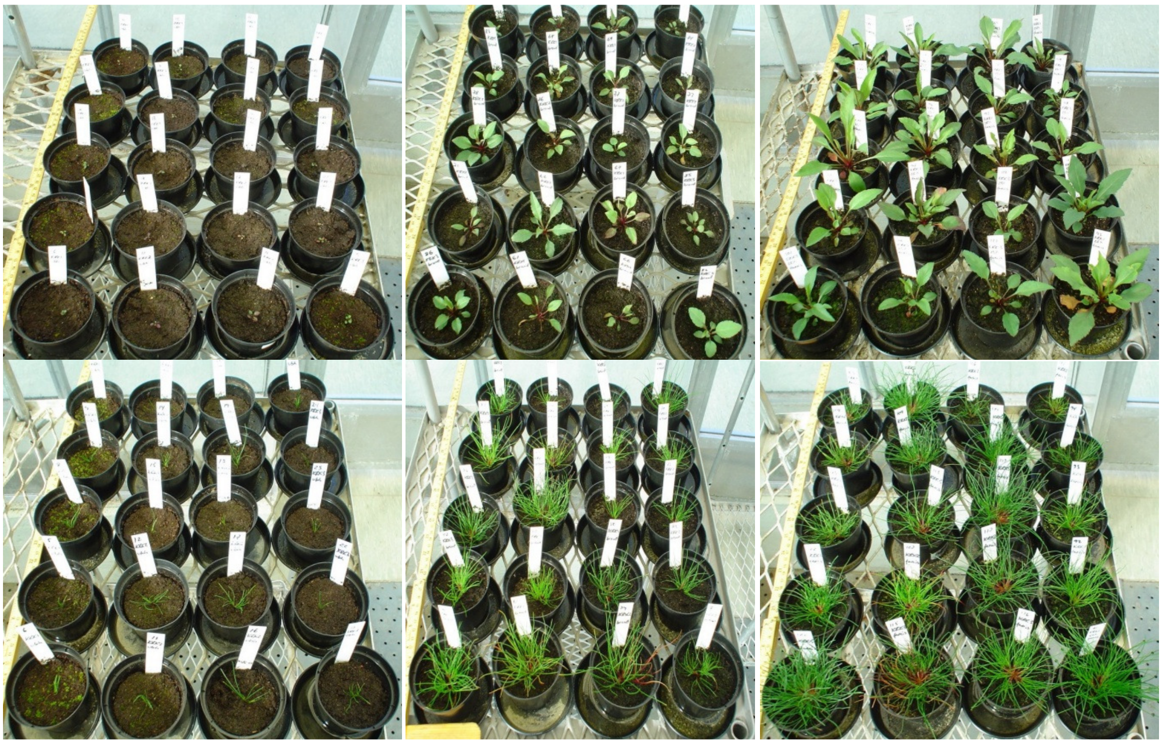
Abstract

Empetrum hermaphroditum is one of the dominant species in many reindeer summer grazing areas in Northern Norway, forming unproductive, late successional stable vegetation covers. As studies of amount, and effect of, plant secondary metabolites emerging from *E. hermaphroditum* indicates strong inhibitory effect on other organisms, it is considered an invasive and allelopathic species. To investigate the effect of two potential ecological disturbances that can cause switch in vegetation cover from unproductive *Empetrum* domination to a more productive herbaceous plant dominated ecosystem, we compared soil pH and growth of *Avenella flexuosa* and *Solidago virgaurea* in heat treated, reindeer faeces fertilized and untreated humus obtained from *E. hermaphroditum* dominated areas. Measures of total plant biomass differed significantly both between treatments and between species, with all treatments having significantly different effects. Largest level of plant dry weight and pH was measured in fertilized humus, medium level in burned humus and the lowest level where obtained in untreated humus. Results indicate that heat treatment and addition of fertilizer to *Empetrum* humus improved growing conditions, by elevating pH or nutrient levels and likely omitting allelopathic effects of *E. hermaphroditum*.



Picture 1 Growth of research plants in humus from *E. hermaphroditum* dominated areas. On top from left; *Solidago Virgaurea* in untreated, burned and fertilized humus, below from left; *Avenella Flexuosa* in untreated, burned and fertilized humus.

Introduction

Northern ecosystems are often characterized by low productivity due to short growing season, low temperatures, acidic soils and low amounts of plant-available nutrients, particularly Nitrogen (N) (Wielgolaski 1975, Chapin et al. 1995, Shaver et al. 1996). *Empetraceae* (crowberry) is a family of long-living evergreen dwarf shrubs thriving under these circumstances in temperate and polar biomes (Hagerup 1927, Elvebakk and Spjelkavik 1995), having advantages in oligothropic environments due to effective intra-plant nutrient recycling and low nutrient uptake demands (Grime and Hunt 1975, Baddeley et al. 1994). The distribution of *Empetraceae* penetrates far north and is one of the dominant species in many reindeer summer grazing areas in Northern Norway (Bråthen et al. 2007), forming late successional stable vegetation covers in the subalpine and low alpine belt (Polunin 1936, Muller 1952, Edvardsen et al. 1988, Elvebakk and Spjelkavik 1995, Bråthen et al. 2007).

Studies of amount, and effect of, plant secondary metabolites emerging from the *Empetraceae*, gives evidence that especially the monoecious *Empetrum hermaphroditum* has a strong inhibitory effect (Gallet et al. 1999). Measures of tannins, phenolic compounds and batatasin III in leaf, litter and *E. hermaphroditum* associated humus indicates that the allelopathic effects of *E. hermaphroditum* are strongest in humus under individual clones and that batatasin-III has the ability to accumulate in soil (Wardle et al. 1998a, Gallet et al. 1999, Wallstedt et al. 2000, Wallstedt et al. 2005). Research indicate that *E. hermaphroditum* can influence ecosystem function by affecting a range of essential processes such as inhibiting seedling establishment and seedling growth of pine (Zackrisson and Nilsson 1992, Nilsson 1994), reduce nutrient uptake by birch (Wallstedt et al. 2001), impose inhibitory effects on aquatic fauna (Brännäs et al. 2004) and soil nematodes (Ruess et al. 1998). *E. hermaphroditum* has also been associated with decreased soil microbial activity and slow decomposition rates of plant litter (Wardle et al. 1997a, 1998a, 2003b), as phenolic compounds can affect nutrient cycling by binding organic nitrogen in protein-phenolic complexes (Northup et al. 1995), slow down decomposition rates by negatively affecting soil micro organisms (Hättenschwiler and Vitousek 2000) and by making plant litter less palatable (Horner et al. 1988).

As evidenced by the distribution of *E. hermaphroditum* and its profound negative effects on other organisms, it is considered an invasive and allelopathic species (Wardle et al. 1998a). Conditions may however change and cause the vegetation to switch from *Empetraceae* dominance into more productive vegetation covers (Olofsson et al. 2001, Nilsson et al. 2002). This study evaluates the effect of two potential ecological disturbance factors that can cause such switches.

Fire is a disturbance to which *Empetraceae* is intolerant (Hale and Cotton 1988), and with prolonged absence of wildfire it can become dominant in the ground layer forming extensive and dense mats (Nilsson 1992, Wardle et al. 1997b). These *Empetrum* dominated environments are associated with humus build up, low pH and low productivity (Edvardsen et al. 1988, Tamm 1991, Elvebakk and Spjelkavik 1995). Fire has a fundamental role in rejuvenating these systems by providing conditions conductive for seedling establishment through mineralizing nutrients and reducing the depth of the humus layer (Tamm 1991, Schimmel and Granstrom 1996, Wardle et al. 2003a), by elevating soil pH (Klingsheim 1996, Skre et al. 1998) and through the sorptive properties of the charcoal it produces (Nilsson 1994, Zackrisson et al. 1996, Wardle et al. 1998b, Keech et al. 2005).

Nutrient addition is another disturbance factor to which *Empetraceae* is challenged. Long term experiments involving application of inorganic N to heath vegetation has resulted in decline of *E. hermaphroditum* cover and an increase in the cover of faster growing species with higher nutrient requirements, such as *Avenella flexuosa* (Håland and Timenes 1980, Chapin et al. 1995, Nilsson et al. 2002). Likewise, animal faeces, by providing nutrients and organic matter free of phenolic compounds, could be suitable in alleviating the inhibitory effects of *E. hermaphroditum* in low-resource environments.

Summer pastures are specially important to reindeer growth as most weight accumulation occurs from June until October (Peterson and Danell 1983, Reimers 1983). In this period reindeer prefer common herbaceous plants like the monocotyledon *A. flexuosa* and the dicotyledon *Solidago virgaurea*, but avoid the *Empetraceae* (Skjenneberg and Slagsvold 1968, Warenberg 1982, Mathisen et al. 1999, Bråthen and Oksanen 2001). Research conducted by Bråthen et al (2001, 2007), on impact of reindeer grazing on standing crop in summer pastures concluded that *A. flexuosa* is a common plant favored by reindeer, being able to tolerate high grazing pressure. Main results indicated however that reindeer reduce abundance of preferred species to an extent that may result in reduced productivity of the herds, suggesting that research involving management methods that may increase abundance of favorable grazing species and elevate primary production in reindeer summer pastures is valid.

We choose to study the growth of *A. flexuosa* and *S. virgaurea* in differently treated humus obtained from *E. hermaphroditum* dominated areas grazed by reindeer in Northern Norway, to investigate how ecological disturbances occurring in these areas can affect growing conditions of preferred grazing species coexisting with *E. hermaphroditum*. The aim of this research is to study the influence of heat treatment and fertilizer addition on the allelopathic properties of *Empetrum* humus. Further we want to evaluate if grass species and herb species are differently affected by the treatments, and if growing conditions are changed in such a way that natural occurring disturbances can cause a switch in vegetation from unproductive *E. hermaphroditum* dominance to more productive pastures for reindeer.

The specific issues of this research are:

- (I) If prescribed or natural occurring fire to the soil can alter growth of *S. virgaurea* and *A. flexuosa* in humus from *E. hermaphroditum* dominated areas.
- (II) If natural fertilization in the form of reindeerfaeces can alter growth of *S. virgaurea* and *A. flexuosa* in humus from *E. hermaphroditum* dominated areas.
- (III) If pH of the soil is altered by heat treatments and fertilizing.

Materials and methods

General characterization of collection area

Material used for this study were collected at Varagerhalvøya, Jakobselvdalen in Finnmark county from the 23rd-28th of august in 2005. All sampling of material were located within the summer grazing area of Várjjatnjárga reindeer herding district, having approx. 4 reindeer per km^2 (Leif Arne Iversen pers comm).

The area is classified as hemiarctic (Moen 1998, Virtanen et al 1999), with mountain birch forest occurring locally at climatically favorable sites up to 150 m a.s.l. (Okasanen and Virtanen 1995). Dwarf shrub tundra is the most common vegetation type, with domination of *Empetrum ssp*, *Betula nana* and *Vaccinium ssp*. Herbaceous species like *Festuca ovina*, *A. flexuosa* and *S. virgaurea* does also occur frequently (K. A. Bråthen pers obs), of witch *S. virgaurea* is a herb occurring in fertile areas and *A. flexuosa* is a grass species having a wider distribution and not so specific habitat demands (Polunin 1936, Muller 1952, Lid and Lid 1994). Soil horizons obtained from Jakobselvdalen has not revealed any charcoal layers, with iron podzol being the typical soil type with a 2-4 cm thick layer of raw humus on top (C. Uhlig pers obs).

Collection, storage and homogenization of research materials

Sampling of *Empetrum* humus was conducted at three different locations as summarized in table 1. Criterion for selecting a sample site was that the location contained *E. hermaphroditum* to a minimum extent of 90% of the total vegetation cover. Other vascular plants present at the sample sites were *Betula nana*, *Vaccinium vitis-idaea* and *Arctostaphylos uva-ursi*, while cryptograms, mainly bryophytes occasionally occurred.

Table 1 Locations and properties of sites for sampling of *Empetrum* humus.

	Location	Meters above sea level	Steepness	Average humus depth
Area 1	35W0574363/UTM7798533	313	15%	2 cm
Area 2	35W0578493/UTM7801818	445	10%	1,5 cm
Area 3	35W0580243/UTM7804189	299	0%	3 cm

Empetrum humus from the different sites was stored separately in polythene bags at 3°C for 5 months before being dried at 30°C for 7 days. All mineral components like small stones or sand, and plant fragments like stems, roots and leafs were removed manually using a 2 mm mesh filter.

Reindeer faeces and seeds from *S. virgaurea* and *A. flexuosa* were collected in the same period and within the same district as the humus. All faeces available to the researcher was collected and stored in polythene bags at 3°C for 5 months before drying at 30°C for 7 days. Dried samples were then homogenized using a Willy-mill, followed by sieving through a 2 mm wide mesh. Seeds from *S. virgaurea* and *A. flexuosa* where collected and stored separately in paper bags at 3°C for 5 months before being blended with wet sand and stored at 0.5°C for a 8 week stratification period. After stratification, seeds from *S. virgaurea* and *A. flexuosa* where allowed to germinate in wet sand at 18°C and with 24 hours artificial lighting.

Experimental design and green house conditions

3 weeks before onset of the experiment the *Empetrum* humus from the different collection sites was divided into three equal parts. The first part was kept untreated, and will be referred to as "untreated". The second part was heat treated, (modified from; Hoffman 1966, Prieto-Fernandez et al. 2004) in an Heraeus oven at 250°C using an 1,5 cm deep iron tray of 425 cm^2. 1/3 of this humus was heated in dry state until catching fire, while 2/3 was heated at field capacity for 30 minutes. The burned and heated humus was then mixed manually. This procedure was followed to simulate a natural occurring fire both burning and heating the soil, and will be referred to as "burned". The third part of the *Empetrum* humus was blended to a volume content of 25% reindeer faeces, and will be referred to as "fertilized".

Samples of untreated humus, burned humus and reindeer faeces were analyzed for nutrient content and pH at Bioforsk, Ås as summarized in table 2. Samples of untreated humus and burned humus were analyzed for contents of batatasin-III and other phenolic compounds in March 2008, by Christiane Gallet, using chromatography (Wallstedt et al. 1997). In average untreated *Empetrum* humus from the three sample sites contained 32.33 µg g-1 batatasin-III, whereas no batatasin-III was detected in the burned humus. Other phenolic compounds were present in the humus, but at higher amounts in the untreated compared to the burned humus. However, no exact amounts were estimated because the identities of the phenolic compounds were not known. All samples for soil analysis were obtained from homogenized and dried humus stored at 3°C and not used in the experiment.

Table 2 Nutrient content and pH of the *Empetrum* humus used in the experiment. Values of fertilized humus are based on calculations simulating the mix of neutral humus and faeces (Neutral*0.75)+(Faeces*0.25).

	Unit	Untreated	Burned	Fertilized	Faeces
Volume weight	Kg/l	0,43	0,56	0,41	0,35
pH		4,3	4,8	ns	7,0
Phosphorous	mg/100g	15	13	48	147
Potassium	mg/100g	49	35	193	624
Magnesium	mg/100g	45	36	157	491
Calsium	mg/100g	176	170	221	357
Sodium	mg/100g	20	15	21	23
Total carbon	g/100g	23	19	29	46
Total nitrogen	g/100g	0,78	0,66	1,41	3,29

Plastic flowerpots, with a diameter of 10 cm was covered in bottom with mosquito net to prevent soil from escaping and filled with 0.5 dl of sand, topped with 1.5 dl of untreated, burned or fertilized *Empetrum* humus. The pots where then watered until field capacity.

Randomly chosen seedlings from *S. virgaurea* where planted in 30 pots with either "untreated", "burned" or "fertilized" *Empetrum* humus, of which 10 pots from each area. Same procedure was followed for *A. flexuosa* seedlings. During the next 3 weeks seedlings which did not establish in the pots where replaced with new ones. A total of 18 seedlings from *S. virgaurea* (12 from untreated, 3 from burned and 3 from fertilized humus), and 9 seedlings from *A. flexuosa* (2 from untreated, 3 from burned and 4 from fertilized humus) where replaced during this period.

All plants were grown at 18°C and 74% air humidity within a phytotron at Climatic Laboratory in Tromsø, Northern Norway from 13th of March until 15th of May. Plants were showered with water daily and additionally to natural daylight conditions in the greenhouse, plants were kept under a 24 hour artificial light regime. Photosynthetic active radiation measured using a photometer, at seven different occasions during the growing period, revealed an average of 192 mikromol/m^2/sec with a range of 180 to 202 mikromol/m^2/sec.

Parameters measured

After the 9 week growing period all trails were destructively sampled, separating all plants into an above and below ground fraction. Dry weight of above and below ground material was measured using a Mettler AT200 electronic analytical balance with an accuracy of ±0.1 mg.

After harvesting the research plants measurements of pH were done by applying Merck universal-indicator paper having a range of pH 0-14 and an accuracy of ±0.5, to soil of all pots at field capacity.

Analysis of data

The data were analyzed using a linear mixed model, fitted using the lme function (Pinheiro and Bates 2000, Pinheiro et al. 2004) using the statistical package of R (R Development Core Team 2004). Response variables were data on dry weight of *A. flexuosa* and *S. virgaurea*, and pH of the humus. Fixed predictor variables were treatment and species, whereas area was treated as a random variable in the model.

The response variables on dry weights were transformed by $\log_e(x+1)$ to be satisfactory for statistical modeling. The size of the random effects was expressed as units of standard deviation, which corresponds to coefficients of variation when calculated on the log scale (e.g. Lande 1977).

Results

Measures of total plant biomass differed significantly both between treatments and between species, with all treatments having significantly different effects and with *A. flexuosa* accumulating more biomass than *S. virgaurea* as shown in table 2 and figure 1. Whereas the species effect was only significant in the aboveground biomass, the treatment effects were present in both above and belowground biomass as shown in table 3.

Measures of pH did also differ significantly between treatments, and there was an interaction between treatments and species with burned humus having pH above 4 in the presence of *S. virgaurea* as opposed to below 4 in the presence of *A. flexuosa* as shown in table 3 and figure 2. Largest level of plant dry weight and humus pH was measured in fertilized soil, medium level in burned humus and the lowest level where obtained in untreated soil.

In general the effect of the random factor area was low, whereas residual variation was of a magnitude larger as shown in table 3.

Table 3 Mixed model anova table for fixed effects of species (S) and treatment (T), and their interaction (S x T) including the standard deviation of the random factor area (A).

Response variable	Predictor variable	d.f.	F	p	*St. dev.*
Total plant biomass (log+1)					
fixed	Intercept	1, 172	105.75	<.0001	
	S	1, 172	5.23	0.0235	
	T	2, 172	38.32	<.0001	
	S x T	2, 172	0.52	0.5969	
random	*A*				*0.020*
	residual				*0.226*
Aboveground plant biomass (log+1)					
fixed	Intercept	1, 172	137.25	<.0001	
	S	1, 172	13.66	0.0003	
	T	2, 172	40.73	<.0001	
	S x T	2, 172	1.01	0.3681	
random	*A*				*0.000*
	residual				*0.155*
Belowground plant biomass (log+1)					
fixed	Intercept	1, 172	75.89	<.0001	
	S	1, 172	0.00	0.9618	
	T	2, 172	22.77	<.0001	
	S x T	2, 172	1.56	0.2124	
random	*A*				*0.009*
	residual				*0.138*
pH					
fixed	Intercept	1, 172	33310.4	<.0001	
	S	1, 172	1.41	0.2364	
	T	2, 172	288.49	<.0001	
	S x T	2, 172	6.03	0.0029	
random	*A*				*0.000*
	residual				*0.313*

Figure 1 Total plant biomass (+95% confidence interval) of *Avenella flexuosa* and *Solidago virgaurea* after 9 weeks of growth in untreated, burned and fertilized *Empetrum* humus, with weight of plants ranging from 0.00 to 0.62 g.

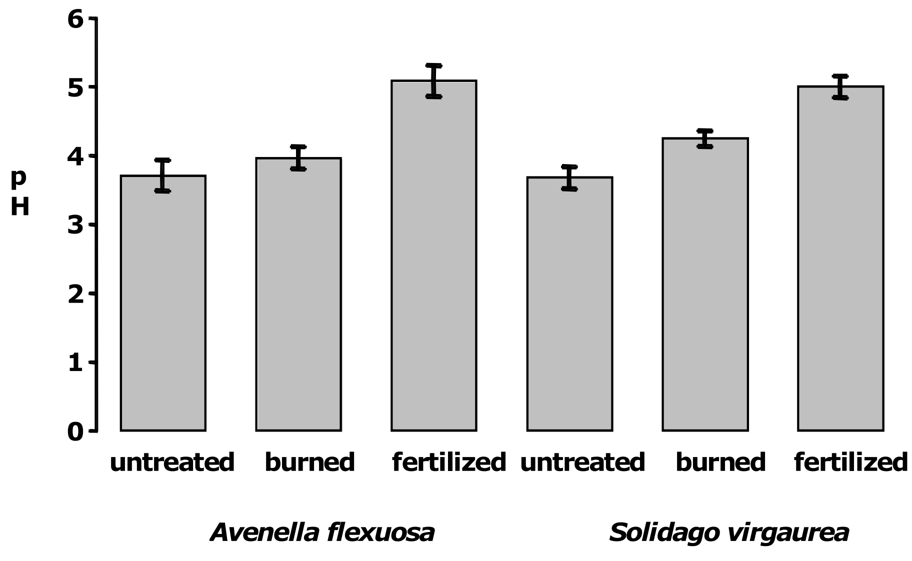


Figure 2 Soil pH (+95% confidence interval) in untreated, burned and fertilized *Empetrum* humus after 9 weeks of growth of *Avenella flexuosa* and *Solidago virgaurea*, with pH ranging from 3.4 to 5.5.

Discussion

The sparse growth of the research plants in untreated humus, suggests that *E. hermaphroditum* has obvious inhibitory effect on the growth of local, herbaceous plants. Also, constant low, or diminished residual variation explained by areal effects indicate that humus from the different sampling sites provided similar growing conditions, and that treatment is the main factor affecting plant growth (Pinheiro et al. 2004).

The species specific responses to the different treatments gives reason to assume that *A. flexuosa* is a plant accumulating more biomass than *S. virgaurea*, both when growing conditions are scarce, as in the untreated humus and when growing conditions are elevated by heat treatment and fertilization. Possibly because *A. flexuosa* is a more robust and faster growing species than *S. virgaurea*, being able to produce a large amount of ramets and leaves during a short period (C. Fodstad pers obs). Furthermore the significantly lowered pH of burned soil in the presence of *A. flexuosa* may indicate a good ability of grass roots to extrude protons during the absorption and assimilation of cations, particularly ammonium, followed by release of organic acids to soil (Taiz and Zeiger 1998). However both species responded to the different treatments at a magnitude indicating that faster growing and more nitrophilous species are able to grow and compete with the slower growing and not so nutrient demanding *E. hermaphroditum* (Grime and Hunt 1975, Baddeley et al. 1994, Stevens et al. 2004), when ecological disturbances such as fire or fertilization alleviates its inhibitory effects.

Effect of burning

Our results show that burning of *Empetrum* humus provides better growing conditions than untreated humus, despite its lower nutrient levels (Table 3). Reduced total N content and increased levels of plant available N in the form of ammonium, has been obtained from soil burned or heated at 150, 210 and 350 ^{o}C (Prieto-Fernandez et al. 2004). Furthermore, increased levels of plant available phosphor has been obtained in soil heated above 150 ^{o}C (Hoffman 1966). We therefore assume that our burning treatment has elevated plant available nutrients, in spite of reduced level of total nutrients, thereby providing better conditions for plant growth.

Analysis of the burned humus revealed elimination of batatasin-III and reduced levels of phenolic compounds compared to untreated humus, suggesting that the heat treatment has had an eliminating effect on the secondary compounds emerging from *E. hermaphroditum*. Heating of the *Empetrum* humus could have caused oxidation of functional groups and reduced the toxic effect of phenolic compounds, including their ability to bind organic nitrogen in protein-phenolic complexes (Northup et al. 1995, Ritter 1996). Furthermore, the sorptive effect of the coal produced in the actual burning could have provided reduced levels of secondary metabolites (Zackrisson et al. 1996, DeLuca et al. 2002, Keech et al. 2005).

Measured batatasin-III contents of up to 50 ng/ml in the untreated humus used in our experiment were relatively low when compared to levels of 350 ng/ml obtained by Wallstedt et al in Swedish boreal forest (2000), and to phenolich extract solutions used in research involving allelopathic effect of E. *hermaphroditum* (Wallstedt et al. 2001, Brännäs et al. 2004). The low batatasin-III levels may be due to the long storage time of the samples before analysis were conducted (Christiane Gallet, personal comm), but the scarce growth of plants in the untreated *Empetrum* humus indicate however that even low levels of batatasin-III can affect plant growth.

Effect of fertilization with reindeer faeces

Our results indicate that addition of plant nutrients can omit allelopathic effects of *E. hermaphroditum* as fertilization in form of reindeer faeces provided better growing conditions for *A. flexuosa* and *S. virgaurea*, compared to untreated and burned *Empetrum* humus. The fertilized humus contained high levels of all measured nutrients particularly, Potassium, Magnesium, Calcium and Nitrogen thereby also providing enhanced growing conditions for plants.

It has been hypotized that allelopathy has evolved as a result of resource competition between plants (Rice 1984), that nutrient-limited conditions may enhance allelophatic effects (Willianson and Weidenhamer 1992, Taiz and Zeiger 1998, Neumann and Römheld 2001), and that addition of fertilizers can eliminate allelochemical inhibition (Einhellig 1989, Inderjit and delMoral 1997, Inderjit and Duke 2003).

It has also been debated that separation of resource competition and allelopathy is unrealistic as both factors occur under natural conditions (Michelsen et al. 1995, Inderjit and delMoral 1997). Nilsson (1994) found, that both below ground competition and alleopathy by *E. hermaphroditum* are important factors in explaining its ability to out-compete other plants, and long term experiments involving application of plant nutrients to heath vegetation has resulted in decline of *E. hermaphroditum* cover and an increase in the cover of faster growing species with higher nutrient requirements (Håland and Timenes 1980, Chapin et al. 1995, Nilsson et al. 2002). Implying that growth inhibiting effects of *Empetrum* humus could be omitted by addition of plant available nutrients, suggesting that the allopathic effect of *Empetrum* humus is, at least partly, due to limited nutrient availability.

Compared to inorganic fertilizer, organic fertilizers is thought to be favorable to soil fertility and soil microbial activity by adding organic matter to soil, provide porosity, stabilize water and temperature fluctuations, and by containing high amounts of carbon and nutrients available to soil microorganisms (Haynes and Naidu 1998, Taiz and Zeiger 1998). Our results indicate that reindeer faeces, by providing nutrients and organic matter possibly free of phenolic compounds, is suitable in omitting the inhibitory effects of *E. hermaphroditum* in low-resource environments.

Soil pH

Fertilization with reindeer faces elevated pH the most, probably due that reindeer faeces had a pH of 7, and its high content of carbon and calcareous substances (Haynes and Naidu 1998). The high pH levels obtained in the fertilized humus can also be a result of elevated nitrate levels due to soil microbial conversion of organic N (Manuel and Molles 1999).

Experiments involving addition of lime to alpine tundra heath vegetation has stimulated graminoid growth and reduced *E. hermaphroditum* abundance, probably due to pH enhancement (Nilsson et al. 2002). Elevation of pH in acidious soils can be favorable for plant growth as pH influences the availability of nutrients (Taiz and Zeiger 1998). The optimum pH for plant nutrient absorption is 5.5, as obtained in the fertilizing treatment, while pH levels below 4, as measured in the untreated humus, strongly reduces plant ability to take up of most nutrients (Lucas and Davis 1961).

Phenolic acids may exert a stronger inhibition at low pH (Harper and Balke 1981) as research by Wallstedt et al (2001) indicate that the inhibitory effects of batatasin-III on N-NH_4^+ uptake is greater at pH 4.2 than at pH 6.8. Furthermore, N bound in phenolic-protein complexes emerging from *E. hermaphroditum* may be released by elevated pH, given that phenolics are less stable in high pH solutions (Harper and Balke 1981, Nilsson et al. 2002), as well as that enhanced microbial activity resulting from elevated pH causes greater N mineralization and elevated mineral nitrogen availability (Madigan et al. 2000, Nilsson et al. 2002). All together this suggests that elevation of pH may omit allelopathic effect of *E. hermaphroditum* and favor growth of herbaceous plants.

Management aspects and further research

Our results indicate that fire to the soil and fertilization with reindeer faeces can enhance growth of attractive grazing species by either elevating pH, increasing plant available nutrients or by reducing the adverse effects of allelochemicals emerging from *E. hermaphroditum*, or by a combination of these effects.

In Finnmark Bråthen et al (2007) found that *Empetrum ssp* was the most common plant in areas heavily grazed by reindeer, indicating that late successional stable vegetation covers dominated by *Empetrum* may have a strong ability to maintain structure despite potential disturbances from reindeer, and that relative high stocking rates are not capable of inducing the same negative effects on *Empetrum* dominated vegetation as obtained near fences by Olofsson (2001). It also appears that dwarf shrubs, are able to re-establish in previously heavily grazed pastures in the absence of reindeer on a short time scale (Olofsson 2006), indicating that a continuous grazing pressure is needed to maintain vegetation changes induced by large herbivores. *Empetrum* dominated ecosystems appears to have a high resistance and high resilience to herbivory by reindeer (Manuel and Molles 1999) despite their addition of organic fertilizer.

Our research involved application of reindeer faeces to an extent that can only occur at a micro scale in nature, even at high stocking rates, implying that faeces emerging from natural occurring reindeer may not have the potential to induce large scale ecosystem changes. Large scale application of organic fertilizer to heath vegetation may however, induce the same effects as obtained by our research.

Studies of post fire successions shows that *Empetrum* becomes dominating 80 – 300 years after fire (Tybirk et al. 2000) and that post fire sites favors graminoid growth (Skre et al. 1998), indicating that *Empetrum* dominated ecosystems has a low resistance and a low resilience to natural occurring fire and prescribed burnings (Manuel and Molles 1999). The area from where our research material was obtained can be described as non pyrogenic with fires occurring very rarely and where prescribed burning is a method not used to heath vegetation in order to elevate primary production (Karl Dag Vorren pers comm). Prescribed burning is however, an applied management method likely to provide long lasting vegetation shift from dwarf shrub domination to graminoid and grass domination.

Field experiments involving fertilization and prescribed burning are necessary for evaluating the generality of our results under natural occurring conditions. Further research is also needed to provide more conclusive results involving the ability of our treatments in omitting allelopathic effect by *E. hermaproditum*. Establishment of parallel control treatments, preferably with different levels of treatments, combined with thorough analysis of phenolic compound content, pH and plant available nutrients, is needed to provide knowledge of treatment threshold levels and the various factor that seem to operate together with, and affecting the allelopathic ability of *E. hermaphroditum*.

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