Estimation of lichen biomass with emphasis on reindeer winter pastures at Hardangervidda, S Norway

Arvid Odland[1], Sylvi M. Sandvik[2], Dag K. Bjerketvedt[1] & Linn L. Myrvold[1]

[1] Telemark University College, Hallvard Eikas plass, 3800 Bø, Norway (Corresponding author: arvid.odland@hit.no).
[2] University of Agder, Department of Natural Sciences. Faculty of Engineering and Science, Service Box 422, NO- 4604 Kristiansand, Norway.

Abstract: Quantification of lichen abundance is important for management of reindeer populations. We measured dry lichen biomass in 876 microplots (16.5 cm × 16.5 cm) systematically sampled within 219 vegetation plots (2 m × 2 m) from 7 different areas in S Norway. Lichen biomass was quantified as: (a) dry weight in g m^{-2}, (b) lichen height in cm, (c) lichen cover, and (d) lichen volume (lichen height × lichen cover). Lichen biomass decreased with increasing precipitation and increasing altitude. On local scale, the variation in lichen biomass varied strongly with snow conditions. The grazed parts of Hardangervidda had in general a low average lichen biomass (an average mostly lower than 150 g m^{-2}). Lichen biomass was much higher in area where reindeer migration was interferred by human activity. Lichen height and lichen volume were strongly linearly correlated with dry lichen biomass. These proxy methods may therefore be used to predict lichen biomass, but deviations from exact measurements should be expected.

Key words: Alpine vegetation; snow index; ordination; proxy methods

Introduction

Lichen heaths are the most important natural winter pasture resources for both wild and semi-domesticated reindeer (*Rangifer tarandus*), and the most abundant generas are *Cladonia* and *Flavocetraria. Cladonia*-species are the highly preferred reindeer winter diet (Danell *et al.,*1994), and one reindeer, depending on age and sex, can consume 2–5 kg of lichen dry matter per day (Holleman *et*

*al.,*1979), given sufficient availability. Hardangervidda is a mountain plateau which has the largest population of wild reindeer in Europe and Norway has therefore an international obligation to manage this population. Estimation of total lichen abundance available for reindeer grazing during the winter is essential when the carrying capacity of an area is determined. The area used by the reindeer is approximately 8000 km[2], but estimations of the total area considered to be available lichen heaths during the winter show highly diverging results, ranging from 431 to more than 2100 km[2] in different studies (Bjerketvedt *et al.,* 2012). Previous measurements of lichen abundances based on lichen cover or lichen volume measurements in the Hardangervidda area show highly diverging results (Gaare *et al.,*2005; Falldorf *et al.,* 2014). The method used by Falldorf et al. 2014 was verified by in-situ measurements of lichen volume combined by robust statistics and should therefore be regarded as much more accurate than the estimates made by Gaare et al. (2005). The reindeer population has varied strongly during the last decades, but a sustainable winter population has been assumed to be between 9000 – 12000 depending on the quality of the winter pastures.

An estimate of the carrying capacity of Hardangervidda based on available winter pastures was first described by A. Tveitnes (1980). His calculation was, however based on seven assumptions which have rarely been mentioned when referring his paper (c.f Bjerketvedt, 2013).

Measurement of lichen biomass (LB) dry weight is therefore an essential component of ecological and reindeer management studies in alpine areas, but often avoided because it is destructive, laborious, and time-consuming (Moen *et al.,*2007). In a destructive sampling strategy, samples are collected within specific vegetation types, weighted after drying and the lichen dry weight is mostly given as g m^{-2}.

Lichen dry biomass has previously only been estimated from one small, fenced area at Hardangervidda ca 40 years ago (Kjelvik & Kärenlampi, 1975). Here the average LB was 380 g m^{-2}, and the annual lichen production was estimated to 0.23 g lichen g[-1] year^{-1} (Kjelvik, 1978).

Four different strategies for not-destructive sampling have previously been used (Kumpula *et al.,*2000; Moen *et al.,*2007; Kastdalen L., 2011, Falldorf *et al.,* 2014): (a) Lichen cover estimated in percentage cover, (b) average lichen podetia height measured in cm, (c) volume estimation calculated as lichen cover x lichen height, and (d) cover estimation based on presence/absence data with a strict criterion of 100 % lichen cover. These proxy methods can never give exact estimates of the actual lichen biomasses, and statistical testing of the relationships between proxy data and lichen biomass data are therefore necessary.

Different methods of estimating LB from ground cover and lichen thallus heights of four common lichen species have previously been compared (Moen *et al.,*2007). It was found that different methods gave mostly similar results with strong linear relationships between LB and mean thallus height, but average thallus heights within the plots were found to explain the variation in LB as well as lichen volume. In northern Finland, dry lichen biomass and other proxies were measured and it was found that LB was best explained by a quadratic relationship to lichen volume (Kumpula *et al.,*2000). Estimated LB was between 260–280 as g m^{-2} (max 700 g m^{-2}) in N Finland.

It is well known that "snow conditions" (thickness or duration) is a major determinant for lichen heath development (Dahl, 1957; Walker *et al.,*2001; Vistnes & Nellemann, 2008; Odland & Munkejord, 2008a), however, quantitative relations between LB and snow conditions have not been investigated. In comparative studies it is essential that data

from sites with approximately the same snow conditions are compared. The amount of snow may vary considerably between years, but due to snow drift the uneven distribution of snow is repeated every year and the snow melt pattern is about the same (Gjærevoll, 1956). Relative estimates of snow layer duration for different plant communities may be calculated by the use of plants as indicators (Odland & Munkejord, 2008a) by the use of Weighted averages for plant communities or vegetation plots (WA_{Si}). This method takes into account both occurring species and their abundances. Species optima along gradients from chionophobous to chionophilous communities have been quantified by giving species with significant responses along the snow layer duration relative snow duration values ranging from 1 to 9. Strictly chionophobous communities will have a WA_{Si} value close to 1, while strictly chionophilous communities have a WA_{Si} value close to 9. In average, during a "normal year" the difference between each step is a 11–12 days difference in snow layer duration (Odland & Munkejord, 2008b). The most exposed sites (with WA_{Si} values between 1 and 2) will normally have no or a very thin snow cover, while the most chionophilous communities will not be melted out before late July. Consequently, the LB in particular sites (vegetation type) should be related to their snow conditions when different areas or sites are compared.

The present study aims at answering the following questions:
• To what extent is "snow condition" as measured by snow indicator values related to the variation in LB?
• How large are the differences in LB between grazed and not-grazed areas as measured on data sampled on sites with approximately the same snow conditions?
• How relieable are not-destructive methods as proxies for LB estimation?
• How large is the average decrease in LB be-

tween oceanic and continental study areas as measured by average annual precipitation?
• How large is the average decrease in LB with increasing altitude as measured from sites with the same "snow conditions"?

Material and methods
Study areas and sampling methods
Nine study areas were selected (Table 1) and these cover variations in climate (oceanity-continentality) and reindeer grazing pressure. Most of the data have been sampled on or in the vicinity of the Hardangervidda mountain plateau. Haukeli lies in the south-western, oceanic part, while Imingfjell W, Imingfjell E, and Mår are situated in the eastern part of Hardangervidda. Imingfjell W and E are separated by a mountain valley with roads, several cabins and a hostel which appears to represent barriers for reindeer migration, with grazing in the western part and also further south to the Mår area (Jordhøy & Strand, 2009). Data from other areas were included to compare the data from Hardangervidda with LB data from other areas in S Norway.

The investigation was based on floristic and environmental data from homogenous stands where lichen abundance data have been systematically sampled. A homogenous stand is defined as an area of vegetation that shows no obvious variation in the spatial distribution or relative abundance of at least the major species present and that shows small substrate variations. Selection of homogenous (Gjærevoll, 1956; Dahl, 1957; Diekmann, 1995) plots is essential when the distribution of plants is related to environmental variables sampled from the actual vegetation plots (Diekmann, 2003).

As the lichen biomass varies strongly with snow conditions, the sampling sites were selected along gradients from exposed ridges to snow-beds. In each area sites at different elevations were also studied. Emphasis has been on low alpine sites from the most exposed sites to

Table 1. The study areas. Tu = Tunhovd, Va = Valdresflya, Sul = Suleskard, Tro = Tronfjell, IE = Imingfjell east, IW = Imingfjell west, M = Mår, V = Vågå, H = Haukeli. The centres of the study areas are given as coordinates. In total 219 vegetation plots (No) have been studied. Gr = grazed (+) or not (-), Prec = Annual precipitation in mm. Average (± standard deviation) snow indicator values WA_{Si} (for plots with a WA_{Si} value <3) have been calculated for the study areas. CoL = Total percentage cover of lichens, LH = Average lichen podetia height (cm), LH x CoL = Lichen height x Lichen cover (Lichen volume), LB = Measured lichen dry biomass (g m^{-2}).

Area	North	East	No	Gr	Prec	Wa_{Si}	Altitude	CoL	LH	LH x CoL	LB
Tu	60°45`	8 °72'	4	-	542	2.0±0.0	760±1	93±8	11.4±2.3	1075±300	1992±405
Va	61°39`	8 °78'	3	+	720	1.6	1428	50	1.0	50.0	76
Sul	59°01`	7 °10'	20	-	990	2.9±0.1	972±80	35±22	6.1±1.9	222±156	245±122
Tro	62°08`	10 °42'	8	-	570	2.3±0.3	990±76	50±25	11.3±3.2	637±414	893±639
IE	60°19`	8 °62'	42	-	600	2.2±0.3	1191±43	81±18	5.9±2.0	501±224	897±440
IW	60°18`	8 °43'	35	+	600	2.3±0.4	127±364	94±6	5.5±1.4	517±120	215±77
M	60°10`	8 °12'	40	+	600	2.4±0.3	1307±49	88±13	3.3±1.3	299±136	133±63
V	62°02`	8 °97'	34	-	370	2.3±0.4	126±529	85±10	6.1±2.0	536±197	713±318
H	59°81`	7 °24'	33	-	1200	2.7±0.1	109±257	47±19	3.8±1.4	182±98	189±132

snow demanding dwarf shrub heaths and early graminoid dominated early snow-beds. Wetland vegetation was omitted because the lichen cover is there generally sparse.

Total cover of all vascular plants and the cover of the most abundant mosses and lichens within the plots were estimated in percentage. Within the plots, four smaller plots (16.5 ×16.5 cm) 60 cm from the corners were systematically selected along the diagonals in the quadrat where total lichen cover estimated in percentage and height of the lichen podetia was measured in cm. All lichens were sampled and brought to the laboratory and the average lichen heights and volumes were calculated for each plot. Lichen samples from the four sample plots were mixed and brought to the laboratory to be carefully sorted, and dried for 24 h at 105ºC. Then it was weighted and an average LB for the whole plot was calculated as g m^{-2}. In the thickest lichen mats, 0.5 - 1.0 cm of the basal part of the podetia were often decaying, and only the living parts were measured.

Weighted averaged snow indexes (WA_{Si}) were calculated for each 2×2 m plot based on plants as snow indicators (Odland & Munkejord, 2008b) occurring in the plots. The weighted average method takes into account the abundances of the different species and calculated according to the following equation:

$$Wa_{Si} = (X_1{*}SI_1 + X_2{*}SI_2 + \ldots + X_n{*}SI_n) / (X_1 + X_2 + \ldots + X_n)$$

Wa_{Si} is the weighted average snow indicator value for the actual plot, X_{1-n} are species abundance values, and SI_{1-n} are the actual snow indicator values.

Numerical analyses

The samples were classified by the TWINSPAN program (Hill, 1979), where six pseudospecies cut-levels (1 – 5 – 10 – 30 – 50 – 70) and five indicator species were selected. Eleven types of vegetation were selected for further analyses, primarily based on their separation along the two main ordination axes. Detrended Correspondence Analysis (DCA) analyzed by the use of CANOCO 5 (ter Braak & Smilauer, 2012) was applied to the floristic data to es-

timate the floristic turnover or compositional change along the main gradient as assessed by standard deviation (SD) units of turnover (detrending by segments, non-linear rescaling, and no down-weighting of rare species). Species abundance data measured as percent cover were square-root transformed. Lumped taxa (some bryophytes and lichens identified to genus only) were deleted in the statistical analyses. The environmental/explanatory variables were log-transformed in the DCA analyses.

Taxa occurrences and abundance (SOA) in the different TWINSPAN community groups are given in percentage, calculated according to the formula given in (Odland *et al.,*1990). Statistical analyses were performed by use of the MINITAB program.

Results

Floristic and environmental gradients

The vegetation plots include a large floristic variation as shown in Figure 1. DCA axis 1 describes a gradient from exposed sites with species such as *Alectoria spp., Flavocetraria spp.,* and *Arctous alpinus* in the left part and meadows with species such as *Geranium sylvaticum and Phleum alpinum* in the right part. DCA axis 2 represents a gradient from moist low alpine communities with *Salix lapponum* and *S. glauca* in the upper part, and snow-bed species mostly at high altitudes in the lower part (*Salix herbacea, Diphasium alpinum, Harrimanella hypnoides, Luzula confusa and Juncus trifidus*). Most of sampled explanatory variables were closely correlated with the floristic gradients as shown in Table 2. The eigenvalues/ gradient length of DCA axes 1, 2, and 3 were 0.457/4.35, 0.326/3.83, and 0.21/2.74 respectively. The main floristic gradient (DCA axis 1) was strongly correlated with snow indicator values and total cover of lichens. DCA axis 2 is best correlated with altitude, and DCA axis 3 with total bryophyte cover. Plots with high LB have a small distribution in the DCA ordina-
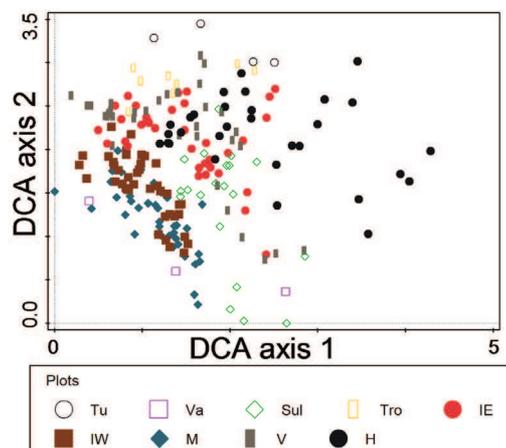

Figure. 1. Positions of the studied plots in relation to DCA axes 1 and 2. Different symbols show in which study area the plots were situated (cf. Table 1). Tu = Tunhovd, Va = Valdresflya, Sul = Suleskard, Tro = Tronfjell, IE = Imingfjell east, IW = Imingfjell west, M = Mår, V = Vågå, H = Haukeli.

tion diagram (approximately 2 SD units both on axis 1 and 2), and are primarily associated with low annual precipitation, low WA_{Si} values, and relatively low altitudes (Table 2).

Table 2. Correlation coefficients between DCA species axes 1-3 and some variables estimated for the study plots. WA_{Si} = Weighted averaged snow indicator value, CoL = Total percentage cover of lichens, CoM = Total percentage cover of mosses, LH = Average lichen podetia height, LH x CoL = Lichen height x Lichen cover (Lichen volume), LB = Measured lichen dry biomass in g m^{-2}.

	DCA 1	DCA 1	DCA 3
WA_{Si}	0.85	-0.38	-0.05
Altitude	-0.36	-0.66	-0.24
CoL	-0.74	-0.30	-0.21
CoM	0.12	-0.26	0.46
LH	-0.45	0.30	-0.11
LH x CoL	-0.60	0.12	-0.32
LB	-0.38	0.33	-0.38

Table 3. Result of the TWINSPAN classification where 11 clusters were selected. Species frequencies and abundances (average pseudospecies cut-levels) are given as SOA in percentage (Odland & Birks, 1999). Average values for environmental and lichen variables are presented in the end of the table. A: *Alectoria nigricans - Flavocetraria* type (Middle alpine), B: *Bryocaulon divergens - Alectoria ochroleuca - Flavocetraria* type (Low alpine), C: *Flavocetraria-Cladonia* type, D: *Betula nana - Cladonia alpestris* type, E: *Cladonia – Cetraria - Vaccinium myrtillus* type, F: *Empetrum – Pleurozium- Cladonia* type, G: *Empetrum – Pleurozium – Cetraria* type, H: *Vaccinium – Nardus stricta* type, I: *Salix herbacea – Juncus trifidus – Cetraria* type, J: *Salix – Geranium* type, K: *Salix herbacea – Nardus stricta* type. WA_{Si} = Weighted averaged snow indicator value, CoL = Total percentage cover of lichens, CoM = Total percentage cover of mosses, LH = Average lichen podetia height, LH x CoL = Lichen height x Lichen cover (Lichen volume), LB = Measured lichen biomass in g m^{-2}.

Vegetation type	A	B	C	D	E	F	G	H	I	J	K
Numbers of plots	6	28	21	43	35	32	8	10	18	3	12
Arctous alpinus	8	8	1	2		5					1
Gymomitrum concinnatum	33	1	10	2	4						
Alectoria nigricans	44	1	2								
Alectoria ochroleuca	67	51	9	2							
Bryocaulon divergens		22				1					
Flavocetraria cucullata	39	29	50	5	5	5					
Flavocetraria nivalis	89	61	75	14	11	6					1
Cladonia alpestris	3	36	24	70	15	2	2				1
Cladonia rangiferina	11	30	61	37	28	23	10	2	3		
Loiseleuria procumbens	11	1		5	1	9	2		3		
Vaccinium vitis-idaea	33	20	41	19	37	19	19	5	17		6
Betula nana	25	59	44	59	40	44	8	55	29		10
Empetrum nigrum	36	49	34	38	59	72	60	37	59	17	
Carex bigelowii	19	12	38	18	31	19	6	8	28	28	24
Polytrichum spp.	47	1	44	8	57	4	6		46		22
Cetraria spp.	19	14	55	29	79	24	40		59		28
Cladonia arbuscula	17	29	56	41	60	48	25	5	44		29
Cladonia spp.	33	10	49	12	46	15	13	2	48		10
Cladonia uncialis	6	5	31	12	38	13	4		27		15
Vaccinium uliginosum	14	8	2	5	11	34	25	38	4	6	
Salix lapponum		3	2	8	1	1		5	1	56	
Pleurozium schreberi		1		4		32	65	25			
Juncus trifidus	22	1	16	1	24				23		7
Avenula flexuosa	3	15	6	9	19	10	27		20	6	22
Pinus sylvestris				2		1	13				
Salix herbacea	22	2	6	4	24	4	2	5	56	11	50
Vaccinium myrtillus		1	3	14	35	26	52	30	44	6	15
Geranium sylvaticum								10		44	
Nardus stricta		1		9		2		38	8	39	40
Salix glauca				1		1		25		44	1
Ave. WA_{Si}	1.8	2.0	2.3	2.7	3.3	3.0	3.4	4.3	4.6	5.3	6.0
Ave. Altitude (m)	1359	1214	1306	1175	1294	1078	934	1073	1251	1062	1181
Ave. CoL (%)	77	82	92	78	82	34	24	3	49	0	22
Ave. CoB (%)	25	0	28	6	39	20	44	11	41	0	19
Ave. LH (cm)	2.9	6.0	4.6	6.9	3.8	4.5	5.2	0.3	2.6	0	2.2
Ave. CoL x LH	244	478	430	561	317	153	159	6	137	0	61
Ave. LB (g m^{-2})	119	652	219	801	129	185	172	7	60	0	84
Ave. LB (Grazed plots)	87		118		103	155					
Ave. LB (Not grazed plots)	183	652	296	802	154	215	172	7	60	0	84

Classification of the studied vegetation plots
The studied vegetation plots as classified by TWINSPAN are shown in Table 3. The first division separated two clusters with *Cladonia rangiferina, C. stellaris* and *Flavocetraria nivalis* as the main indicators (Types A-F, n = 165) from the rest (Types G-K, n = 51) . The second division separated two clusters: (Type A-C, n=55) with high abundance of *Flavocetraria nivalis, F. cucullata,* and *Alectoria ochroleuca* and (Types D-T, n = 110) where 43 plots had high abundance of *Cladonia stellaris.* The cluster (Type G-K, n = 51) included a group of different vegetation types dominated by species such *Salix glauca, S. lapponum, S. herbacea, Vaccinium myrtillus, Nardus stricta, Pleurozium schreberi,* and low abundances of lichens.

Eleven separated types (clusters) were selected to be compared with previously described vegetation types. SOA values for the different species in the different types and also average values for WA$_{Si}$, LB, CoL, CoB, LH and lichen volume were calculated for each type (Table 3).

LB was much higher in type B and D as compared to the other types. Type A represents highly exposed sites at high altitudes (mainly the Middle alpine zone). Type C represents less exposed sites but at relatively high altitudes
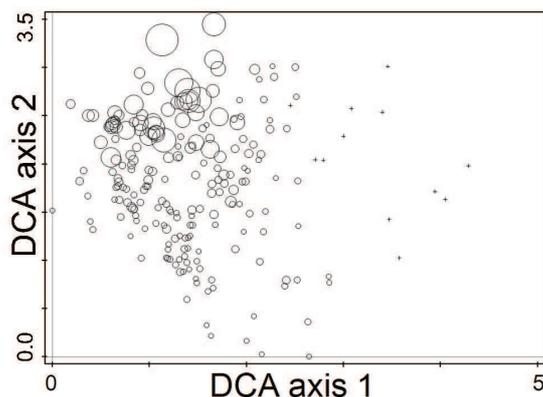
(upper Low alpine and Middle alpine zone). Types E, F, G, H, I , and J represents lee-side communities which are dependent on a stable and relatively thick and longlasting snow cover, while type K represents an early snow-bed community. Within some of the vegetation types, plots were both grazed and not-grazed, and therefore average values were calculated for both groups. In type B and D no plots were grazed, while in type A and C both grazed and not grazed plots were grouped together. In type A and C, LB in the grazed areas were around 50 % of the LB in not grazed areas. The differences in LB between grazed and not grazed plots within type E and F were smaller.

Lichen abundance estimations
LB and different proxies in vegetation types with or without grazing and in differerent areas are shown in Table 3 and 4. In all study areas the standard deviations of the means were high which is a result of variations in snow conditions between the plots. High LB were also found in dry, not grazed *Pinus sylvestris* vegetation in the Tunhovd area where *Cladonia stellaris* had developed thick mats. Relationships between measured LB and the different proxies for LB estimation are shown in Figure 3. The Lowess smoothers show that the relationship between CoL and LB is very different to the trends between LB, LH, and LH × CoL. All three proxies show significant linear relationships, but lichen volume (LH × CoL) was best correlated with measured LB. Lichen height (LH) also explained LB well, but there were several deviating plots. Lichen cover (CoL), however, was poorly linearly related to the LB measurements. Based on these data, LB may be estimated on the proxy data by the following equations:

Eq.1 $LB = -70.8 + 1.5 \times (LH \times CoL)$, ($R^2$ = 74.1% , P < 0.0001)

Eq.2 $LB = -170.7 + 113.4 \times LH$,   ($R^2$ = 52.6% , p <0.0001)

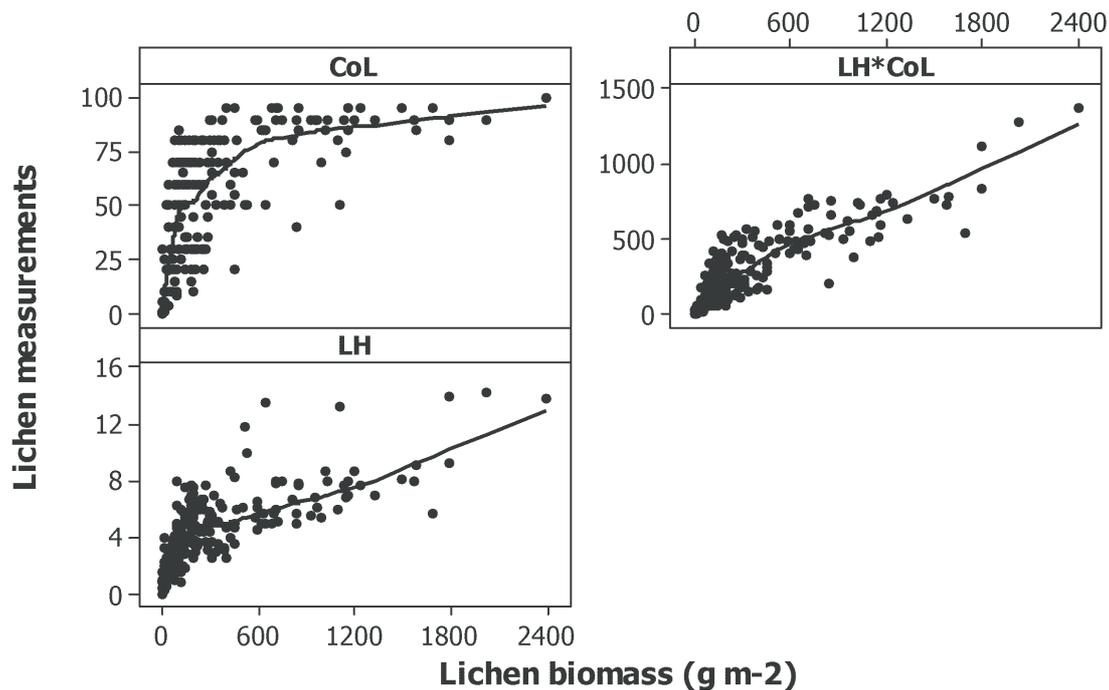Figure 2. The relative differences in lichen biomass according to the plot positions along DCA axes 1 and 2 (cf. Figure 1).

Figure 3. Relationship between measured lichen cover (CoL), lichen height (LH), and lichen volume as estimated by LH × CoL. Lowess smoothers are drawn. Results of the linear regression analyses are shown in the text.

Eq.3   LB = -113.8 + 8.6 × CoL,   (R^2 = 37.4%, P < 0.0001)

Variation in LB along snow duration gradients
Variations in LB and the three different proxies along gradients in the WA_{Si} show poor linear trends (Figure 4). LB higher than 500 g m^{-2} were mainly found in plots with WA_{Si} values lower than 3.0, and the highest LB values were found in plots with WA_{Si} values around 2.0, decreasing toward the most exposed sites (WA_{Si} values below 1.7). Similar patterns were also shown for lichen volume and lichen height. Lichen cover (mainly dominated by *Cetraria islandica*), however, could be higher than 75 % in plots with WA_{Si} around 5.0 (*i.e.* snow-bed communities).

Estimation of available lichen resources for reindeer during the winter have often been based on average data from the most exposed sites (Figure 5). Therefore, average values for LB from the different areas where WA_{Si} was lower than 3.0 were calculated, and these results are given in Table 1. In continental areas without reindeer grazing (Vågå, Imingfjell E, and Tronfjell), the average LB was higher than 700 g m^{-2}, while in the grazed areas LB was mostly below 150 g m^{-2}. The oceanic areas, also with little or no grazing (Haukelifjell and Suleskard) have average LB below 250 g m^{-2}. A quadratic regression analyses on plots with WA_{Si} values between 3.0 and 1.7 showed a trend in LB as measured on data from continental, ungrazed areas with a maximum LB at a WA_{Si} value of 2.3. Regression analysis gave the following equation:
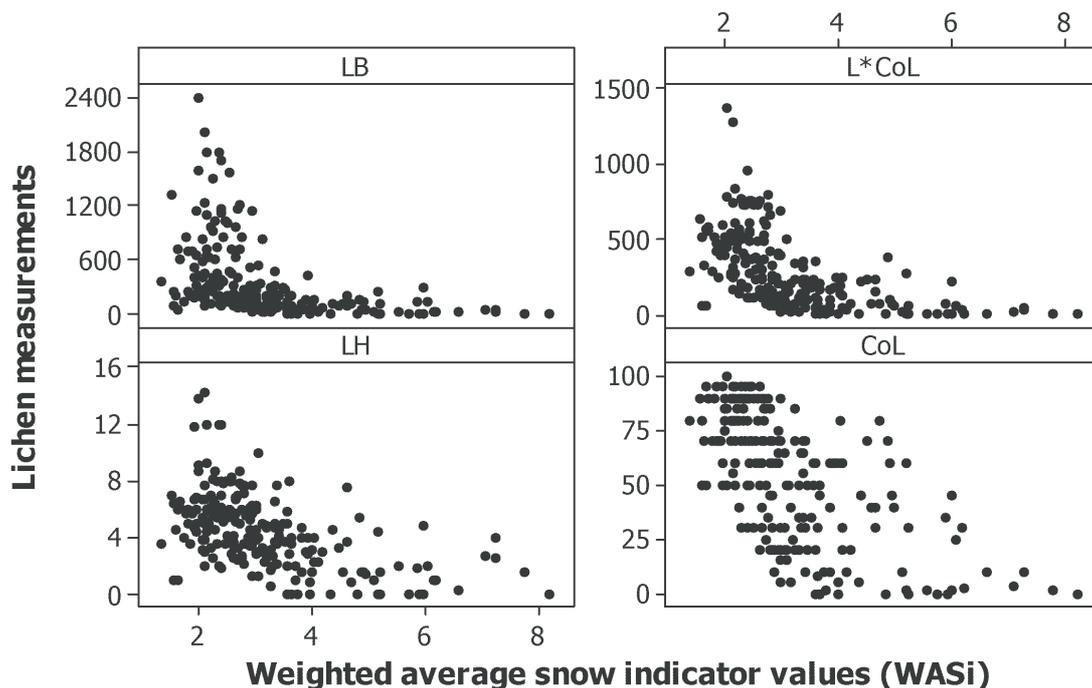Eq.4   LB = -1361 + 1925 × WA_{Si} - 418 x WA_{Si}^2, (R^2 = 27.3, p < 0.0001)

Figure 4. Relationships between average snow indicator value (WA_{Si}) for the plots and associated values for lichen biomass (LB), lichen cover (CoL), lichen height (LH), and lichen volume as estimated by LH × CoL.

Regional differences in LB

There was a strong significant general decrease in LB and CoL (lichen cover) from oceanic areas (1200 mm at Haukeli) to a strongly continental area (370 mm at Vågå), but in all areas there were major variations in LB according to snow conditions. Regression analyses gave the following equations:

Eq. 5 LH × CoL = 554.5 - 0.42 × Precipitation,

(R^2 = 18.5, p < 0.0001)

Eq. 6 LB = 98.3 - 0.07 × Precipitation,

(R^2 = 37.4, p < 0.0001)

A regression analysis showed that there was a general decrease in LB with increasing altitude. All plots (both grazed and ungrazed) from the continental areas where WA_{Si} < 3.0 gave the following equation:

Eq. 7 LB = 2420 - 1.604 × Altitude,

(R^2 = 16.7%, p < 0.0001)

The main results of the study showed that the variation in average LB between the areas was strongly influenced both by altitude, snow condition, reindeer grazing, and annual precipitation. Three main areas may be separated: oceanic areas with annual precipitation higher than 1200 mm where LB generally was below 200 g m² even where reindeer grazing was low or absent; continental areas without grazing, where average LB (calculated on all plots where WA_{Si} < 3.0) was higher than 650 g m⁻², and LB was about 100 g m⁻² in grazed areas.

Discussion

LB in different vegetation types and total lichen production

Different vegetation types include major variation in LB from exposed ridges to snow-bed veg-

etation, as previously shown by vegetation transects analyses (Gjærevoll, 1956; Dahl, 1957), it is therefore essential to relate the lichen measurements to actual vegetation types and their snow conditions. Types A-D are similar to previously described as oligotrophic chionophobous belonging to Loiseleurio-Arctostaphylion (Nordhagen, 1943) or Arctostaphyleto-Cetrarion nivalis (Dahl, 1957). It includes alpine dwarf-shrub- and lichen heaths, *Juncus trifidus* heaths as well as subalpine (northern boreal) chionophobous coniferous and *Betula pubescens* forests. The most exposed (A and B) include several differential species against other groups, *e.g. Arctous alpinus, Alectoria nigricans, Bryocaulon divergens, Coelocaulon aculeatum, Flavocetraria nivalis, Gymnomitrium concinnatum* and *Thamnolia vermicularis.* Similar communities are previously included in the A group (Odland, 2005). Such vegetation types appear to have been the basis for previous estimates of LB (Wielgolaski, 1975), Type E-I can be described as oligotrophic lee-side communities similar to previously allocated to Phyllodoco-Vaccinion myrtilli (Nordhagen, 1943; Odland, 2005). The limit towards the chionophobous community Arctostaphyleto-Cetrarion nivalis is drawn where *Cladonia stellaris* and *Flavocetraria nivalis* begin to dominate. Oligotrophic lee-side communities have not been included in previous LB-studies on Hardangervidda.

Type J includes edaphically richer meadow stands belonging to Lactucion alpinae alliance (Nordhagen, 1943) with species such as *Geranium sylvaticum, Salix glauca,* and *S. lapponum.* The 12 plots in type K may be described as early snow-bed communities similar to communities referred to Nardo-Caricion bigelowii (Nordhagen, 1943) or Deschampsio-Anthoxanthion (Gjærevoll, 1956).

A vegetation map based on vegetation classifications has been published where the area of the different vegetation types were calculated, and also their distribution in relation to altitude (Hesjedal, 1975). The two lichen communities available for reindeer grazing were there described as *Loiseleuria procumbens* heaths (1a) and *Flavocetraria nivalis-Juncus trifidus* heaths (1b). The first covered 7.1 % of the total area (8310 km^2), while the second covered 3.0 %, but this was mainly confined to high altitudes (>1350 m a.s.l.).

Effects of grazing on LB
Studied plots classified to the same vegetation types had highly different LB when grazed and not grazed areas were compared, with a 50 % reduction in the grazed areas. Types with a higher WA$_{Si}$ value had a lower (ca 30 %) reduction (Table 3). Average LB from the grazed areas at Hardangervidda were around 100 g m^{-2}, while not-grazed continental areas had LB higher than 700 g m^{-2}. During the period from 2001 to 2011 the reindeer population at Hardangervidda increased from ca 5200 to 11000 animals (Bjerketvedt *et al.,* 2014), and the estimated average LB may be considered to reflect this grazing pressure. This value indicates that LB at Hardangervidda lie close to a critical value adequate to ensure survival of the present reindeer population size. It is remarkable that Imingfjell east in the outskirts of Hardangervidda situated only one km from the grazed Imingfjell west appear to remain ungrazed. The main reason for this is presumably that Imingfjell east is separated from Hardangervidda by human activities (roads and cabins). Migration of reindeer supplied with GPS collars (Jordhøy & Strand, 2009) showed that they hardly crossed the valley during winter. It has previously been found (Nelleman *et al.,*2000) that available LB was ca 1200 g m^{-2} 0-5 km from a tourist resort decreasing to a low of ca. 250 g m^{-2} at 15-25 km distance, a pattern that was assumed to reflect overgrazing as a result of avoiding a tourist resort in the Rondane national part, S Norway.

A reindeer consumes 70 % of the entire

amount of lichens within a grazing area and can dig and graze 30 m² day⁻¹, and then on average 90-100 g m⁻² of lichens should be available (Kumpula *et al.,*2000). This represents on average around 50 % lichen cover 3 cm thick which is equivalent to earlier presented lichen biomass data. A lichen cover of 50 % with a thickness of 3 cm will according to Eq.1 represent an estimated LB of 86 g m⁻². A general model for the dependence of lichen range condition on the mean density of semidomesticated reindeer in Finland indicates that a LB at such a condition level, the number of reindeer on lichen ranges in winter should not exceed 5-7 reindeer km⁻². It has also been found that LB lower than 200 g m⁻² was associated with reindeer densities of 4-8 reindeer km⁻² (Kumpula *et al.,*2000).

It has been estimated that the highest annual yield of lichens (120–160 kg ha⁻¹) is achieved from lichen stands that contain LB of 600–1200 kg ha⁻¹ (Helle *et al.,*1990). Studies of vegetation in protected ungrazed sites in the Finnish reindeer management area (Väre *et al.,*1996) estimated an average of nearly 8000 kg ha⁻¹ of lichen (total amount) at ungrazed sites. Theis value fit quite well the average LB value found here from ungrazed areas in continental parts of S Norway.

In general, there was a strong increase in lichen abundance from oceanic to continental areas. As shown by Eq. 5 and 6, the lichen abundance (based on not-grazed plots with $WA_{Si} < 4$) increased from approximately 20 % in an oceanic site to 80 % in a continental site. It has previously been estimated that exposed heaths have often a 75-85 % lichen cover in areas where annual precipitation is less than 400 mm, and 40 % or less where the annual precipitation is 1200 mm (Heggberget *et al.,*2002).

Lichen height, cover and volume as proxies for biomass
The present study shows that lichen height and lichen volume were well linearly correlated

with LB. There were, however frequently major discrepancies between LB and lichen volume (Fig. 3). This can partly be explained by the fact that volume measurements in the most exposed vegetation types may deviate strongly from the measured LB (cf. Eq. 4). Fig. 3 also show that LH (and thereby also the volume) is particularly a poor estimate for LB when the lichen mat is heigher then 10 cm. This is because the podetia density decrease strongly the the top to the bottom. Relationship between LB and CoL indicate that lichen cover was generally a poor estimate for LB. In plots where CoL was high (>75 %), LB varied from <100 g m⁻² to >2000 g m⁻², and plots with a CoL of 90 % could have a variation in LB from less than 400 g m⁻² to1800 g m⁻² (Figure 4). This is particularly evident in grazed area where the lichen cover could be quite high, but where the lichen heights were very low. Consequently, we suggest that reindeer management evaluations should not be based on lichen cover data only.

It has also previously been found (Moen *et al.,*2007) that different not-destructive methods gave fairly similar results, except when cover estimation was based on presence/absence data with a strict criterion of 100 % lichen cover. Average thallus heights within the plot explained the variation in LB as well as lichen volume (estimated from cover and average heights). Relationships between biomass and volume or height were also very similar for four lichen species studied (*Cladonia arbuscula, C. rangiferina*, *C. stellaris,* and *Cetraria islandica*), and the separation into species thus did not seem necessary for practical purposes.

In a recent published study estimating reindeer pasture quality at Hardangervidda, lichen volumes measurements on the ground were performed and combined with Landsat image analyses (Falldorf *et al.,*2014). Sampling data over a large area, they found that the maximum lichen volume was 600 (6 cm height × 100 % cover), and the average value within alpine

Figure 5. Exposed alpine lichen heaths have often no or a thin snow cover during the winter and are therefore available for reindeer grazing. These areas are most distinctly separated from areas (vegetation types) with a thicker snow layer that has not melted during late winter-early spring. The exposed vegetation on the picture belongs to Type C in Table 3.

heaths was approximately 154. By the use of Eq. 1, this will translate to a maximum LB of 829 g m^{-2}, and a mean of ca 160 g m^{-2} which do not deviate much from results of the present study. We agree with Falldorf et al. (2014) who maintained that in future studies one should discriminate between dominant lichen species on alpine heaths, *e.g.* by the use of three lichen catogeries which have slightly different distribution optima: (i) *Cladonia stellaris* dominant heaths (primarily type D), (ii) C. *rangifer*ina and *C. arbuscula* dominant heaths (primarily type C, D, and E), and (iii) *Flavocetraria nivalis* dominant ridges (cf. type A and B) (cf. Figure 5).
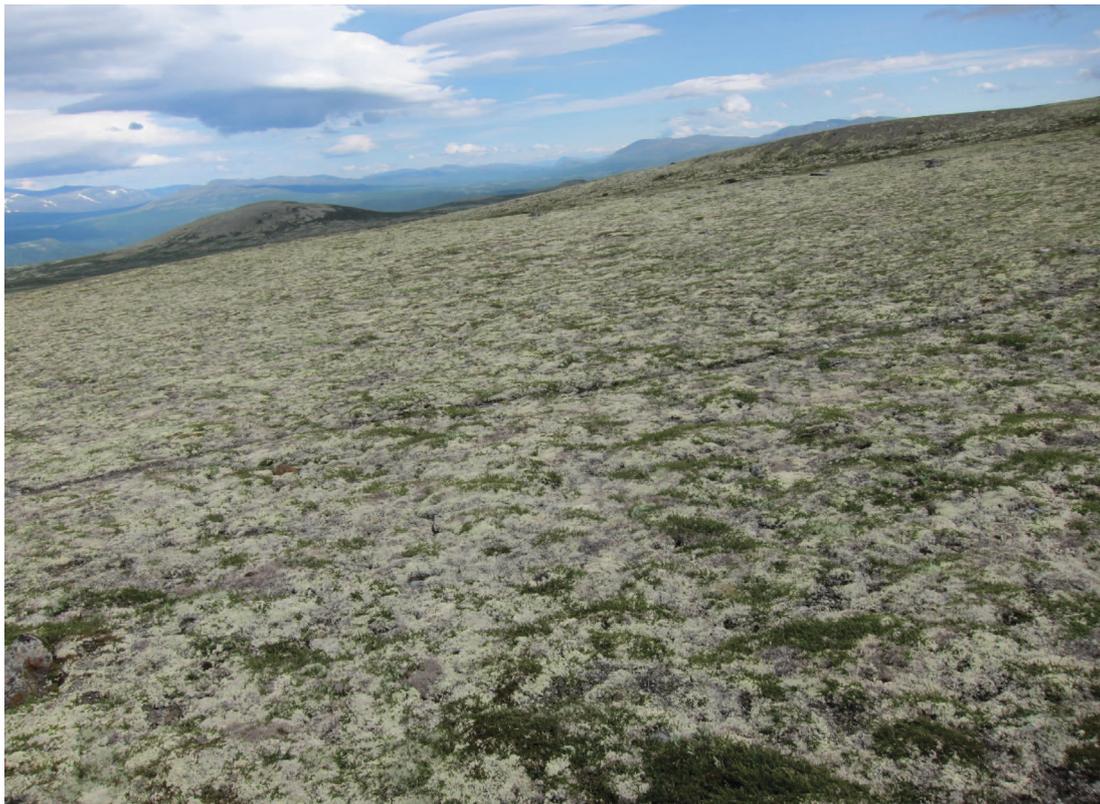

Figure 6. In continental areas with a gently sloping terrain where wind blows the snow away, large stands with a vegetation cover similar to Type A and B (Table 3) may occur. The picture is from the Vågå area, ca 1250 m a.s.l.

Use of snow indicators to predict variation in LB
In comparative LB studies it is essential that sampling has been performed in the same environments, *i.e.*, under similar snow conditions. One way to control that LB has been measured under the same snow conditions are to relate the biomass to average Snow index in the sampled plots.

Plants have for a long time been recognized as potential indicators of environmental conditions, and there are several reasons for, and advantages of using plant indicators instead of physical or chemical measurements (Diekmann, 1995). Studies have shown that vegetation, especially long-established vegetation, provides a sensitive integrated measure of the environment.

Species with an optimum on exposed sites with no or little snow during the winter have indicator value 1, and species with an indicator values 5 (lee-side species such as *Vaccinium myrtillus*) are normally melted out around medio May (Odland & Munkejord, 2008b). As compared with a previous study (Dahl, 1957), Caricetum nivalis communities (type A and B) had a snow-depths <50 cm, and the calculated Wa_{Si}-value was 1.49 ± 0.30, Cladonietum alpestris betuletosum communities (type C and D) had snow-depths between 0.3 and 2.0 m (Wa_{Si} = 2.16 ± 0.35), Phyllodoco-Vaccinium myrtilli communities (type E-I) had snow-depths between 1.6 and 4.5 m (Wa_{Si} = 3.3 ± 0.31), and Deschampsieto-Dicranetum fuscae communities (type K) had depths between 2.0 and 4.2 m (Wa_{Si} = 5.66 ± 0.35) (cf. 15). Maximum snow depths and Wa_{Si}-values are not always well correlated because the snowmelt rates may differ highly according to variation in altitude and aspect.

An essential question related to available grazing resources for the reindeer population in an area is the snow thickness and hardness. The snow thickness is highly variable both during the year and between years, and evaluations must therfore be based on "normal values". Studies show that reindeer can dig craters 70–80 cm deep, but the depth depends on snow hardness and possible layers of ice (Helle, 1984; Nelleman, 1996; Heggberget *et al.,* 2002). According to this, mainly the two most exposed types studied will normally be available for reindeer grazing. LB are estimated to 119 g m^{-2} (Wa_{Si} = 1.8) in the middle alpine zone and 652 g m^{-2} (Wa_{Si} = 2.0) in the low alpine zone, but the spatial distribution is relatively small. Vegetation types where LB is highest (type B and D, LB = 802 g m^{-2} and Wa_{Si} = 2.7) would therfore probably not be available for wintergrazing in a normal year.

Conclusions

As to the main questions raised in the study, the following answers can be given:
• There were large variations in LB in relation to average snow layer duration as quantified by average snow indicator values for the studied sites (Wa_{Si}). The relationship was not linear and highest average LB (650 g m^{-2}) was found in sites with an average WA_{Si} value of 2.0 (*i.e.* snow layer lasts until medio April). Average LB decreased on sites where the snow duration was both shorter and longer.
• The two vegetation types considered to be available for reindeer grazing at Hardangervidda had average LB of 87 and 118 g m^{-2}, representing an average decrease of LB of approximately 60 % compared to similar vegetation in ungrazed areas.
• Lichen volume and lichen height were both significantly linearly correlated with LB and are therefore useful proxies for LB. Lichen percentage cover was, however a poor proxy for LB.
• Annual precipitation (oceanity) was strongly negatively correlated with average LB. In areas with annual precipitation higher than 900 mm, LB was generally low and rarely higher than 200 g m^{-2}.

- There was a significant decrease of LB with increasing altitude. On average, LB decreased with approximately 20% for each hundred m increase in elevation.

Acknowledgements

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Estimering av lavbiomasse med fokus på reinsdyrenes vinterbeiteområder på Hardangervidda, S Norge

Abstract in Norwegian/Sammendrag: Kvantifisering av lavbiomasse er svært viktig i forvaltningen av reinsdyrpopulasjoner. Vi målte lavbiomassen (tørrvekt) i 876 mikroruter (16.5 cm × 16.5 cm) systematisk innsamlet i 219 vegetasjonsruter (2 m × 2 m) fra 7 ulike fjellområder. Lavmengden ble estimert ved fire ulike metoder, kvantifisert som: (a) tørrvekt i g m^{-2}, (b) lavdekkets høyde, (c) lavenes totale dekning i prosent, og (d) lavvolum (lavenes høyde × lavenes totale dekning). Undersøkelsen viste at lavbiomassen minket med økende gjennomsnittlig nedbørsmengde og økende høyde over havet. Lokalt var det stor variasjon i lavbiomasse, noe som avspeiler snøforholdene på stedet. De undersøkte områdene som var beita på Hardangervidda hadde generelt en lav gjennomsnittlig lavbiomasse (oftenst et gjennomsnitt under 150 g m^{-2}). Undersøkelsen viser at måling av lavdekkets gjennomsnittlige høyde og volum var godt korrelert med målt lavbiomasse, og disse metodene kan derfor benyttes til å få et relativt godt estimat av lavbiomassen, men en må regne med at verdier avviker fra eksakte målinger. Lavbiomassen var mye høyere i områder der reinsdyrenes trekk synes å være forhindret av menneskelig aktivitet og inngrep.