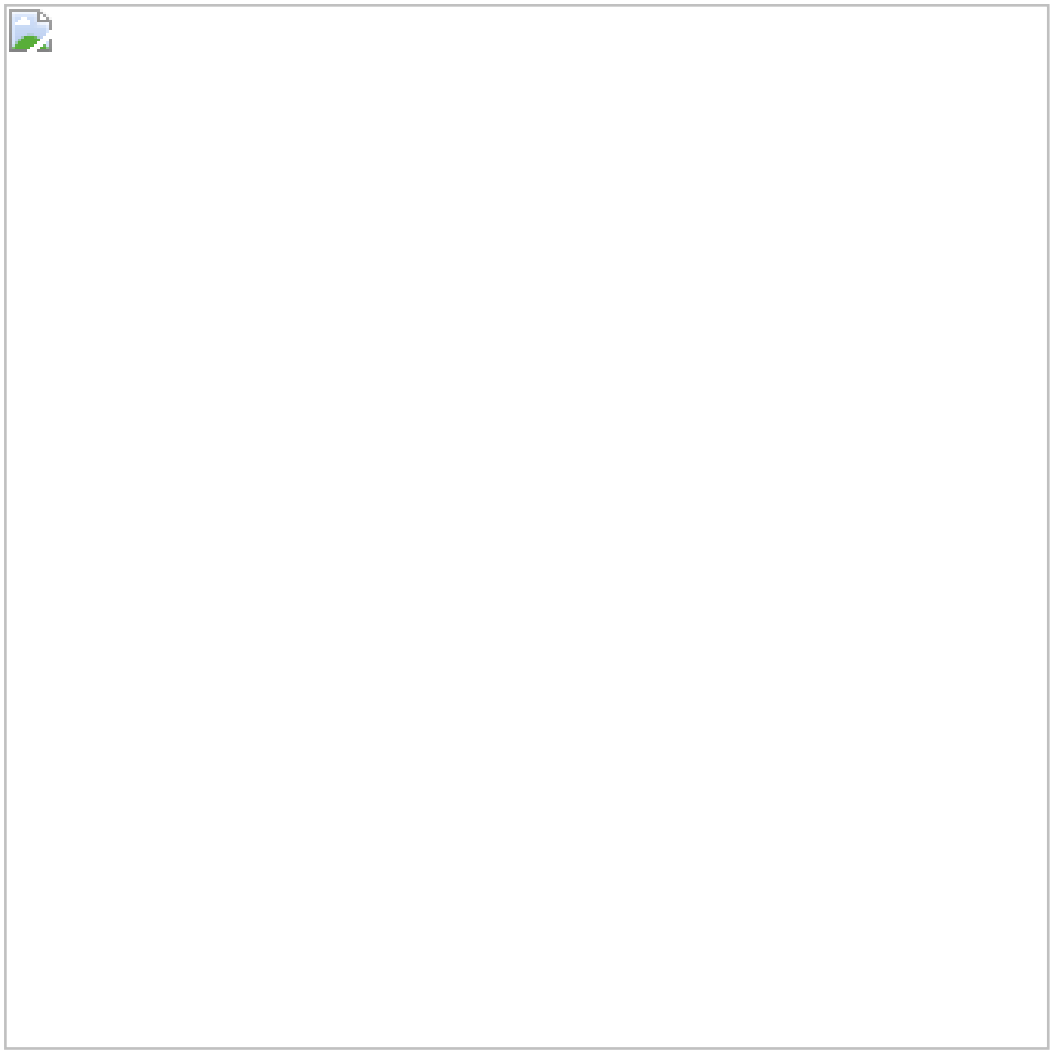

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Source: Lindbergia, 40(5) : 1-10

Published By: Dutch Bryological and Lichenological Society and Nordic Bryological Society

URL: https://doi.org/10.25227/linbg.01072

Lindbergia 40: 001–010, 2017
ISSN 2001-5909

Accepted 28 February 2017

How does microclimate affect the growth of the rare liverwort *Scapania nimbosa*?

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Vegetative growth of bryophytes is dependent on water and will stop as soon as the plants dry out. The growth rate depends on the quality of the micro-habitat. Clonal growth and dispersal of plant fragments are important parameters to understand local distribution of bryophytes lacking spore and gemmae production. Species of the mixed northern hepatic mat mainly rely on plant fragments and vegetative growth to disperse and maintain local populations. Understanding a species' means for population maintenance and dispersal potential is important for a successful management. This study aims to investigate the micro-scale climatic requirements and growth rate of the mixed northern hepatic mat species *Scapania nimbosa* through measuring its growth in situ in Norway, and through comparison of micro-climate between presence localities and seemingly suitable absence localities. The results show that *S. nimbosa* grows approximately 4.38 ± 2.78 mm during one growing season. No difference in micro-climate was found between the presence and absence localities, suggesting that *S. nimbosa* is limited by dispersal, not by suitable habitats. The availability of suitable habitat, and the ability to identify these, opens up the possibility to expand its range through transplantation of plant fragments.

In clonal plants not known to reproduce sexually, growth rate is an approximation to measure plant fitness across environments (Shaw and Beer 1999). Bryophytes are the only land plants for which the gametophyte is the dominant life stage, gametophore growth rate is therefore important in relation to competition and reproduction (Hassel et al. 2005). Gametophore growth varies through the season, and water availability seems to be the most important factor for growth (Hanslin 1999a). Differences in gametophore growth rates may thus reflect differences in quality of the microhabitat they occupy.

Reproduction in liverworts can be sexual through spore production, or asexual through production of gemmae, or through regeneration of plant fragments (Vanderpoorten and Goffinet 2009). The mixed northern hepatic mat community is characterized by a group of large and rather rare leafy liverworts, but also some more widespread species (Ratcliffe 1968). All the characteristic species of this community are dioicous, have seldom been recorded producing sporophytes in Europe, and only a few, such as *Scapania ornithopodioides* (With.) Waddell and *S. nimbosa* Taylor, produce gemmae, and then only very rarely (Paton 1999, Damsholt 2002). Thus, these species today seem to mainly rely on vegetative growth and fragmentation to maintain populations and to disperse (Flagmeier 2013). The mixed northern hepatic mat community has a northern Atlantic distribution in Europe (Ratcliffe 1968), where it is found in the most oceanic parts of the British Isles and Ireland, the Faeroe Islands and in southwestern Norway (Paton 1999, Damsholt 2002). Many species of this community have disjunct populations in northwestern North America, eastern Himalayas and eastern Asia (Schofield and Crum 1972). Many of the species are considered rare or scarce both in the UK (Preston 2006, 2010) and Norway (Hassel et al. 2010).

The distribution of species is determined by many factors, including historical factors such as continental drift and glacial history (Schuster 1983), and climatic and topographic factors that determine the potential distribution (Dahl 1998). Life history traits affect their ability to disperse and establish in suitable habitats (During 1979, 1992, Longton 1992, Laaka-Lindberg et al. 2000, Flagmeier et al. 2013).

Rarity may be due to habitat specialisation with few available places to grow, or due to dispersal limitation (Rabinowitz 1981). The degree of habitat limitation can be thought of as the proportion of the suitable habitat that are colonized, and is constrained by the distance between suitable habitat patches and dispersal ability (Herben and Söderström 1992). Restricted dispersal seems to be range-limiting for at least some species of this community as they

are absent from localities where their climatic requirements seem to be fulfilled (Jordal and Hassel 2010, Flagmeier et al. 2013, Wangen et al. 2016). Some studies have tested the regeneration capacity of mixed northern hepatic mat species from fragments and from whole shoots, both in situ and ex situ (Løe and Söderström 2001, Flagmeier et al. 2013). Such studies are important to understand the means of population maintenance and dispersal potential. The experience from such studies also provides essential knowledge for the introduction of rare mixed northern hepatic mat species into new localities as a conservation strategy. Conservation strategies may be necessary to preserve some of these species for the future since many of these species are threatened (ECCB 1995, Hassel et al. 2010), and may decrease in range in the face of climate change (Hodd and Skeffington 2011, Hodd et al. 2014). This study aims to investigate the micro-scale climatic requirements and the growth rate of the threatened northern hepatic mat species *S. nimbosa*, in Norway. The specific aims of the study were to: 1) test if microclimatic variables differs between localities where *S. nimbosa* is present and absent; 2) test if there are differences in how much *S. nimbosa* grows during one growing season across the study area; and 3) explore which environmental factors that affect the growth rate of *S. nimbosa.* Microclimatic variables were considered likely to differ between presence and absence localities if the absence localities had unsuitable micro-climate. Findings are discussed in terms of habitat and dispersal limitation within Norway, and in relation to the future conservation of this species.

Method

Study species

The globally-disjunct liverwort *Scapania nimbosa* is only known from the eastern Himalaya (Nepal, Sikkim), western China (Yunnan) and northwestern Europe. *Scapania nimbosa* is one of nine species in section sect. *Planifoliae* (Müll.Frib.) Potemkin together with the rare *Scapania rotundifolia* W.E. Nicholson and *S. ornithopodioides* (Heinrichs et al. 2012, Söderström et al. 2016). *Scapania nimbosa* was first discovered in Norway in 1907. Norwegian localities with *S. nimbosa* are usually open habitats facing towards the northwest, north or northeast. The typical habitat is a protected depression on a north facing slope, just above the forest limit. The localities often have a rough topography, the landscape thus offering a great variety of different microhabitats; for further details on the ecology and associated species see Jordal and Hassel (2010).

Study area

The study area comprises the known geographical range of *S. nimbosa* in Norway, which is located on the northwestern coast of Møre and Romsdal County. Here it is restricted to a small area covering about 20 × 12 km in the municipalities of Eide, Gjemnes and Fræna (Fig. 1, Norwegian Biodiversity Information Centre 2015). Today there are more than 30 localities from which *S. nimbosa* is known; these are 5–20 km from the coast, and ranging from approximately 200–550 m a.s.l., with mean elevation increasing with the distance from the coast (Jordal and Hassel 2010). Lower altitudes are covered by forests (pine or birch, but with scattered spruce plantations), mires and coastal *Calluna* heaths. At higher altitudes birch forest dominates and forms the forest limit. Above the forest there are moist heaths and mires, but also large scree areas with ferns, grasses or tall herb vegetation, and rock walls with more scattered vegetation. The climate in the study area is characterized as highly oceanic (Moen 1999), with mild winters and cool summers. The mean temperature (1961–1990) of the coldest month (January) at local meteorological stations near sea level in Fræna and Eide is between –0.2 and + 0.2°C, but colder at higher altitudes. The mean annual temperature is between 5.9 and 6.2°C and of the warmest month (August) between 12.7 and 12.9°C. There are 220–250 days with precipitation > 0.1 mm per year, and annual precipitation of 1400–2300 mm (Jordal and Hassel 2010).

Data collection

We collected microclimatic temperature and humidity data at ground level and growth data from several localities in the known geographical range of *S. nimbosa*. Figure 1 shows the set-up of the climatic loggers and growth measurements. Three mountain chains are situated along the coast at increasing distance to the ocean. We selected two mountains from each mountain chain. At presence localities (localities with *S. nimbosa* present) both microclimate data and growth data were collected (blue circles), while at absence-localities only microclimate data were collected (green triangles). Macro-climate, geography, geology and plant communities were similar on the presence and absence localities.

Microclimate data

Measurements of microclimatic data that are relevant for the species in question is difficult due to steep gradients of temperature and water vapour in the laminar boundary layer (Proctor 2011). Microclimatic data were collected from data loggers placed in the field between June 2012 and medio September 2014, using three types of loggers (iBCod Temperature logger, EL-USB-2 Humidity and temperature USB data logger, RHTemp1000 Humidity and temperature recorder) that measured temperature and in some places humidity once every hour. The data loggers were placed such that their sensor were at the same level as the surrounding mat of bryophytes, with no extra protection. The loggers were placed to make minimal disturbance of the bryophyte mat. The most frequent associated species with *S. nimbosa* at our study localities were *Racomitrium lanuginosum, Diplophyllum albicans, Sphagnum* spp., *Hypnum jutlandicum* and *Scapania ornithopodioides*. Among vascular plants the most frequent associated species with *S. nimbosa* were *Narthecium ossifragum, Trichophorum cespitosum, Calluna vulgaris, Andromeda polifolia* and *Nardus stricta* (Jordal et al. 2010). Vascular plants may cast shadows on the bryophyte mat and data loggers, however this effect were thought to be similar across the studied plots. Microclimatic data were collected in pairs from one mountain where *S. nimbosa* was found,

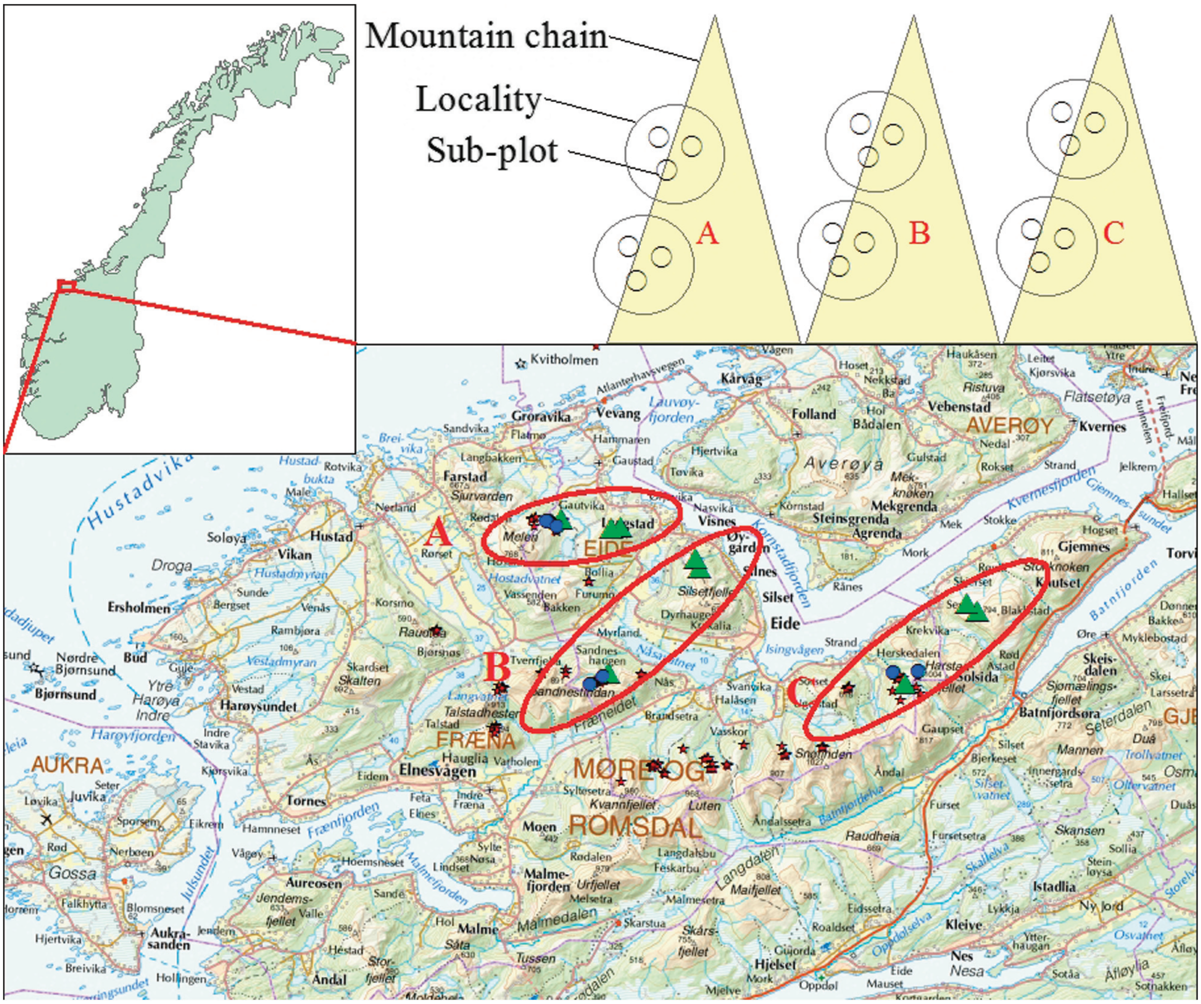

Figure 1. Set-up of the growth and microclimatic measurements. Loggers were placed out in localities indicated with green and blue dots. Blue dots show absence localities, and green triangles show presence localities where growth measurements were made. The three mountain chains (A, B and C) are marked in red circles. The known geographical range of *S. nimbosa* is shown as red stars (Norwegian Biodiversity Information Centre 2015). The illustration above the map shows how the growth measurements were set up: in upper and lower range in each mountain, a locality with three sub-plots was set up, 10 shoots were measured in each sub-plot. This sums up to 180 shoots measured.

and a nearby mountain where it was not known to occur. The absence-localities were selected on the basis of where conditions seemed suitable i.e. northwest, north or northeast facing slopes with protected depressions from the forest limit and upwards. In addition the absence localities should have similar species composition as localities with *S. nimbosa* (Jordal and Hassel 2010). To capture the breadth of the environmental range in which the species currently grows, we placed the loggers at the upper and lower range for the species on each mountain (at one locality loggers were also placed in the middle range). The lower part of the range was usually in the transition between tree line and open moist heath, and the upper range was in open moist heath dominated by *Narthecium ossifragum, Trichophorum cespitosum* and *Calluna vulgaris*. In addition, one absence locality with seemingly similar conditions and associated species was set up on the three mountains with presence of *S. nimbosa* to see whether these localities differ in microclimate compared with the presence localities. Microclimatic data was collected from six presence localities and nine absence localities, in total 15 localities spread out on six different mountains along three mountain chains, which covered most of the current range of *S. nimbosa* in Norway.

Growth measurements

The growth data for *S. nimbosa* were collected during the summer of 2014 with a method using a sewing thread (Longton and Greene 1967, Jägerbrand 2007; see evaluation of measuring methods in Appendix 1). Threads of different colour were tied around the shoots, between 2–7 mm below the apex, which was assumed to be just below the area of elongation. The shoots were in their natural position in the canopy while the thread was tied on. The thread was tied tight enough to avoid sliding off, and loose enough to not affect the shoot negatively. We measured the distance between the thread and the apex with a calliper. At the end of the growing season, the distance between the thread and the

apex were measured again. All measurements were done by the first author. The increased growth in mm could thus be derived from the difference in distance between the thread and apex from May to September. We did the first growth measurements as soon as the snow had disappeared the 5 to 7 of May and the 11 to 12 of June (leading to a five weeks difference in measurement period between plots), and the second measurements the 15 to 17 of September before the snow arrived.

We measured the growth for 30 shoots divided between three sub-plots in each of the six localities, summing up to 180 shoots measured. Each shoot was measured three times in succession at each measurement to reduce the measurement error. Using the increase in shoot length as a measurement for growth is quite straightforward because *S. nimbosa* has a low degree of branching. By using this as a measure of growth, it is also assumed that there was relatively low variation among shoots in other traits such as leaf size, shoot diameter and distance between leaves (which are species specific traits with low intra specific variation cf. taxonomic treatments of Nordic liverworts; Damsholt 2002). Growth rate was calculated as the total growth divided by the number of days between the two measurements. This value was used as a measure of habitat quality. To account for variation in length of the growing season, an estimate of total growth for one season was calculated as the growth rate multiplied by the number of days in the growing season (defined in Table 1), as estimated by the logger data. The growth rate is likely to vary somewhat within the growing season (Rincon and Grime 1989, Martínez-Abaigar et al. 1994), which has to be taken into consideration when interpreting the results.

Out of the 180 shoots measured before the summer, 107 shoots were available for the analysis due to disturbance, uncertainty in measurements due to loose threads etc. (Appendix 1). Temperature was logged in each of the sub-plots, but relative humidity only in one sub-plot per locality, both was logged once an hour.

Data analysis

Microclimatic variables

To investigate whether the microclimatic conditions differed between absence and presence localities, the following variables were extracted from the logger data: snow days; frost days; frost events and mild days during the winter; the length of the growing season; and the mean, median, maximum and minimum relative humidity and temperature during the measurement period. The choice of these microclimatic variables was based on current knowledge about the ecology of *S. nimbosa* (Ratcliffe 1968, Jordal and Hassel 2010). Explanation and ecological relevance of the chosen variables is presented in detail in Table 1. Periods with snow cover could be detected from the logged temperature data as periods with stable temperatures in contrast to the fluctuating temperatures when there was no snow. Frost/mild periods were defined as days without snow and with temperatures at or below/above –1/+ 1°C for 4 h in a 6-h period. See Table 2 for correlation between variables.

Hypothesis testing

The effect of the derived microclimatic variables on the growth rate was tested with likelihood ratio tests, where the intercept-only model (null model) was compared with each single-variable model. To take into consideration the dependency between the growth measurements within sub-plots, linear mixed models (Pinheiro et al. 2014) were made, with sub-plot ID set to random factor. All model residuals were visually inspected to check against model assumptions.

To test whether there was a significant difference in each microclimatic variable between the selected presence and absence localities, individual two-sided t-tests were carried out. To investigate whether presence and absence localities varied in multi-dimensional microclimatic space we used ordination-based analyses. First we created a principle components analysis using the following variables for each site: growing season length, number of snow days, number

Table 1. Description of the variables used to test the difference in micro-climate between the selected presence and absence localities for *S. nimbosa*, their ecological significance, and the time period over which the measurements were collected.

Variable	Description	Ecological significance	Time period
Snow days	days with snow cover during the winter.	*S. nimbosa* is associated with fairly prolonged snow cover...	Oct 2012 to May 2013
Frost days	days with no snow cover and with frost during the winter.	...which is thought to protect it from severe winter frost (Ratcliffe 1968).	Oct 2012 to May 2013
Frost events	number of times when the temperature went from positive to negative.	repeated freeze-thaw events may reduce survival of the plant since it is associated with loss of macro-nutrients in other bryophytes (Wynn-Williams 1980, Melick and Seppelt 1992, Seppelt 2011).	Oct 2012 to May 2013
Mild days	days with no snow and positive temperatures during the winter.	mild periods during the winter may be associated with poor protection from snow, and thus lower chance for survival.	Oct 2012 to May 2013
Length of growing season	period between last and first snow period.	the length of the growing season may reflect the time the plant will have for growth...	2013
Mean % RH	mean relative humidity from the logger data during the measurement period.	...although it depends on staying moist to sustain metabolism and photosynthesis (Vanderpoorten and Goffinet 2009, chap. 8)	13 June to 15 Sep 2013
Mean temperature	mean temperature from the logger data during the measurement period.	*S. nimbosa* is considered limited by high summer temperatures (Ratcliffe 1968).	13 June to 15 Sep 2013

Table 2. Pearson correlation matrix with correlation coefficient for all pairs of the variables used to test the difference in micro climate between presence and absence localities. Abbreviations: gs = growing season estimated for 2013. Mean temperature and % RH was calculated for the period 13-06–15-09 2013. See Table 1 and the data analysis section for variable description.

Variables	Snow days	Frost days	Frost events	Mild days	Length gs.	Mean temp	Mean % RH
Snow days	1						
Frost days	0.92	1					
Frost events	0.87	0.85	1				
Mild days	0.85	0.77	0.91	1			
Length gs.	0.87	0.79	0.74	0.74	1		
Mean temp	0.58	0.50	0.37	0.51	0.36	1	
Mean % RH	0.0091	0.10	0.22	0.27	0.26	0.029	1

of frost days, number of mild days, number of frost events, mean temperature, median temperature, minimum temperature and maximum temperature. Humidity data were not included due to the missing data. We fitted the binary variable of *S. nimbosa* presence or absence onto this ordination and tested the significance of this using a permutational goodness of fit test. All statistical analysis were done with the software R (<www.r-project.org>). The R package vegan was used for the ordination (Oksanen et al. 2014).

Method evaluation

To control for differences in measurement error when the distance from the tread to the shoot apex is short or long, each shoot was measured three times. To test for any systematic errors related to measured shoot length we used a linear model including all shoot length measurements and their corresponding standard deviation.

Results

Growth

The mean, minimum and maximum seasonal growth across all shoots was 4.38 mm, –2.96 mm and 12.45 mm, with a standard deviation (SD) of 2.78 mm. The growth data approximates a normal distribution (Fig. 2).

The minimum and maximum measured daily growth rate per shoot was, –0.015 mm and 0.060 mm day^{-1} respectively (note that the length of the growing season differs between localities). The mean across all shoots was 0.023 mm day^{-1} SD ± 0.014. The growth rate measurements across all the localities approximates a normal distribution (Fig. 3). There was a significant negative effect of relative humidity ($p = 0.03$) on the growth rate, but growth rate was unrelated to all other microclimatic variables ($p > 0.05$, Table 3). However, relative humidity was measured at only a few localities and some of these also showed questionably measurement quality during the summer season. Altogether 28 growth measurements had corresponding relative humidity data. However, questionable values and high uncertainty about the relative humidity measurements, probably due to the sensors being in water during snow melt and when there was heavy rain, leading to dust on the sensors and interfering with the readings, these data was omitted from further analysis.

Microclimate in presence and absence localities

It was not possible to detect a difference in microclimate between presence and absence localities (Table 4). The result from the analysis of the temperature logger data for each locality, which was the basis for testing the effect of microclimatic variables on the growth rate, is presented in Table 5. The logger from one locality (Bjørndal-Low) failed, and is thus excluded from the analysis. The temperature data nicely showed the periods where they were covered by snow as very stable temperature readings by the data loggers. During a 24-h period temperatures were fluctuating most in spring after snow melt and in autumn before the snow covered the ground. During mid-summer there was much less variation in temperature during the 24-h period, the sun is below the horizon for only four ours at mid-summer.

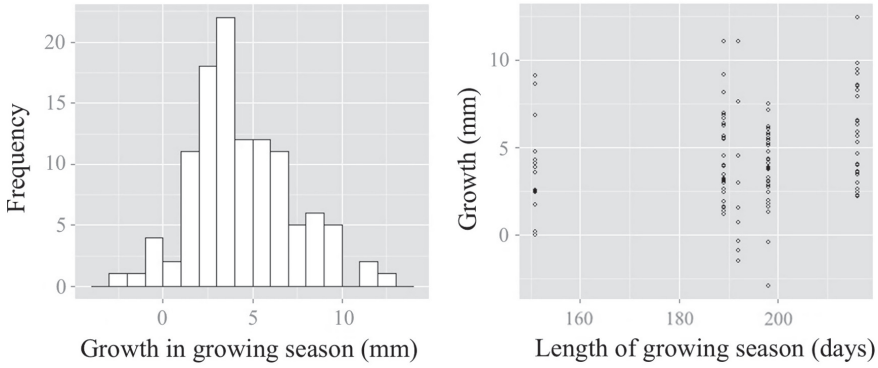

Figure 2. Left: histogram of the estimated growth during the growing season, length of growing season was estimated from the logger data. Mean, minimum and maximum growth equals 4.38 mm, –2.96 mm and 12.45 mm respectively. n = 113. Right: the response of growth to the length of the growth season.

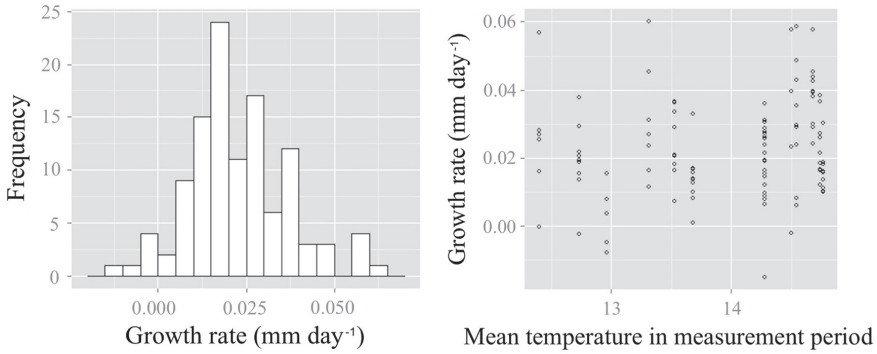

Figure 3. Left: the distribution of estimated growth rate across all localities. Right: growth rate plotted against mean temperature from the period that the shoots were measured. n = 113.

Fitting of the presence:absence sites onto an unconstrained ordination of the site microclimatic data showed no significant difference in microclimatic space in sites where *S. nimbosa* was present or absent (Fig. 4, squared correlation coefficient $r^2 = 0.092$, $p = 0.462$).

Method evaluation

Each shoot was measured three times, and the mean standard deviation of all the shoot measurements was 0.185 mm. The distance from the thread to the apex did not significantly affect the standard deviation ($p = 0.85$).

Discussion

Growth rate is a key trait for bryophytes and is partly determined by the quality of the micro-habitat. Vegetative growth is especially important for species not known to reproduce sexually as they will depend on clonal growth and dispersal by fragmentation for their survival. *Scapania nimbosa* is a rare liverwort species within its European range, not known to reproduce by spores. This study indicates that *S. nimbosa* has a mean seasonal growth rate of 4.38 ± 2.78 mm, however, there is large variation within its Norwegian geographical range. We were not able to detect any difference in micro-climate between presence localities and seemingly suitable absence localities, which indicates that the species is dispersal-limited rather than habitat-limited in Norway (see also Wangen et al. 2016). It also suggests that we have a reasonably good understanding of its ecology. The transplantation of turfs of plants can be considered as a possible conservation strategy for *S. nimbosa*. To evaluate possible effects of transplanting plants one should first do an in situ transplantation.

Growth and habitat quality

The mean growth during the estimated growing season was 4.38 ± 2.78 mm, with the minimum and maximum extremes of –2.96 mm and 12.45 mm respectively. The extreme values might partially be due to measurement error (notably the estimates of negative growth) or other sources of error. Considering the relatively small measurement error (SD = 0.185 mm for all measurements), this indicates a very large variation among the shoots. The mean growth corresponded to a growth rate of 0.73 mm × month^{-1}. Flagmeier et al. (2013) found the ex situ mean growth rate of *S. nimbosa* in growth chambers to be 1.44 mm × month^{-1} in the main stem. The reason why they found better growth may be because they grew the shoots in growth chambers with stable and suitable growing conditions, and quite low light levels, which would lead to etiolation. Our shoots were measured in situ and during the summer, which is the part of the growing season when shoots are most likely to dry out. Bryophyte species likely to dry out during the summer have shown to decrease in chlorophyll content during the summer compared to early spring and late fall (Martínez-Abaigar et al. 1994). Our measurement probably includes both favourable and less favourable periods of growth (cf. Rincon and Grime 1989), leading to less growth per month, compared to results in Flagmeier et al. (2013). In addition, our measurements were done at the limit of the upper and lower elevational range within

Table 3. Output from linear mixed models testing the effect of microclimatic variables on the growth rate by comparing the intercept-only (null) model with each single-variable model. All models used sub-plot ID set to random factor. Mean temperatures and relative humidity are from the period where growth was measured at the corresponding locality (not 13 June to 15 Sep).

Model	Estimate	SE	Likelihood ratio	p-value	n
Growth rate ~ snow days	0.000015	0.000045	0.11	0.73	113
Growth rate ~ frost days	–0.00016	0.00016	0.99	0.32	113
Growth rate ~ frost events	0.00017	0.0017	0.01	0.92	113
Growth rate ~ mild days	–0.00008	0.00026	0.10	0.75	113
Growth rate ~ length gs.	–0.000007	0.0001	0.003	0.95	113
Growth rate ~ mean temp	0.003	0.003	1.30	0.25	113
Growth rate ~ % RH	–0.002	0.0008	4.45	**0.03**	31

Table 4. Results from testing the difference in microclimatic variables between presence and absence localities using a two-sided t-test. The mean value of each variable in the presence and absence localities is presented along with the test statistic, the p-value and total number of presence and absence localities.

Variable	Mean presence	Mean absence	T-stat.	p-value	n
Snow days	151.5	127.4	0.982	0.35	13
Frost days	28.5	37.1	–0.769	0.46	13
Frost events	2.3	3.4	–0.871	0.40	13
Mild days	16.5	22.4	–0.821	0.43	13
Mean temperature	12.82	12.17	1.144	0.28	13
Length gs.	185	196	–0.905	0.39	12

the study area, where there might be less growth than in the intermediate ranges.

None of the microclimatic variables had a significant effect on the growth rate. The mean summer temperature among the sub-plots varied between 12.4°C and 14.8°C, but there was no significant effect on the growth rate. One possible reason for this may be that the environmental range within the currently known geographical range of *S. nimbosa* in Norway is too small to see any difference in the growth rate. Some bryophytes have shown to have a weak response in growth rate to temperature (Furness and Grime 1982). If this is true also for *S. nimbosa*, then growth would have to be measured over a much larger range, which is more suitable for laboratory experiments, or the sample size would have to be larger in order to see any response. Air humidity is probably an important factor for plant growth, but due to our unreliable logger data on this, we could not include it in the analysis. It is likely that *S. nimbosa* has a much broader potential environmental range than that exhibited in Norway, since it in the British Isles covers almost the same geographical range as *S. ornithopodioides* (Blockeel et al. 2014). Another possibility is that the response to temperature is hidden due to the effect of other, possibly more important variables such as relative humidity. Since liverworts are poikilohydric, their metabolism and photosynthesis will stop when they dry out, and water availability thus has a major impact on their growth (Vanderpoorten and Goffinet 2009). Thus, it is likely that there is an interaction effect between temperature and wetness factors on the growth rate. Confounding effects could have been ruled out by doing such measurements in the laboratory. There is a large variation in growth rate especially within some of the sub-plots. This indicates that there are variables at even larger scale affecting the growth rate, which is expected. This could be due to the actual neighbour with its competing or facilitating effect (van der Hoeven 1999), or due to edaphic factors or soil moisture at that specific locality (Kooijman and Whilde 1993, Hanslin 1999b, Arróniz-Crespo et al. 2011). Our results on length growth is generally less than 10 mm per growing season, and is less than in most other field studies reporting 5–80 mm. All but one of the species included in these studies are mosses, and the only other liverwort *Barbilophozia lycopodioides* had an annual length growth of about 20 mm (Kooijman and Whilde 1993, van der Hoeven 1999, Arróniz-Crespo et al. 2011).

Water vapour deficit is thought to be an important factor for growth in liverworts (Clausen 1952), and air humidity is recognised as one of the main factors driving the distribution of hepatic mat species at regional scale (Ratcliffe 1968). However, at a local scale air humidity may also be related to the soil type. Species growing on wet peaty soils like *S. nimbosa*, may have lower risk for drying

Table 5. Results from the analysis of the logged temperature data from one sub-plot in each locality, and mean daily growth rate ± SD mm day^{-1} across all sub-plots in each locality. Data on snow days, frost days, frost periods and frost events based on measurements during the winter 2012–2013. Mean temperature based on the period 13 June to 15 Sep 2013. Abbreviations: U/M/L = upper/middle/lower locality; MC = mountain chain – see Fig. 1; gs = growing season estimated for 2013. * = Estimate. ** = Logger data was available from two sub-plots in Hældal L.

Locality	Presence	MC	Snow days	Frost days	Mild days	Frost events	Length gs	Mean temp	Mean daily growth rate ± SD mm day^{-1}
Melen U	1	A	148	33	13	2	198	12.89	0.02089 ± 0.00907 (n = 22)
Melen L	1	A	116	33	27	4	216	13.89	0.02614 ± 0.01288 (n = 29)
Melen L	0	A	88	51	43	8	211	11.94	–
Lyngstadfj U	0	A	97	67	31	6	–	12.90	–
Lyngstadfj L	0	A	105	44	24	3	–	13.06	–
Hældal L	1	B	136	50	14	3	192	11.76	0.02264 ± 0.13729 (n = 15)
Hældal U	1	B	208	0	0	0	151	11.43	0.03071 ± 0.01537 (n = 5)
Hældal L	0	B	133	34	25	2	200	12.98	–
Hældal L**	1	B	119	38	36	4	198	–	
Silsetfj U	0	B	215	0	3	0	174	10.39	–
Silsetfj L	0	B	76	49	20	4	217	12.46	–
Herskedal U	1	C	182	17	9	1	151	13.02	0.25914 ± 0.17955 (n = 9)
Herskedal M	0	C	177	17	10	1	187	12.02	–
Herskedal L	1	C	–	–	–	–	189*	13.97	0.02378 ± 0.01353 (n = 27)
Bjørndal U	0	C	178	15	11	1	180	11.47	–
Bjørndal L	0	C	–	–	–	–	–	–	–

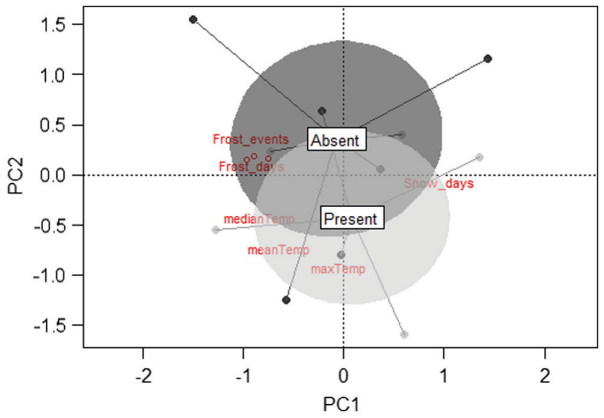

Figure 4. Principle components analysis plot showing the microclimatic varaibles recorded in sites where *S. nimbosa* was present or absent. The plot is based on an unconstrained ordination, and the presence:absence data subsequently added. Sites are joined to the centroid for each site type by lines. The centroid for each type of site is shown by text, and the 95% confidence interval of centroid location is shown by the shaded ellipses. The scores for climatic variables are shown by red coloured text.

out, and this is probably related to the thickness of the soil.

Habitat limitation and conservation

The absence of *S. nimbosa* in the seemingly suitable absence localities is either because it has not been able to arrive and establish there, or because the locality is actually unsuitable due to unmeasured factors, which may be of climatic, edaphic or biotic nature. We were not able to detect a significant difference in micro-climate between the selected presence and absence localities. This indicates that *S. nimbosa* is limited by dispersal rather than by suitable habitats, and that there is a possibility for the species to grow if it spreads to new localities. It also indicates that we have a reasonably good understanding of the ecology of this species. This is useful in a conservation perspective. A possible conservation measure is to expand its distribution by translocating turfs or plant fragments to suitable absence localities, in which case it is important to choose localities that are actually suitable. The study by (Flagmeier et al. 2013) shows that regeneration in the field from plant fragments is possible for the mixed northern hepatic mat species *Herbertus hutchinsiae* (Gottsche) A.Evans. Their study also suggests that other species belonging to this community will be able to establish from fragments in the field. Such conservation measures are especially relevant for *S. nimbosa* in Norway, since it has a geographically small distribution and limited dispersal potential, which makes it vulnerable to climate change (Jordal and Hassel 2010). Flagmeier et al (2014) found a significant decline of *S. nimbosa* over 50 year period in oceanic–montane liverwort heath in Scotland, with grazing, eutrophication and warmer and drier conditions as the potentially most important drivers of the change. Decline of the oceanic liverwort species (*S. nimbosa* included) was also found by Moore and Crawley (2015) who studied the impact of red deer. However in Norwegian localities decreased grazing is associated with tree and shrub expansion in mountain areas (Speed et al. 2010) that potentially threatens the hepatic map communities.

Conclusion

The estimated mean growth of *S. nimbosa* during one growing season was 4.38 ± 2.78 mm, and the variation in growth was large within its geographical range. We were not able to find an effect of temperature or humidity on the growth rate in this study, probably due to a low environmental variation within the Norwegian distribution range of *S. nimbosa*. We did not find any differences in microclimate between localities where the species was present and where it was absent, suggesting that *S. nimbosa* is dispersal limited within Norway. The availability of suitable habitats and the ability to identify them opens up the possibility to expand its range and abundance with conservation measures such as translocating of turfs or plant fragments. Such conservation measures are especially relevant for *S. nimbosa* since in Norway it is restricted to a small geographical area and has limited dispersal potential, making it particularly vulnerable to climate change.

Acknowledgements – We thank the field assistants Ingvil Kålås, John Bjarne Jordal and Kristine Sundsdal. H. During and A. Jägerbrand are thanked for their constructive criticism of an earlier version of the manuscript.
Funding – We thank the Norwegian Environment Agency for funding through the Nature Index project.

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Appendix 1

Evaluation of growth measurement methods

Thread method

Generally, the thread method used in this study (Fig. A1) gave a small standard deviation (based on three measurements of all shoots made on a row), thus the results are relatively reliable if other sources of error can be eliminated. The method is also likely to work for other species with similar growth forms to *Scapania nimbosa*, as long as the species is large enough to allow the thread to be placed between the leaves without tying the thread too tight. That includes species that have a low degree of branching and low variation in traits such as leaf size, distance between leaves and shoot diameter, which will allow growth of shoot length to work as a good measure of energy spent on growth. The biggest source of error is probably the possibility of the thread to move out along the shoot during the summer if the thread is tied too loose. Outwards movement of the thread would lead to a measured growth lower than the actual growth. Another possible source of error is the effect of the treatment on the shoots. Slightly pulling the shoot out of the ground when tying the thread or by animals passing by during the summer is presumably the most harmful effect, since this would make them more vulnerable to desiccation. Such sources of error and the disturbance by animals during the summer were the biggest source of sample size reduction in this study.

Suggestions for improvements

Some suggestions for improvement of the method, sorted by importance, include: 1) Avoiding disturbance from animals by covering the plots with a fence (e.g. chicken wire); 2) do the field work in good enough weather. Especially when it was raining, condensation formed on the hand lens, and the chance of measuring the wrong species increases. It was also a harder to do high precision work such as tying threads around the shoots in wet and cold conditions; 3) be sure to tie the thread tight enough to avoid that it will move, but not too tight. Bring plenty of extra threads to the field in order to allow for some unsuccessful attempts; 4) it was easier to measure short than long distances and it did not affect the measurement error. Tying the thread approximately 2–3 mm below the apex was perfect in my opinion.

Figure A1. Measuring of *S. nimbosa* in the field using a calliper. The area marked with yellow in the right bottom corner was measured in the beginning and the end of the growing season (Photo: K. Hassel).

Figure A2. Illustration of the cranked wire method. The picture is from the beginning of the growing season. The tip of the shoots that were measured were aligned with horizontal part of the wire, and the position along the shoot indicated by a black mark on the wire to avoid measuring the wrong shoots at the end of the growing season. Identifying the shoots that were measured was the main challenge with this method (Photo: K. Wangen).

Cranked wire method

During the summer 2013, the growth of *S. nimbosa* was measured based on the cranked wire method, which has been used for measuring growth in *Sphagnum* (Clymo 1970). The method is illustrated in Figure A2. Cranked wires of stainless steel shaped like an L were placed upside down into the ground. The horizontal part of the wire was aligned with the tip of the shoot, and the location of the shoot along the wire was marked with permanent marker. At the end of the summer, the part of the shoot that had passed above the wire was measured as the growth.

This method did not work well for *S. nimbosa*. The main reason was that the position of the shoot above the ground differed, thus only one to four shoots could be measured by one wire. Thus it was difficult to identify which shoot was measured at the end of the summer. In addition, the wire seemed to negatively affect some of the shoots that had been touching the wire, since they had changed colour, and had not grown anything at all.