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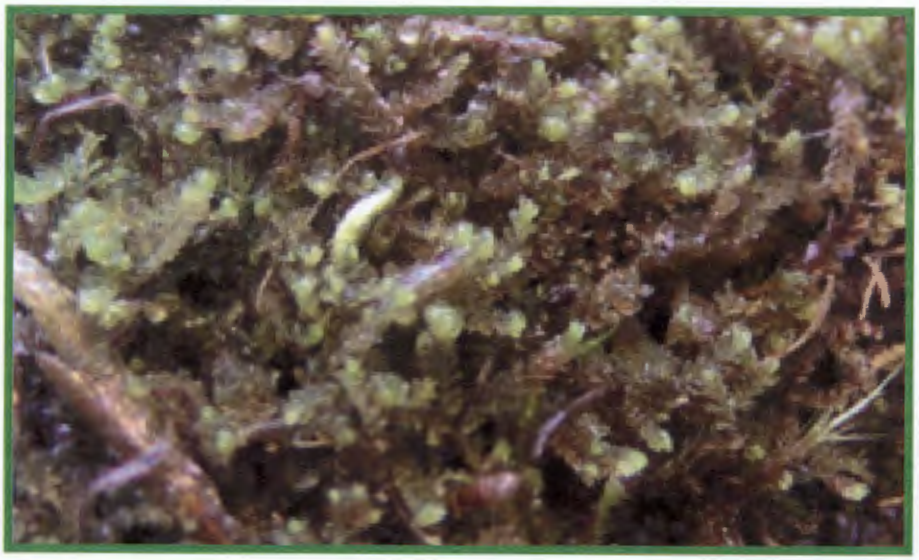
Determinants of gemmae output in the liverwort *Lophozia ventricosa*



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for a BSc (Hons) degree in Botany

KD ALGA
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Abstract

The spacial variation and population parameters affecting gemmae output of a boreal and arctic liverwort species, *Lophozia ventricosa*, were studied in Trøndelag, a boreal region of central Norway and in the arctic tundra on Svalbard. The population parameters investigated included colony size, colony shoot density, number of gemmae per shoot, proportion of gemmiferous shoots and gemmiferous shoot density. The gemmae output in a colony was calculated as the product of the number of gemmae per shoot, colony size and gemmifeorus shoot density. A Nested Analysis of Variance was used to partition population parameters spacially and a Pearsons Product-Moment Correlation was used to evaluate which of these population parameters affect gemmae output in a colony. The number of gemmae per shoot differed significantly between areas, populations and colonies, and was significantly varied between populations and colonies on Svalbard. No significant variation in the number of gemmae per shoot was found in Trøndelag. Population influences on shoot density, gemmiferous shoot density and gemmae output were significant in Trøndelag. This was expected, as more shoots in a colony is thought to influence gemmiferous shoot density and gemmae output. In Trøndelag, the only significant relation that can explain gemmae output is colony size whereas on Svalbard, gemmae output in a colony is affected by colony size, shoot density and number of gemmae per shoot. The results indicate that most of the variation in gemmae output occurs at the population level and that gemmae output differs between the arctic and boreal regions.

Introduction

The long-term survival of a species is determined largely by its life-history (or reproductive) strategy, population structure and dynamics, and its ability to disperse its diaspores to new available habitats (Söderström 1994; Söderström & Herben 1997). Variation in life-history strategies among bryophytes (as well as other plants) is due to various complex variables (ecological and environmental) interacting with one another (Hedderson & Longton 1996), and the strategy favoured depends on the duration and predictability of the environment (During 1979) as well as spatial structure of habitats (Söderström & Herben 1997).

Liverworts have two forms of reproduction: asexual and sexual. Sexual reproduction involves the fusion of male and female gametes to produce a sporophyte which produces spores. Asexual reproduction, on the other hand, is reproduction without the fusion of male and female gametes, producing asexual propagules on the gametophore (Söderström 1994). 'Growth' of populations of bryophytes is often very much dependent on asexual reproduction (Schofield 1985). The term growth can be seen as 'an increase in size of a single physiological individual' (Mishler 1988) and in that sense is no form of reproduction and Mishler (1988) defines reproduction in bryophytes as the production of a new, physiologically independent plant.

In general, the cost of sexual reproduction is much higher than the cost of asexual reproduction but provides greater genetic diversity. Green & Noakes (1985) suggest that occasional sexual reproduction is enough to maintain genetic diversity in normally asexually reproducing species, so genetic variability may not be the determining factor. Pohjamo & Laaka-Lindberg (2003) suggest that a trade-off exists between asexual and sexual reproduction at the colony level in the liverwort *Anastrophyllum hellerianum* as the proportion of gemmiferous shoots was higher in bisexual colonies without sporophytes than in bisexual colonies with sporophytes.

Asexual reproduction in bryophytes can provide the means for population persistence in a habitat in species where sexual reproduction is rare (Longton 1997) Asexual reproduction is very common in liverworts (Laaka-Lindberg 2000). In the British flora, for example, 46% of liverwort species produce asexual propagules (Laaka-Lindberg et al. 2000), while only 18% of mosses produce special asexual propagules (Longton & Schuster 1983). The production of asexual propagules occurs in various forms and positions on the plant (Longton & Schuster 1983). In liverworts they include the production of special propagules like gemmae, caducous leaves and shoots, and tubers (Laaka-Lindberg 2000). Gemmae develop from specialised mother cells on the edges of the upper leaves of shoots in leafy liverworts (Buch 1911 in Laaka-Lindberg 2000). These mother cells produce gemmae once adequately mature and only for a specific period of time (Buch 1911 in Laaka-Lindberg 2000). Asexual reproduction also includes gametophore fragmentation and branching of the mature gametophore that becomes independent (Söderström 1994). Fragmentation is rarer in liverworts than in mosses and this mode of asexual reproduction produce diaspores that are effective only in short-distance dispersal (Longton & Schuster 1983). Branching of mature plants is a common form of cloning in liverworts, with the subsequent death of older branches. This process may be stimulated by the removal or death of apical shoots (Longton & Schuster 1983).

The output of gemmae by a colony will affect its local survival where more gemmae produced by a colony will result in more shoots being established and a larger colony being formed. The output of gemmae by a colony will, however, not be affected only by the number of gemmae per shoot and colony size. Various population parameters will have an effect on the gemmae output by a colony. A simple model relating various characters within a colony, all leading to the gemmae output per colony is hypothesized as follows (Figure 1).

A high number of gemmae per shoot will increase the number of new shoots establishing and this will increase colony size which increases the gemmae output of the colony. A high number of gemmae per shoot will result in more shoots establishing within the colony (a higher density) which would increase colony gemmae output. Shoot density

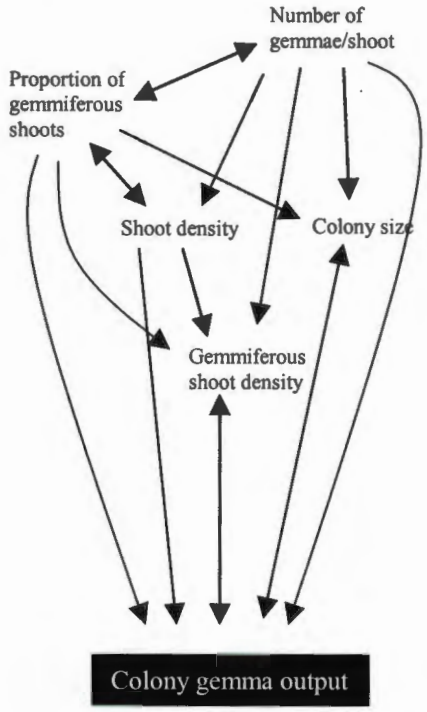


Figure 1: Hypothetical pathway of parameters affecting gemmae output of colonies in liverworts

and the proportion of gemmiferous shoots are inter-related where a higher density could increase the proportion of gemmiferous shoots, or a higher proportion of gemmiferous shoots could lead to a higher shoot density. Both pathways increase gemmae output in a colony. A higher number of gemmae per shoot may also increase the proportion of gemmiferous to shoots resulting in a higher gemmae output in a colony.

Reproduction is involved in the survival and dynamics of populations (Kimmerer 1991; Söderström 1994), which in turn is important in the long-term survival of a species (Söderström 1994). Sexually and asexually produced diaspores tend have different roles in the life-history strategy (Söderström 1994). Asexual propagules tend to be larger and are associated with short-distance dispersal whereas the usually smaller sexually produced spores are associated with long-distance dispersal. In mainly asexually reproducing species, the local population dynamics is likely to be affected by the

seasonality and extent of asexual reproduction (Laaka-Lindberg 1999). However, studies quantifying the production of asexual propagules are uncommon (Söderström 1994). The spatial distribution of individuals, habitats and populations will also affect population dynamics (Söderström 1995). Describing this distribution is essential in understanding the dynamics of the populations. Quantifying spatial variation of gemmae output in two geographically separated areas, Trøndelag in Central Norway and Svalbard archipelago, and evaluating the hypothesized model will offer an understanding into the local survival ability of a species.

Many bryophyte species are also widespread in boreal, or in boreal and temperate regions, commonly expanding to alpine regions (Longton 1988). As the liverwort *Lophozia ventricosa* is found in both arctic and boreal regions, it will be a good species to use for this study.

Aims of this study

This study aims to evaluate the main factors determining gemmae output in the liverwort *Lophozia ventricosa* and determine the spacial scale of variation in gemmae output. The main questions are: (1) How many gemmae are produced by individual shoots? (2) Does gemmae production vary in space and if so at what level? (3) Is the number of gemmae produced density dependent? (4) Does gemmae production influence colony size?

Methods

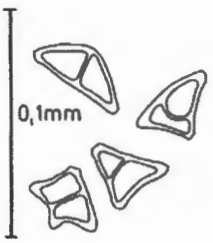
Studied species

Lophozia ventricosa (Dicks.) Dumort. is a leafy hepatic species belonging to the family Lophoziaceae. It is common in boreal and arctic areas occurring in bright green to yellow-green patches with shoots 0.8-4 mm wide and 1-5 cm long (Figure 2) (Damsholt 2002). *L. ventricosa* is a very variable species. All five varieties (Table 1), recognized by Damsholt (2002), produce yellow-green to green gemmae in abundance. The gemmae are two-celled, 18-20 × 20-25 μm and vary from pyriform to rhombic, quadrate to stellate with protuberant angles (Damsholt 2002).

Study sites

The first study site is located in the province of Sør-Trøndelag in Central Norway (Figure 3). The area belongs to the boreal zone dominanted by *Picea abies* (Figure 4a). Population samples of *Lophozia ventricosa* were collected from three different localities in this area (Table 2). The second study site is on Spitzbergen, one of the Svalbard

(a)



(b)

Figure 2: (a) A shoot of ***Lophozia ventricosa*** (b) Gemmae of *L. ventricosa*

Table 1: Descriptions of the five varieties of *Lophozia ventricosa* (Damsholt 2002).

Lophozia ventricosa **variety**	**Distribution**	**Habitat**
ventricosa	Boreal-arctic	Growing in shaded, moist places on rock-ledges, on the ground in forest (esp. along footpaths) and decaying logs.
silvicola	Boreal	Grows on acidic sites, such as humid rock faces, over exposed peat, on decaying logs in forests.
grandiretis	Arctic-alpine	Grows in rills or fissures of acidic rock, and along rushing streams
confusa	arctic	Grows in exposed places such as sandy ridges or rock fissures
uliginosa	boreal	Grows over organic substrate, often among *Sphagnum* in mires

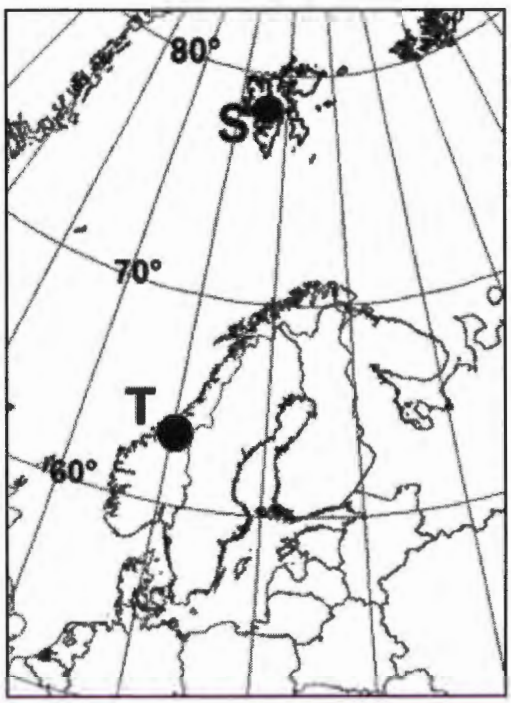


Figure 3: Map showing the study sites, Trøndelag (T) and Svalbard (S)

Figure 4: (a) Boreal forest dominated by *Picea abies* in Sør-Trøndelag, Central Norway; (b) A quadrat on a steep peaty slope in the Boreal forest

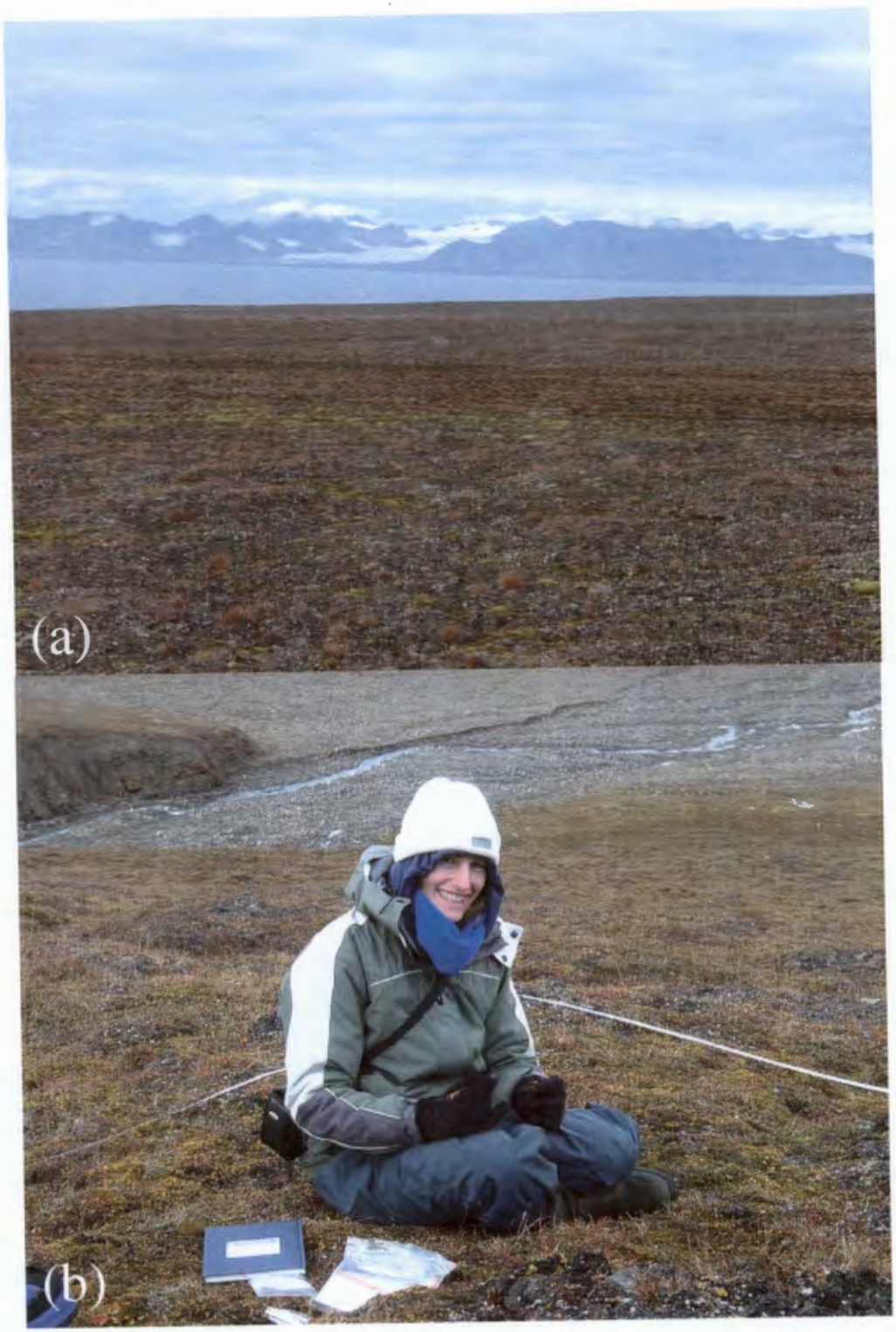


Figure 5: (a) Tundra on Svalbard; (b) The author in a quadrat in the tundra setting.

Table 2: Co-ordinates of collecting localities in Trøndelag (T) and on Svalbard (S).

Area	Locality name	Longitude	Latitude
T1	Elgsetheia	63° 25' 13" N	10° 12' 04" E
T2	Urvatnet	63° 07' 21" N	9° 48' 26" E
T3	Vintervatnet	63° 24' 50" N	10° 15' 16" E
S1	Platåberget	78° 13' 38" N	15° 23' 25" E
S2	Platåberget	78° 13' 06" N	15° 35' 20" E
S3	Endalen	78° 11' 48" N	15° 44' 19" E
S4	Bjørndalen	78° 13' 10" N	15° 19' 17" E
S5	Adventdalen	78° 10' 15" N	16° 01' 10" E
S6	Todalen	78° 09' 23" N	15° 59' 31" E

Islands (Figure 3). This area is middle arctic tundra (Figure 5a). Population samples of *Lophozia ventricosa* were collected from six different localities in this area (Table 2).

Field sampling

Material was collected at the end of August and early September (late summer in Norway 2004). Colonies were located and a five-by-five metre quadrat was placed around the located colony(ies) (Figure 4b). Within each quadrat, the size of each colony present was measured for all colonies with a standard metal ruler, 10 shoots with gemmae were collected from each colony and a two-by-two centimetre (minimum size) sample of each colony was collected to estimate the proportion of gemmiferous shoots (Figure 5b). Each sampled gemmiferous shoot was placed in a numbered snap-lid microtube and samples from each colony were placed individually in a labeled plastic bag.

The parameters measured are outlined in Table 3.

Table 3: Description of population parameters used in the analyses.

Parameter	Description
Number of gemmae/shoot	-
Colony shoot density (no./cm^2)	-
Proportion of gemmiferous shoots	-
Density of gemmiferous Shoots (no./cm^2)	-
Colony size (cm^2)	-
Colony gemmae output	Calculated as the number of gemmae/shoot × the colony size × density of gemmiferous shoots

Gemmae production

The number of gemmae per shoot was counted by placing each shoot individually in a drop of water on a microscope slide and the gemmae were scraped loose under a dissecting microscope with a fine needle. The water droplets containing the gemmae were rinsed back into the original tube with distilled water. The tube was weighed to calculate the volume of the water-gemmae solution. This was done using the equation:

V_s = (0.4755g/weight of water and gemmae in tube) × 1000

where 0.4755g is the weight of the tube with no contents

V_s = Volume of solution in tube

The solution was shaken to homogenise the gemmae in the tube. A drop of solution was placed on a haemocytometer and the number of gemmae per shoot was calculated using the equation:

$N_{sh} = (V_s \times N_x)/V_c$

where N_{sh} = number of gemmae per shoot

N_x = number of gemmae counted

V_c = volume of the haemocytometer chamber

The mean of four haemocytometer counts per sample was used as an estimate of the number of gemmae per shoot.

Shoot density

The collected sample from each colony was cut into a one-by-one cm square and placed under a dissecting microscope. The number of shoots with gemmae and the number of shoots without gemmae were counted to give a ratio of shoots with asexual propagules to those shoots without. This additionally provided a measure of colony shoot density.

Statistical analyses

All analyses were performed using JMP version 5.0.1.2. Examination of frequency distribution revealed strong skewness in all variables except for proportion of gemmiferous shoots. This was corrected by log-transforming the variables and after transformation, no variables departed significantly from normal.

To analyse the spatial variation of the individual variables a Nested Analysis of Variance (ANOVA) was performed using area, population and quadrat as nested classification variables, except for the number of gemmae per shoot which included colonies nested within quadrats.

Relationships among the measured variables were evaluated using the Pearson Product-Moment Correlation.

As Svalbard and Trøndelag are two ecologically distinct areas (Figure 4a and 5b), they were considered separately as well as together in all analyses.

Results

A total of 31 colonies (13 from Sør-Trøndelag and 18 from Svalbard) of *Lophozia ventricosa* were used in this study. In Trøndelag, the number of gemmae per shoot ranged from 105 to 8244 with a mean of 2002 ± 137 whereas on Svalbard the number of gemmae ranged from 169 to 10907 with a mean of 2920 ± 222. Colony size in *L. ventricosa* ranged from 5.5 cm^2 to 444 cm^2 with a mean size of 98.5 ± 35.7 cm^2 in Trøndelag and from 8.8 cm^2 to 468 cm^2 with a mean size of 52.9 ± 25.4 cm^2 on Svalbard. Shoot density ranged from 14 to 150 shoots per cm^2 with a mean of 75 ± 10 shoots per cm^2 in Trøndelag and from 14 to 436 shoots per cm^2 with a mean 105 ± 26 shoots per cm^2 on Svalbard.

Spatial variation of population size and gemmae production

A comparison of the spatial variation between parameters is shown in Table 4. The overall nested ANOVA reveals significant differences in (a) the number of gemmae per shoot between areas, populations and colonies although variation amongst shoots within colonies accounts for 77.3% of the variation; (b) colony size between populations accounting for 44.3% of the variation.

In Trøndelag, statistically significant variation exists between populations in shoot density (63.5% of variation), gemmiferous shoot density (57.6%) and total gemma output (24%). Although there is statistical significance among populations in the total gemma output, a much higher percentage of the variation occurs between colonies (66%).

On Svalbard, statistically significant variation exists in the number of gemmae per shoot at the population level and at the colony level although variation between shoots accounts for 75% of the variation. Statistically significant variation in colony size exists between populations, accounting for 62% of the variation.

Interactions between parameters

Table 5 shows the results of the pairwise comparisons of parameters using all localities as well as Svalbard and Trøndelag separately. The correlations indicate a significant relationship between the number of gemmae per shoot and the proportion

Table 4: Summary of variation of the six parameters for the studies populations. Parameters showing significant differences at the different spatial scales are indicated by asterisks: * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

	Number of gemmae/ shoot			Colony shoot density			Proportion of gemmiferous shoots			Density of gemmiferous shoots			Colony size			Colony gemmae output		
	d.f	%var	F	d.f.	%var	F	d.f	%var	F	d.f.	%var	F	d.f	%var	F	d.f.	%var	F
Total:																		
Area	1	3.5	11.03***	1	0.8	0.30	1	0.1	0.05	1	0.2	0.08	1	1.3	0.84	1	1.9	0.75
Population	7	8.0	3.65***	7	43.6	2.15	7	9.8	0.30	7	30.0	1.22	7	44.3	3.38*	7	43.0	2.50
Quadrat	6	1.8	0.96	6	12.8	0.68	6	9.8	0.55	6	14.0	0.66	6	15.2	1.38	6	6.3	0.42
Colony	16	9.4	1.90*	-	42.8	-	-	80.3	-	-	55.8	-	-	39.2	-	-	48.8	-
Shoot	-	77.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trøndelag																		
Population	2	3.2	1.57	2	63.5	15.78**	2	3.6	0.29	2	57.6	9.39*	2	35.5	3.22	2	24.4	8.73*
Quadrat	5	3.2	0.61	5	30.5	3.03	5	57.1	1.77	5	15.3	2.54	5	28.4	1.03	5	9.8	0.93
Colony	5	3.8	0.73	-	6.0	-	-	39.3	-	-	27.1	-	-	36.1	-	-	65.8	-
Shoot	-	89.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Svalbard																		
Population	5	10.9	4.46***	5	37.7	1.49	5	10.4	0.29	5	42.3	0.84	5	61.8	3.66*	5	42.1	1.68
Quadrat	1	1.3	2.75	1	6.6	1.31	1	7.5	0.92	1	3.1	1.52	1	0.9	0.25	1	2.8	0.56
Colony	11	13.0	2.42**	-	55.7	-	-	82.1	-	-	54.6	-	-	37.3	-	-	55.1	-
Shoot	-	74.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

of gemmiferous shoots, the density of gemmiferous shoots and colony gemmae output. The three relationships above are also significant on Svalbard but not in Trøndelag. Significant relationships exist also between the gemmae output of a colony and shoot density, proportion and density of gemmiferous shoots, and colony size when both areas are considered together. All of the relationships with gemmae output are significant on Svalbard, but in Trøndelag only colony size and gemmae output are significantly related. In Trøndelag, the only other significant relationship is between gemmiferous shoot density and shoot density. On Svalbard, gemmiferous shoot density is additionally significantly related to shoot density and proportion of gemmifeorus shoots. The relationship between colony size and shoot density is marginally significant ($r = 0.45$; $p = 0.06$) (Figure 6).

Table 5: Pairwise correlations between parameters indicated by correlation coefficients in (a) the total area, (b) Trøndelag and on (c) Svalbard with significant differences between parameters indicated by asterisks where * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

(a)

	Number of gemmae/ shoot	Shoot density	Proportion of gemmiferous shoots	Density of gemmiferous shoots	Colony size
Number of gemmae/ shoot					
Shoot density	0.24				
Proportion of gemmiferous shoots	0.53**	0.25			
Density of gemmiferous shoots	0.39*	0.95***	0.54**		
Colony size	0.21	0.27	0.14	0.29	
Colony gemmae output	0.55**	0.69***	0.47**	0.76***	0.81***

(b)

	Number of gemmae/ shoot	Shoot density	Proportion of gemmiferous shoots	Density of gemmiferous shoots	Colony size
Number of gemmae/ shoot					
Shoot density	0.20				
Proportion of gemmiferous shoots	0.02	- 0.00			
Density of gemmiferous shoots	0.21	0.97***	0.25		
Colony size	0.17	0.08	- 0.09	0.06	
Colony gemmae output	0.39	0.47	0.03	0.47	0.89***

(c)

	Number of gemmae/ shoot	Shoot density	Proportion of gemmiferous shoots	Density of gemmiferous shoots	Colony size
Number of gemmae/ shoot					
Shoot density	0.32				
Proportion of gemmiferous shoots	0.70***	0.32			
Density of gemmiferous shoots	0.50*	0.95***	0.60**		
Colony size	0.06	0.45	0.24	0.46	0.77***
Colony gemmae output	0.52*	0.82***	0.61**	0.90***	0.77***

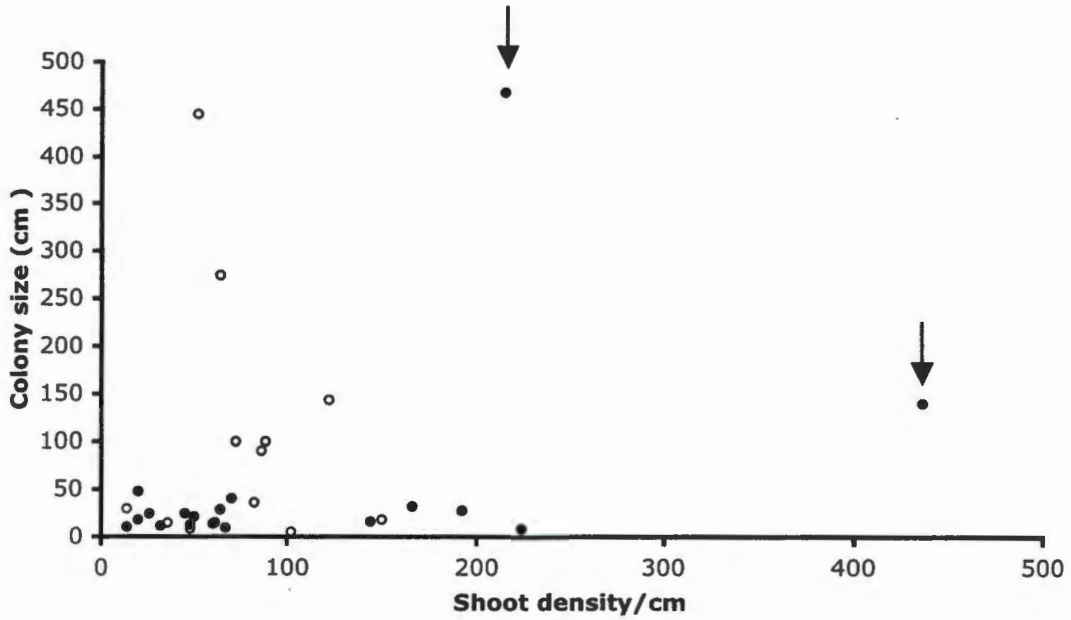


Figure 6: Relationship between shoot density and colony size in Trondelag (open circles) and Svalbard (closed circles). No significant relationship exists between shoot density and colony size in Trondelag, however a relationship approaching significance ($R = 0.45$; $p = 0.06$) exists in Svalbard as a result of two colonies with high shoot density (arrowed). Exclusion of the two outliers reveals no significant relationship between colony size and shoot density on Svalbard ($R^2 = 0.004$; $p = 0.81$).

Discussion

Little of the observed variation in the measured variables could be attributed to differences between Svalbard and Trøndelag. Only number of gemmae per shoot differed significantly between the areas, but this varied also between populations and between colonies, with variation among shoots explaining the vast majority (77%) (Table 4). In Trøndelag, no significant differences exists at any spatial level and the number of gemmae per shoot explains almost 90% of the variation. On Svalbard, however, significant variation exists between populations and between colonies but 75% of the variation in the number of gemmae per shoot is explained by variation between shoots. Variation in the number of gemmae produced per shoot may be due to differences in conditions affecting the growth rate of shoots (Laaka-Lindberg 1999). If so, both macroclimate (Trøndelag and Svalbard) and microclimate differences play a role and may explain the differences noted. It is, however, noticeable that no differences were found among populations in the boreal region.

Of the other measured characters very few significant differences were discovered. Shoot density did, however, vary significantly between populations in Trøndelag and this spatial level accounted for 64% of the variation. From our hypothesis we expected shoot density to influence gemmiferous shoot density and colony gemmae output (Figure 7), which may explain the significant difference of gemmiferous shoot density and colony gemmae output between populations in the same area.

Colony size varied between populations on Svalbard and in the whole data set. This can be explained by a significant difference in the number of gemmae per shoot which was hypothesized to influence colony size, where more gemmae on a shoot would result in a larger colony.

Our initial model hypothesized various pathways that influence gemmae output of colonies. No formal path analysis was done. Instead pairwise correlation data was used for significance test of the relations. In Trøndelag only two relations were significant: shoot density was positively related to gemmiferous shoot density which is expected if

the proportion of gemmiferous shoots is not density-dependent , as we found and agrees with studies on the liverwort *Anastrophyllum hellerianum* (Pohjamo & Laaka-Lindberg 2004). The only significant relation in the boreal region that can explain the gemmae ouput is colony size (Figure 7a).

The interactions between characters is very different on Svalbard (Figure 7b). The direct relationship between a high number of gemmae produced per shoot within a colony and a higher gemmae output within a colony is significant. The original suggestion that the number of gemmae per shoot influences colony size as well as shoot density is not supported as no significant relationship exists between these variables but all three variables directly influence gemmae output in a colony. Additionally, shoot density influences gemmiferous shoot density which in turn influences gemmae output. As the number of gemmae per shoot is related to the proportion of gemmiferous shoots, this explains the significant positive dependence that gemmae output of the colony has on the proportion of gemmiferus shoots. When the model is considered as a whole and all characters evaluated, gemmae output in a colony on Svalbard is affected by the colony size, shoot density and the number of gemmae produced per shoot.

Kimmerer (1991) showed that shoot density in mosses was highly correlated with the mode of reproduction used. She found that colonies of *Tetraphis pellucida* with densities above 100 shoots/cm^2 reproduce sexually by spores whereas colonies with a density of less than 75 shoots/cm^2 reproduce asexually through the production of gemmae. She hypothesised that at low shoot densities, there is available substrate and asexual reproduction allows rapid colonisation. However, in the liverwort *Lophozia silvicola*, Laaka-Lindberg (1999) and Pohjamo & Laaka-Lindberg (2004) showed that no correlation exists between shoot density and the number of gemmae per shoot. Our results from both Trøndelag and Svalbard agree with previous studies, suggesting that asexual reproduction is not density-dependent.

No correlation exists for either area between shoot density and colony size. On Svalbard, however, the relationship approached significance. This correlation may exist as a result

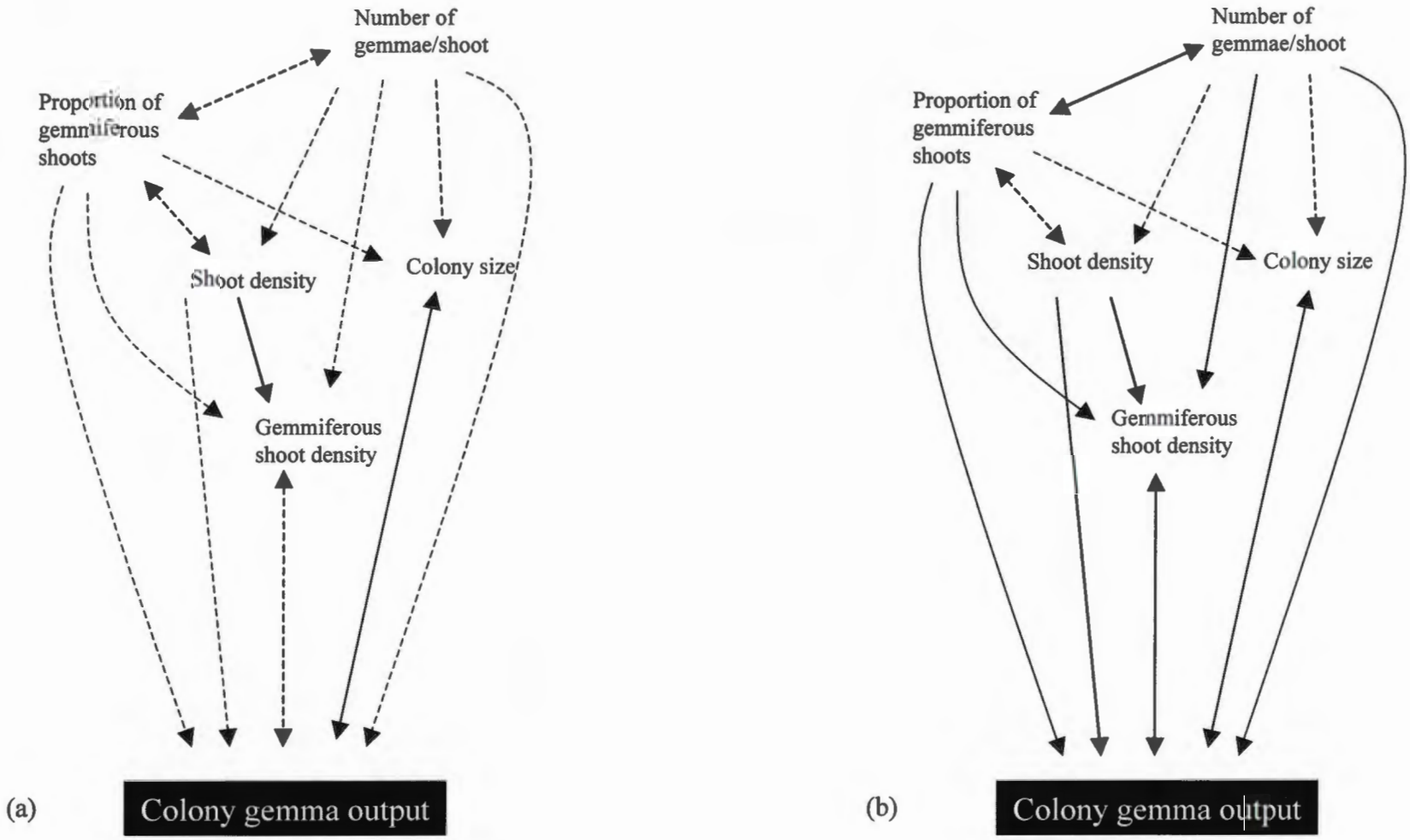


Figure 7: An overview of the results of the pairwise comparisons of parameters affecting gemmae output of colonies in *Lophozia ventricosa* (a) in Trondelag and (b) on Svalbard.

of two colonies,within the same quadrat, which are large with high shoot densities (Figure 6). If the two outliers are excluded, no significant relationship between shoot density and colony size exist ($r^2 = 0.004$; $p = 0.81$).

Understanding the nature of bryophyte populations, especially those in dynamic habitats, allows an understanding into long-term survival. Gemmae output leads to long-term survival through the growth of a colony, either in size or the density. It appears that gemmae output in colonies from different habitats rely on different population parameters to ensure survival and the number of gemmae produced per shoot may be the cause of these differences.

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