Substrate preference and reproduction in *Lophozia silvicola* (Hepaticopsida) in southern Finland

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I studied colonies of *Lophozia silvicola* Buch on wood, rock and soil in an old-growth forest in southern Finland. The frequency of fertile colonies is highest on wood. Rock is considered suboptimal on the basis of rare occurrences and lowest frequency of fertile colonies on boulders. On logs, *L. silvicola* is most frequent on *Picea abies* in late stages of decay and on middle-sized logs. The colonies were on average 1.94 m apart from each other, what indicated relatively good colonization ability. The overall distribution pattern of *L. silvicola* colonies is aggregated. Sexual and asexual colonies do not differ in a distance to the closest neighbouring colony.

Keywords: asexual, colony size, fertile, *Lophozia silvicola*, nearest neighbour, substrate type, wood quality

INTRODUCTION

Population size and dynamics, dispersal ability and reproductive system are important in determining a species' general distribution pattern and rarity (Hansson *et al.* 1992, Longton 1992). Asexual and sexual reproductions have different roles in the population ecology of a species (Newton & Mishler 1994, Green & Noakes 1995). In bryophytes, spores are often considered as means of long-distance dispersal (e.g. Miles & Longton 1990), while asexual and vegetative modes of multiplication are considered as means of maintenance of local populations (Mishler 1988, Hansson *et al.* 1992). Thus, asexual reproduction com-

pensates for insecure and costly sexual reproduction (Newton & Mishler 1994, Kimmerer 1994). In hepatics, the reproductive traits have rarely been studied in relation to environmental variables (however *see*, Benson-Evans 1964).

Ecological requirements of many boreal hepatic species are poorly known. Some species are generally considered to be confined to old-growth forests (Söderström 1988a, Laaka 1992). I chose to study the ecological traits of a common species to provide better understanding of the general picture of that species relative to ecologically adjacent species.

Characteristically, habitats of bryophytes are patchy in space and time. Production, dispersal
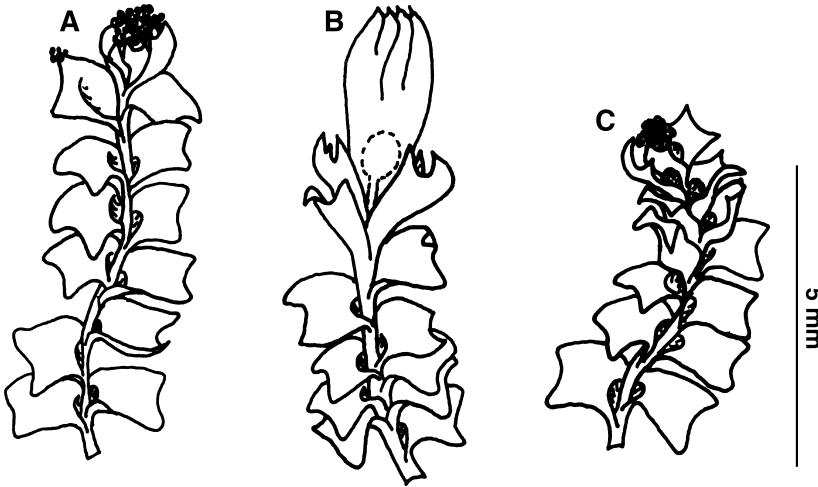
Fig. 1. Shoots of *Lophozia silvicola* representing different reproductive modes. — A: Asexual shoot with gemmae on the tips of uppermost leaves. — B: Female shoot with a perianth and a sporophyte embryo. — C: Male shoot with antheridia in axils of perigonial leaves. A and B drawn from Sanna Laaka-Lindberg 56-97 (H), and C from Sanna Laaka-Lindberg 96-97 (H).

and survival of diaspores are among central population parameters in survival of a species in a system of habitat patches. Spatial distribution of habitats and the distance between habitat patches are key parameters for species' survival in such an environment (Söderström & Herben 1997, *see* also Husband & Barrett 1996). The distribution of suitable habitat patches varies among habitat types. In a boreal forest environment, trees and stumps are more or less regularly distributed, whereas distribution of boulders is random. Spatial distribution of dead, fallen tree trunks is typically aggregated (e.g. Söderström & Herben 1997), and patches of open humus or mineral soil are nearly uniformly available. However, aggregation of suitable habitat patches varies on different scale (Addicott *et al.* 1987). As a consequence, facultative modes of reproduction may function in different roles and on different scales in population dynamics of bryophytes (*see* Newton & Mishler 1994). Asexual propagules should function on a local, short-distance scale, and sexually produced spores on regional, long-distance scale (Kimmerer 1994, Söderström & Herben 1997).

Difficulties in collecting field data and establishing experimental studies on reproduction in hepatics have often been noted (Wyatt 1982, *see* also Newton & Mishler 1994). I studied *Lophozia silvicola*, a boreal hepatic species in an old-growth forest in southern Finland. I provide ecological data on substrate preference and local distribution of colonies in connection to modes of reproduction. I put forward the following questions:

(1) does *L. silvicola* show preferences in relation to substrate types, (2) what are substrate preferences of *L. silvicola* in relation to reproduction, and (3) how are the colonies of *L. silvicola* distributed in the study area?

MATERIAL AND METHODS

In this study, I differentiate between reproductive modes (sexual vs. asexual). In asexual colonies, all shoots lack gametangia, but asexual gemmae are present in abundance on tips of uppermost leaves of shoots (Fig. 1A). In sexual colonies, shoots with initials or mature gametangia either of one sex (unisexual) or both (bisexual) sexes (Fig. 1B and C) are present. As sexual shoots often bear asexual gemmae simultaneously with gametangia, the asexual mode of reproduction is considered prevalent. In fertile colonies, female shoots with fertilized archegonia (swollen venter, *see* Greene 1960) or maturing sporophytes are present as an indication of a previous event of fertilization. Because this phase of my study was done in late summer, practically all bisexual colonies were fertile.

Studied species

In addition to the aforementioned sexual and asexual modes of reproduction, *Lophozia silvicola* can spread vegetatively by branching. It has a wide

circumboreal distribution in the taiga zone, where it grows in closed, often somewhat paludified forests, occasionally also on forested peatlands. It belongs to a group of closely related taxa within *Lophozia* subgenus *Lophozia*, the taxonomy of which is inadequately understood (*see* Schuster 1969, Paton 1999). I follow here the taxonomic treatment by Buch in Herzog *et al.* (1933).

Study area and sampling

The study area was the Kotinen Forest Reserve in Lammi commune in the biogeographical province of South Häme, southern Finland (61°14´N, 25°03´E). The vegetation is southboreal (*see* Ahti *et al.* 1968) old-growth forest dominated by Norwegian spruce (*Picea abies* (L.) Karst.), with patches of spruce-swamp along a brooklet.

I sampled during late July and early August 1997 in a 50×50 m plot along a small brooklet. All the colonies of *Lophozia silvicola* were scored on substrate, colony size, distance to the closest neighbouring colony within the plot frame, and reproductive mode of the colonies. The substrates on which *L. silvicola* colonies were found are divided in three types: wood (presence on fallen logs, branches and stumps), rock (presence on surfaces of boulders) and soil (presence on mineral soil and humus). The colony shape was estimated as an ellipse, with the principal axes measured for colony size (cm²). The distances to the closest neighbouring colony of *L. silvicola* were measured (m) from the closest edges. If possible, the reproductive mode of each colony was determined in the field, but portions of colonies were collected for the study under a microscope.

Logs in the study plot were recorded as to tree species. Their diameter (cm), decay stage and percentage cover of bark remaining on them were measured. The decay stage was estimated following Söderström (1988c): 1 to 2 = newly fallen tree trunk with intact bark and smooth, hard wood texture, 3 to 4 = early stages of decay; small parts of bark gradually loosening and wood becoming softened, 5 to 6 = middle stages of decay; wood texture becoming rough, wood softening, 7 = late stage of decay; wood texture deeply fissured and softened, and 8 = completely decayed log, with outlines gradually merging to soil, bark often

undetectable, wood uniformly softened. In addition, the above-mentioned variables were recorded on the patches with colonies of *Lophozia silvicola*.

Statistical analysis

The differences in size and distance between colonies representing different reproductive modes and substrate types were tested with Kruskall-Wallis one-way analysis of variance with adjustment for unequal sample size (Zar 1984). Spatial distribution of *Lophozia silvicola* colonies was analysed by applying one-tailed nearest-neighbour analysis (Campbell 1996). In this study, colonies separated by at least 0.1 m were treated as corresponding to "individuals" in Campbell's model. Corrections for edge-effect bias and reciprocal pairs were applied. χ^2 goodness-of-fit tests were performed for observed occurrences of colonies on wood against proportion of logs representing different wood quality variables found in the study plot.

RESULTS

Substrate preferences and reproductive mode

Altogether 112 colonies of *Lophozia silvicola* were found in the 50×50 m plot. Of these, 43.8% grew on wood, 11.6% on rock and 44.6% on soil. Of all the colonies 78.6% were asexual, 15.2% fertile, and 6.2% unisexual.

The distribution of wood quality variables of the logs ($n = 207$) found in the study plot is shown in Table 1. Proportions of occurrences of *L. silvicola* colonies on wood of different quality are also given in Table 1. Tree species that could not be identified are shown in this table as "other".

Of all the *Lophozia silvicola* colonies on wood, 85.7% grew on *Picea abies*, the most common log tree species in the study plot. The occurrences on logs of other tree species in the study plot were less frequent than expected, $\chi^2 = 10.936$, df = 4, $p < 0.05$ (Fig. 2). On *P. abies* logs fertile colonies were more common ($\chi^2 = 107.092$, df = 4, $p < 0.001$) than asexual ones. These asexual colonies showed no preference on the basis of log tree species ($\chi^2 = 9.222$, df = 4, n.s.).

Average diameter of the logs on which colo-

nies of *Lophozia silvicola* were found was 11.6 cm (n = 39, S.D. = 7.70). In the study plot, *L. silvicola* colonies occupied to a variable degree logs in different size classes (Table 1 and Fig. 3). The result of the χ^2-test = 11.208, df = 4, p < 0.05, showed preference on the basis of log size, as occurrences on middle-sized logs in diameter classes 5.5–15 cm and 15.5–25 cm were more frequent than expected.

The wood quality variables, decay stage and bark cover, correspond to the successional stage of decomposition of a log (Figs. 4 and 5). The majority of the logs in t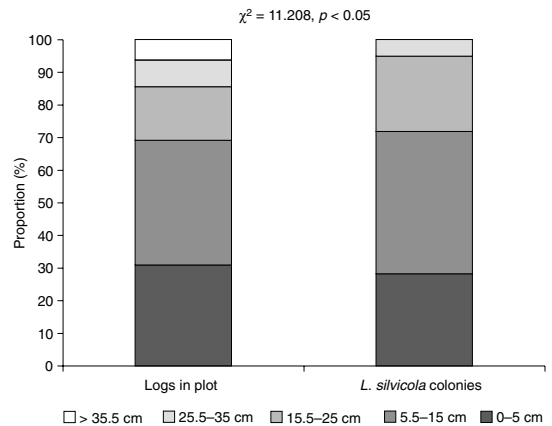he study plot were in late stages of decay. Colonies of *Lophozia silvicola* most often grew on totally decorticated logs (bark cover class 0%–< 10%, Fig. 4) or logs with only small patches of bark remaining (10%–20%, Fig. 4), χ^2 = 24.435, df = 5, p < 0.001. Colonies of *L. silvicola* were totally absent from the earliest stages of decay and first became established on logs in middle stages (Fig. 5), χ^2 = 21.547, df = 3, p < 0.001. Both asexual and fertile colonies prefered decorticated logs (χ^2 = 35.606, df = 5, p < 0.001, and χ^2 = 59.825, df = 5, p < 0.001, respectively), and late stages of decay (χ^2 = 21.821, df = 3, p < 0.001, and χ^2 = 43.566, df = 3, p < 0.001, respectively).

Table 1. Proportions (%) of logs (N = 207) in different wood quality classes in the study plot at Kotinen Nature Reserve, and of *Lophozia silvicola* colonies growing on patches representing different wood quality variables. Sample size for *L. silvicola* varies between the variables, since it was not possible to measure all variables in every case. Proportions on different wood quality variables are given for total number of *L. silvicola* colonies, and for asexual and fertile colonies.
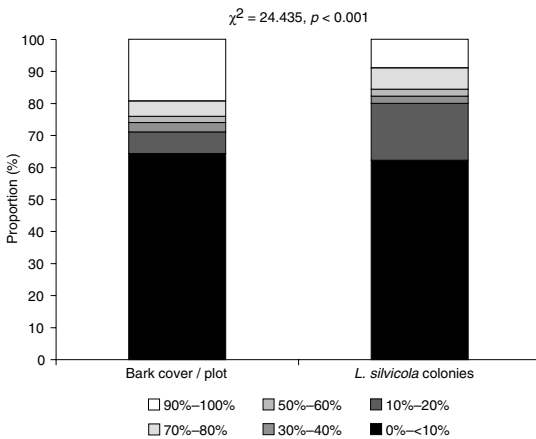
Wood quality	*L. silvicola* colonies			
	%	Total (%)	Asexual (%)	Fertile (%)
Log species				
Picea abies	77.3	85.7	87.9	76.9
Pinus sylvestris	7.7	2	3	0
Betula spp.	10.1	8.2	9.1	7.7
Populus tremula	2.9	0	0	0
Other	1.9	4.1	0	15.4
	N = 207	N = 49	N = 36	N = 13
Log size class				
0–5 cm	30.9	28.2	32.1	18.2
5.5–15 cm	38.2	43.6	42.9	45.5
15.5–25 cm	16.4	23.1	21.4	27.3
25.5–35 cm	8.2	5.1	3.6	9.1
> 35.5 cm	6.3	0	0	0
	N = 207	N = 39	N = 28	N = 11
Decay stage				
1	1	0	0	0
2	4.8	0	0	0
3	4.4	0	0	0
4	7.3	0	0	0
5	6.8	11.9	12.5	0
6	18.8	16.7	21.9	11.1
7	24.6	35.7	15.6	77.8
8	32.4	35.7	50	11.1
	N = 207	N = 42	N = 33	N = 9
Bark cover (%)				
0–< 10	64.3	62.2	48.5	81.8
10–20	6.8	17.8	18.2	9.1
30–40	2.9	2.2	3	0
50–60	1.9	2.2	3	9.1
70–80	4.8	6.7	12.1	0
90–100	19.3	8.9	15.2	0
	N = 207	N = 45	N = 33	N = 12
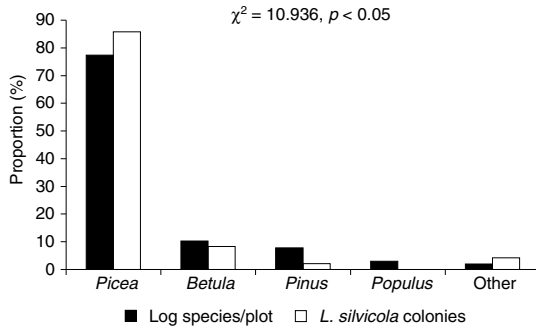
Fig. 2. Presence of log tree species (black bars) in the study plot in Kotinen Nature Reserve and occurrence of *Lophozia silvicola* colonies (white bars) on different log species. The bars represent the proportions of total log species and colony occurrences. χ^2-test value was calculated for observed frequency of *L. silvicola* colonies against expected frequency on the basis of log species present.

Fig. 4. Proportions (%) of logs representing different bark cover classes, and of occurrences of *Lophozia silvicola* on corresponding logs. Bark cover is estimated on scale of 10% intervals further grouped in six classes. χ^2-test value was calculated for observed occurrences of *L. silvicola* colonies against expected frequencies on the basis of logs in different bark cover classes present in the study plot.

Colony size and distance to the nearest neighbour

An average colony size of *Lophozia silvicola* was 99.6 cm^2 (N = 112, S.D. = 255.3). The average colony sizes (Table 2) did not differ among the substrate types (H_c = 2.22, df = 2, p > 0.1). Average size of colonies in different reproductive modes (Table 2) was significant between asexual
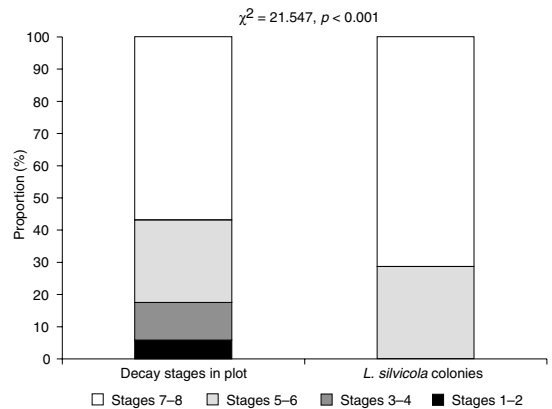

Fig. 3. Proportions (%) of logs in different size (diameter) classes, and of occurrences of *Lophozia silvicola* colonies on logs of different sizes. Log size is measured as diameter (cm) in the middle of the trunk, and presented in five classes. χ^2-test value was calculated for observed occurrencies of *L. silvicola* against expected frequencies on the basis of log size class distribution present on the study plot.

Fig. 5. Proportions of logs in different decay stages, and of occurrences of *Lophozia silvicola* on logs in different stages of decomposition. Decay stage of the logs is estimated on an eight stage scale, here combined in four classes: 1–2 = newly fallen trunk, beginning of decomposition, 3–4 = early stage of decay, 5–6 = advanced (middle) stage of decay, 7–8 = late stages of decay. For a more detailed description, *see* Söderström (1988c). χ^2-test value was calculated for observed occurrencies of *L. silvicola* colonies against expected frequencies on the basis of logs in different stages of decay present on the study plot.

and fertile colonies (H_c = 3.912, df = 2, p < 0.05).

The mean distance (r_A) to the closest neighbouring conspecific colony was 1.94 m (n = 112,

S.D. = 2.81). The distances to the closest neighbour did not differ between the reproductive modes ($H_c = 4.44$, df = 2, $p > 0.1$). On the basis of colony density ($m = 0.045$) and expected variance ($\sigma^2_R = 1.569$) in the plot, expected mean distance between colonies was $r_E = 2.36$ m. Thus Campbell's (1996) test gave as result $c = -4.392$, $p < 0.004$, indicating aggregated distribution, which is in agreement with generally aggregated distribution of suitable habitat patches in the plot.

DISCUSSION

Difference between asexual reproduction and vegetative growth is often a matter of definition (Mogie 1992). In the case of *Lophozia silvicola*, and in many other gemmiferous hepatics (Buch 1911), production of uni- to bicellular gemmae meets the criteria for reproduction, as the gemma mother cell can be interpreted as an unicellular zygote equivalent (*see* definitions in Mogie 1992). As gemma mother cells are formed by mitotic cell divisions on the gametophyte, and the gemmae are produced without fusion of gametes, and function ontogenetically analogously (Buch 1911) to sexually produced spores, the mode of reproduction is asexual instead of mere growth (*see* also Mishler 1988). Growth, sexual and asexual reproduction in *L. silvicola* will be discussed further elsewhere.

Spatial distribution and availability of habitat patches influence the distribution of colonies (e.g. Söderström & Herben 1997). When considering the substrate preference by comparing frequencies of occurrence of *Lophozia silvicola* on potential substrates, all substrates available can be considered equally suitable. However, the observed distribution of colonies on different substrate types showed that *L. silvicola* grows less frequently on rock as compared with other substrates. In the study plot, small disturbance of the forest soil created open patches of humus and mineral soil. Of the logs in the plot, only 24% were occupied by *L. silvicola* colonies. The fact that all logs were not equally occupied indicates a degree of substrate preference in regard to a tree species of origin, log size, stage of decay and degree of decortication. The quality of the wood seems to have an effect on the ability of *L. silvicola* to establish new colonies. In previous studies on substrate preference in epixylic bryophytes, the availablity of substrate (Söderström 1988a) was reported to be an important factor determining species occurrences. Furthermore, large logs are favoured by most of the epixylic species (Söderström 1988c). In this study, colonies of *L. silvicola* grew most frequently on middle-sized logs. As a consequence of log size, wood decomposition process creates ecologically different conditions (Rayner & Boddy 1988, Renvall 1995) which, in turn, form different substrate niches for epixylic species (Söderström 1988b).

The amount of bark remaining on logs corresponds to the duration of that log as a substrate, since bark gradually falls off, forming open patches of bare wood surface. Colonies of *Lopho-*

Table 2. Sizes of *Lophozia silvicola* colonies on different substrate types, and of colonies representing different reproductive modes. In unisexual colonies, only one of the sexes is present. The colony shape is estimated as an ellipse, and surface area in cm² is measured on the basis of the length of principle axes.

	Substrate type		
	Wood	Rock	Soil
Average colony size (cm²)	48.4	52.2	162.1
S.D.	50.7	35.1	371
N	49	13	50
	Reproductive mode		
	Asexual	Fertile	Unisexual
Average colony size (cm²)	68.3	293.3	22.5
S.D.	118.7	572.4	16.5
N	88	17	7

zia silvicola grew most often on decorticated logs, and were practically absent from newly fallen logs with an intact bark cover. The bark is not only of shorter duration than the wood but it often has a lower pH. In addition to the bark condition *L. silvicola* was affected by the degree of decay. The late stages of decay were favoured by both asexual and fertile colonies.

Lophozia silvicola colonies grew more frequently than expected on *Picea abies* logs, and less frequently on hardwood species such as *Betula* spp. In the study plot, I found no *L. silvicola* colonies on *Populus tremula* logs. The decomposition process differs between those tree species (Rayner & Boddy 1988). *Picea abies* is perhaps especially suitable for *L. silvicola* because of rapid decortication (*see* Renvall 1995).

Different substrate types affect the relative proportion of fertile and asexual colonies of *Lophozia silvicola*. In hepatics, environmental parameters are one of the factors contributing to sex organ induction (Benson-Evans 1964, Knoop 1984). Thus, habitat quality affects the potential for sexual reproduction in the colonies. At the study site, the proportion of fertile colonies with sporophytes was highest on wood, 20.4%. The proportion of colonies with gametangia (26.5% on wood, 18% on soil, and 15.4% on rock) shows that there is a strong effect of substrate. *L. silvicola* colonies on soil and rock reproduced mainly asexually. The lower proportion of fertile colonies (7.7%) on rock substrate is in agreement with Söderström's (1993) interpretation of rock substrate being suboptimal for *L. silvicola* (*see* also Laaka-Lindberg 1999). As reproductive modes are at least in some degree facultative in *L. silvicola*, asexual propagation may facilitate establishment on less optimal substrates (Mishler 1988, Kimmerer 1994). However, sexual reproduction with consequent highly dispersable spores has alternatively been considered as an escape from unfavourable conditions (but *see* Cockburn 1991). In contrast, I emphasize the energetic cost of sexual reproduction, and prefer the hypothesis that successful sporophyte production in hepatics requires favourable conditions, and is not an escape mechanism.

The average colony size of *Lophozia silvicola* was large in the population at the Kotinen Forest Reserve (84.1 cm^2). A previous study in a Norwegian population showed smaller colony sizes

(3.0–32.1 cm^2; Laaka-Lindberg 1999). The colony size did not differ significantly among the substrate types (*see* also Laaka-Lindberg 1999). It correlates with the availability of substrate patches in time, which in turn, is connected to stability of the environment (e.g. Herben & Söderström 1992, Söderström & Herben 1997). The conditions in the Kotinen old-growth forest are more stable than in the more disturbed Norwegian locality (*see* Laaka-Lindberg 1999). The small colony size on wood as compared with the colonies on soil may demonstrate a trade-off between reproduction (sexual or asexual) and vegetative growth (*see* Piquot *et al.* 1998). On such an unfavourable substrate as rock, maintenance of colonies requires investment on vegetative growth at the cost of reproduction.

The size of fertile colonies is significantly larger than that of asexual colonies. In a dioicous species, presence of both sexes, which is obligatory for sexual reproduction, requires at least two separate successful colonizations (Söderström 1992). In unisexual colonies, lack of one of the sexes and a small colony size may point to a recent colonization (Söderström 1992). Large size of fertile colonies is interpreted as indicating their old age with several colonization events followed by merging of separate colonies.

The average distance to the closest neighbouring conspecific colony did not differ between sexually and asexually reproducing colonies in *Lophozia silvicola* in the study plot. The scale on which the spatial distribution is here defined for *L. silvicola* is likely to influence the significance of spores as the means of long-distance dispersal (*see* Addicott *et al.* 1987, Söderström & Herben 1997). Average distance to the closest neighbouring colony illustrates the pattern of colonized substrate patches, but does not show how far the propagules are actually able to disperse from the parent colony. Obviously the provenance of the propagule is unknowable. Kimmerer (1991) studied the reproductively versatile moss *Tetraphis pellucida* adapted to effective colonization of a patchily distributed substrate. In her study, *T. pellucida* showed a more or less regular spatial distribution of colonies, occupying practically all available substrate patches. The situation is similar in *L. silvicola*, even though the overall spatial pattern of the colonies tends to be aggregated. This

greater aggregation of *L. silvicola* colonies as compared with *T. pellucida* may reflect a greater amplitude of substrates. Spatial pattern of suitable substrates is a key factor in the formation of the population pattern (Söderström & Herben 1997, *see* also Addicott *et al.* 1987), and eventually in survival of the population. The availability of optimal substrate for sexual reproduction secures survival on a large scale, while the ability to reproduce asexually even on suboptimal substrates and to spread vegetatively together provide means of maintaining a local population. Further analyses of spatial distribution of *L. silvicola* populations will be presented in a subsequent paper.

In conclusion, *Lophozia silvicola* shows substrate preference for decorticated, middle-sized *Picea abies* logs in late stages of decay. Gametangia and fertile shoots of *L. silvicola* were more frequent in colonies on wood than on other substrate types. Fertile colonies were larger than asexual ones, likely reflecting the older age of such colonies on a more optimal substrate. Overall distribution of the colonies tended to be aggregated, likely because of the pattern of distribution of suitable substrate patches. On the average, distances between colonies were relatively short, indicating a relatively good colonization ability on a local scale.

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